

The attentional boost effect and related phenomena: New insights into the relation between attention and memory

Edited by

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The attentional boost effect and related phenomena: New insights into the relation between attention and memory

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Editorial: The attentional boost effect and related phenomena: new insights into the relation between attention and memory

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attention, memory, cognition, attentional boost effect, recognition

Editorial on the Research Topic

The attentional boost effect and related phenomena: new insights into the relation between attention and memory

The relation between attention and memory has been unanimously recognized as a key theme of modern cognitive psychology (e.g., [Baddeley et al., 1984](#); [Craik et al., 1996](#)). Starting from this consideration, our Research Topic was aimed at putting together a selected set of papers which illustrate the latest advancements in the field. We were particularly interested in the examination of a phenomenon called the *Attentional Boost Effect* (ABE) but, as we will show below, the contributions extended to the discussion of a wide range of related findings.

The Research Topic includes a comprehensive review of the latest evidence on ABE and an updated version of the Dual-Task Interaction Model ([Swallow et al.](#)), previously proposed by [Swallow and Jiang](#). Briefly, the ABE arises when stimuli encoded with to-be-responded items are remembered better than stimuli encoded with to-be-ignored items. This target-induced enhancement generalizes to both visual material (images: [Swallow and Jiang, 2010](#); [Sisk and Lee, 2022](#)) and verbal material ([Mulligan et al., 2014](#); [Spataro et al., 2015](#)). The Dual-Task Interaction model suggests that the detection of a target item leads to a transient increase in the amount of resources devoted to the perceptual processing of co-occurring stimuli, likely instantiated by the phasic release of norepinephrine from the locus coeruleus. The Dual-Task Interaction Model 2.0 maintains these tenets, but additionally proposes that the perceptual boost occurs whenever the state of the world does not coincide with the state of the neurocognitive system and a response is needed to bring them back into alignment. In addition, to account for emerging results showing that the ABE can extend to the encoding of contextual details ([Turker and Swallow, 2019, 2022](#); [Spataro et al., 2020, 2022](#); [Mulligan et al., 2021](#)), the model assumes that the target-related boost may enhance the formation of bound, multi-item representations in the MTL.

Consistent with the notion that subcortical noradrenergic structures play a key role in the ABE, the fMRI study by [Moyal et al.](#) found that auditory target detection produced broad physiological and neural effects. These include increases in phasic pupil responses, increases in the activation of the locus coeruleus and the ventral visual cortex, enhancements of the multi-voxel pattern classification of image category in the fusiform gyrus and

parahippocampal gyrus, and enhancements in functional connectivity between the ventral visual cortex and the hippocampus. The latter result seems particularly relevant, because it suggests that the ABE-related manipulation benefits working memory maintenance and long-term memory encoding by enhancing communication between perceptual and medial temporal regions at behaviorally relevant times (such as when participants need to respond to target items).

An early finding in the ABE literature was that the memory enhancement following target detection was only significant for images that overlapped in time with the targets; no increase was observed when the images were presented 100 ms before or 100 ms after the targets (Swallow and Jiang, 2011). The study by Shimane et al. used a similar paradigm, in which participants responded to visual Go or No-go cues by pressing a key (the motor task) or by counting (the cognitive task). After each cue, two images were presented (a pre-item and a post-item). Memory for these images was later tested in a surprise recognition task. In line with the Swallow and Jiang (2011) conclusions, the results showed no significant difference in the recognition of pre- and post-items between Go and No-go trials in the motor task. However, in the cognitive task, post-items were better recognized in the Go than in the No-go trials. Moreover, No-go post-items were better memorized in the motor task than in the cognitive task. Jointly, these findings suggest that (a) in some conditions (i.e., with a non-motor task), target presentation may enhance memory for stimuli presented after its disappearance, and (b) covert motor engagement and response inhibition in No-go trials may promote memory encoding for task-irrelevant stimuli.

Another interesting finding in the ABE literature was that the memory enhancement induced by target detection may be reduced for distinctive stimuli that are already subject to heightened attention during an early encoding phase. Interactive effects of this type have been previously reported by Mulligan et al. (2014) for low-frequency words (but see Prull, 2019; for a different conclusion) and by Spataro et al. (2015) for words with rare orthographic features. An exception to this pattern has been reported in this Research Topic by LaPointe et al. They showed that perceptual degradation and target detection had significant, but independent effects on recognition memory, such that the ABE was similar in magnitude for clear and blurry words. Although these results are not necessarily inconsistent with the early-phase elevated attention hypothesis of the ABE, they nonetheless suggest that further research is needed to understand which manipulations are structurally redundant with the ABE.

As discussed above, the contributions included in this Research Topic cover a wide range of phenomena that are not limited to the ABE. Glicksohn et al., for example, demonstrated that the encoding

of visual objects benefited from the association with unusual sounds, and that reactivating these sounds strengthened the entire multisensory representation, resulting in better memory for contextual details (such as the objects' locations). Muhmenthaler and Meier showed that objects presented during switch trials (i.e., trials in which participants had to switch between different classification tasks) were recognized worse than those presented during repeat trials, that the effect was still robust after a 1-week delay and that it was mainly due to recollection processes. Yu et al. used a three-phase sequential paradigm and found that the recognition of semantically-encoded words reduced the incidental encoding of new "foil" words, as compared to the recognition of orthographically-encoded words. They suggested that the detrimental effect occurred because semantic tasks relied primarily on recollection processes, whereas non-semantic tasks relied more strongly on familiarity processes. Lastly, a three-phase sequential paradigm was also adopted by Zhao et al., who reported that objects encoded with self-referential cues were recognized better than objects encoded with other-referential cues.

In conclusion, while we are still far from having a comprehensive understanding of the cognitive and neural underpinnings of the complex interactions between attention and memory, the studies briefly summarized in this editorial represent a promising starting point that should motivate enduring research efforts.

Author contributions

PS wrote the first draft of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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Attentional load and attentional boost: a review of data and theory

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Both perceptual and cognitive processes are limited in capacity. As a result, attention is selective, prioritizing items and tasks that are important for adaptive behavior. However, a number of recent behavioral and neuroimaging studies suggest that, at least under some circumstances, increasing attention to one task can enhance performance in a second task (e.g., the attentional boost effect). Here we review these findings and suggest a new theoretical framework, the dual-task interaction model, that integrates these findings with current views of attentional selection. To reconcile the attentional boost effect with the effects of attentional load, we suggest that temporal selection results in a temporally specific enhancement across modalities, tasks, and spatial locations. Moreover, the effects of temporal selection may be best observed when the attentional system is optimally tuned to the temporal dynamics of incoming stimuli. Several avenues of research motivated by the dual-task interaction model are then discussed.

Keywords: attention, temporal selection, dual-task interference, attentional boost effect, load theory

Even the earliest writings on attention indicate that it is both limited in capacity and selective in nature (James, 1890; Johnston and Dark, 1986). Since then, extensive controversy has surrounded the nature of those limits and the processing stage at which they occur (Pashler, 1994; Driver, 2001). In all of this, however, few studies challenge the idea that attentional capacity is limited. Increasing attention to one task almost always impairs, or at best has no effect on, performance on a second task (Kinchla, 1992). In contrast to these findings, however, a number of recent reports suggest that transient increases in attention to one task can boost performance in a second encoding task (Lin et al., 2010; Swallow and Jiang, 2010). In this review, we briefly present an influential view of attentional selection (Lavie and Tsai, 1994; Lavie, 2005) that is based on the assumptions that perceptual and cognitive resources are limited. We then review recent findings that challenge these assumptions by demonstrating that increasing attention to one task can sometimes enhance performance in a second task. We propose a new model to account for how a limited-capacity system like attention produces these enhancements.

LOAD AND SELECTION

Because attention is limited in capacity (Kinchla, 1992), one must prioritize behaviorally relevant items to ensure that they drive task performance. For decades, attention research has sought to place selective attention within the broader perceptual and cognitive framework (Pashler, 1998). *Early selection* theories (e.g., Broadbent, 1958) suggest that attention acts as a perceptual filter, preventing the identification and semantic analysis of unattended sensory information. *Late selection* theories (e.g., Deutsch and Deutsch, 1963; Duncan, 1980) suggest that selection occurs after sensory stimuli have been identified but before they reach awareness.

The load theory of attentional selection (Lavie and Tsai, 1994; Lavie, 1995; Lavie et al., 2004) reconciled these views by suggesting that attentional selection occurs both early and late in processing, but that early selection varies according to the perceptual and cognitive demands of the attended stimuli. Load theory originated from combining two influential ideas: that attention has limited-capacity (Kahneman, 1973), and that all available perceptual resources will be obligatorily used to process sensory input (Treisman, 1969). This combination leads load theory to two assertions.

First, because perceptual resources are used obligatorily, the upper limit to perceptual processing is also its lower limit. Control processes first direct perceptual resources to goal-relevant (attended) stimuli. Any remaining resources will spill over to irrelevant (unattended) stimuli. As a result, if an attended item (target) requires few perceptual resources to process and identify, then the remaining perceptual resources will “spill over” to process unattended (distractor) stimuli. Late selection then reduces the effect of these irrelevant items on behavior. In contrast, if an attended item requires more perceptual resources, then fewer should spill over to unattended items. Early selection occurs under these circumstances because irrelevant items undergo little perceptual processing. Several factors influence the amount of resources that are needed to perceive an attended item, including the number of distractors (set size), the perceptual similarity between targets and distractors, and stimulus quality (e.g., whether it has been degraded; Lavie and Tsai, 1994; Lavie, 2005).

Evidence for the assertion that excess perceptual resources spill over to distractors came from studies that used the Eriksen flanker paradigm (e.g., Lavie, 1995). Participants indicated which of two-target letters (e.g., a Z or an X) was presented in a central region of the screen. Letters presented in the periphery were task-irrelevant but were associated with a response that was the

same as (congruent) or different than (incongruent) the response to the central letter. When the central region contained few letters (low perceptual load), the irrelevant peripheral letter influenced performance, and produced a congruency effect. In contrast, when more letters were present and perceptual load was high, the irrelevant letter's influence on performance was substantially reduced. This pattern of data has been replicated in studies using other manipulations of perceptual load, including those that increase load by requiring conjunction, rather than feature search, and by degrading the perceptual quality of the stimuli (Lavie, 2005). Moreover, increasing perceptual load decreases the response of brain regions involved in processing task-irrelevant stimuli (e.g., Yi et al., 2004; Bahrami et al., 2007).

A second assertion of load theory accounts for the effects of irrelevant items on task performance (Lavie et al., 2004). Because control processes direct perceptual resources to attended stimuli, any manipulations that impair control processes will disrupt their ability to do so. Therefore, increasing demands on control processes should impair selection, increasing the likelihood that irrelevant items will influence performance. This prediction was confirmed when the low perceptual load condition used in earlier studies was combined with a working memory task (Lavie et al., 2004): The effects of an irrelevant item on task performance were stronger when six items were maintained in memory, rather than one. Importantly, manipulations of cognitive load only affect the processing of irrelevant items when they conflict with relevant items (e.g., both involve spatial processing; de Fockert et al., 2001; Carmel et al., 2012).

Although it is not without controversy (Lavie and Torralbo, 2010; Tsal and Benoni, 2010; Wilson et al., 2011), load theory can account for a large amount of data (Lavie and Tsal, 1994; Lavie, 2005), and encompasses processes that occur throughout task performance. Like other accounts of attention and control, load theory focuses on capacity limitations, both in perception and in control. Here we review evidence that challenges the ubiquity of these limitations, demonstrating that increasing attention to one task can sometimes enhance performance in another task (Lin et al., 2010; Swallow and Jiang, 2010; Swallow et al., 2012).

DETECTING A TARGET FOR ONE TASK BROADLY ENHANCES PERCEPTUAL PROCESSING

Behaviorally relevant or novel events often signal the need to adapt one's goals and activities to a new context. In everyday life, such events might constitute a knock at the door, an email notification, or the appearance of a friend one has been waiting for. In the lab, behaviorally relevant events are often pre-defined targets to which participants have been instructed to respond¹. In all cases, selective attention is needed to identify the stimulus and determine an appropriate response (Chun and Potter, 1995; Nieuwenhuis et al., 2005). Perhaps less obviously, because these

events represent a change in the current situation, they may also lead to enhanced perceptual processing of their broader context (Donchin and Coles, 1988; Chun and Jiang, 1998; Bouret and Sara, 2005; Zacks et al., 2007). Consistent with this possibility, extensive data indicate that perceptual and conceptual information that is present when observed activities change form an important component of long-term episodic memory (Newtson and Engquist, 1976; Hanson and Hirst, 1989; Lassiter and Slaw, 1991; Schwan and Garsoffky, 2004; Swallow et al., 2009). However, these data apply almost exclusively to changes in observed activities, rather than to situations in which an event cues an observer to act. Whereas increased attention to context may be expected when activities change, load theory (Lavie, 2005) suggests that increasing attention to a relevant item should decrease the processing of concurrent perceptual information.

The limited-capacity of perceptual processing and attention (Lavie, 2005) necessitates that attending to a relevant event, such as a target, decreases attention to unrelated information that coincides with it. Indeed, most of what is understood about attention predicts that attending to a target should impair, rather than enhance, the processing of concurrently presented but unrelated information. For example, in the attentional blink, participants are typically asked to report the identity of two-target letters that appear in a stream of distractors (Raymond et al., 1992; Chun and Potter, 1995; Dux and Marois, 2009). Items are presented quickly, often at a rate of 10 per second, making their identification difficult. Detecting the first target in the stream reduces the ability to report the identity of the second target when it appears approximately 200–500 ms later. Similarly, in the two-target cost, Duncan (1980) demonstrated that the ability to detect a target is impaired when it coincides with another target, rather than a distractor. Thus, relative to distractor rejection, detecting and responding to a target produces significant demands on attention that reduce the availability of attentional resources for other items.

Over the last several years, however, several studies have presented data that seemingly challenge the ubiquity of interference from target detection. Data from multiple sources, including studies of memory, priming, brain activity, and perceptual learning suggest that attending to a behaviorally relevant target item can actually boost the perceptual processing of concurrent, but unrelated information.

In one study, Swallow and Jiang (2010) asked participants to perform two continuous tasks at the same time (**Figure 1A**). For one task participants were shown a series of scenes, one at a time (500 ms/item), at the center of the screen. Participants encoded all of the scenes for a subsequent memory test. For a second task a stream of squares was presented at fixation (also 500 ms/item). The square could be black or white, and participants pressed a key as quickly as possible whenever a white target square appeared. Importantly, the square was completely unrelated to the scene. To examine the effect of target squares on encoding the background scenes, the scenes were assigned to thirteen serial positions around the target square. Scene memory was assessed in a forced choice recognition test at the end of the experiment. If increasing attention to a target leads to widespread increases in perceptual processing, then scenes that are presented at the same time as a target square should be better remembered than those presented with

¹ Although targets are typically construed as items that lead to an overt or covert response, we define targets as items that lead to a change in planned behavior, including a no-go cue (cf. Makovski et al., 2012). These items require the updating of goal states and could therefore also lead to greater perceptual processing (e.g., Donchin and Coles, 1988; Aston-Jones and Cohen, 2005; Bouret and Sara, 2005; Zacks et al., 2007).

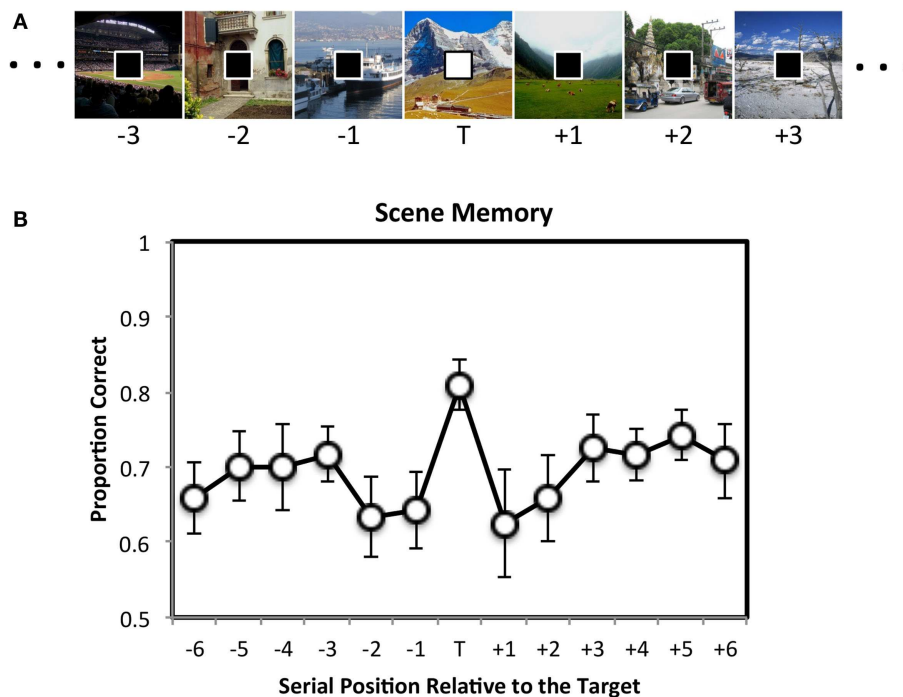


FIGURE 1 | The attentional boost effect. (A) Participants memorized scenes (500 ms duration, 0 ms ISI) for a later memory test. At the same time, they also pressed a key as quickly as possible whenever the square presented at fixation was white instead of black. Stimuli are not drawn to

scale. **(B)** Later recognition memory for the scenes was enhanced if the scene was presented at the same time as a target square during encoding. Error bars = ± 1 standard error of the mean. Adapted from Swallow and Jiang (2010).

a distractor square² (*enhancement hypothesis*). However, because perceptual and control processes are limited (Lavie, 2005), targets should also reduce the availability of attention for processing the scene. Encoding scenes into memory requires attention (Wolfe et al., 2007). Target detection should therefore interfere with memory for images that coincide with, and even closely follow a target (*interference hypothesis*). This, however, did not occur. Instead, memory for scenes that were presented at the same time as a target square was enhanced relative to those presented with a distractor square (Figure 1B). No consistent differences were observed in memory for scenes that appeared with a distractor in the other serial positions. These data suggest that perceptual processing increases when behaviorally relevant events occur, resulting in a global enhancement of multiple competing tasks.

Importantly, this pattern of data could not be attributed to the perceptual salience of the rare, white square (Swallow and Jiang, 2010). No memory advantage was observed for scenes that were presented at the same time as a white square when the squares were ignored. In addition, the effect was not due to a motor response, as it also occurred when participants were asked to covertly count the number of target squares (Swallow and Jiang, 2012). Although

detecting the target square required more attention than rejecting a distractor square (Duncan, 1980; Raymond et al., 1992), increasing attention to the square task boosted performance in the second task – an *attentional boost effect* (Swallow and Jiang, 2010)³.

The attentional boost effect is not limited to tasks that require participants to actively encode stimuli for a later memory test. In an experiment examining implicit memory (Spataro et al., 2013), participants read aloud words that were individually presented at a rate of 2 per second. Each time a word appeared a green or red circle appeared below it. In the divided attention condition, participants pressed a button when the circle was green. In the full attention condition, they ignored the circle. After completing the encoding task and a brief delay, participants performed a lexical decision task on exposed and unexposed words. Remarkably, words that coincided with targets produced nearly twice as much priming as words that coincided with distractors. Moreover, this advantage was absolute: priming was greater for words presented with targets than for words in the full attention condition. This pattern of data was replicated in a word fragment completion task. It did not, however, occur in a conceptual priming task, suggesting that target detection enhanced the perceptual encoding of concurrently presented words.

The effects of detecting a target on concurrent image processing can also be observed in short-term memory tasks. In their study,

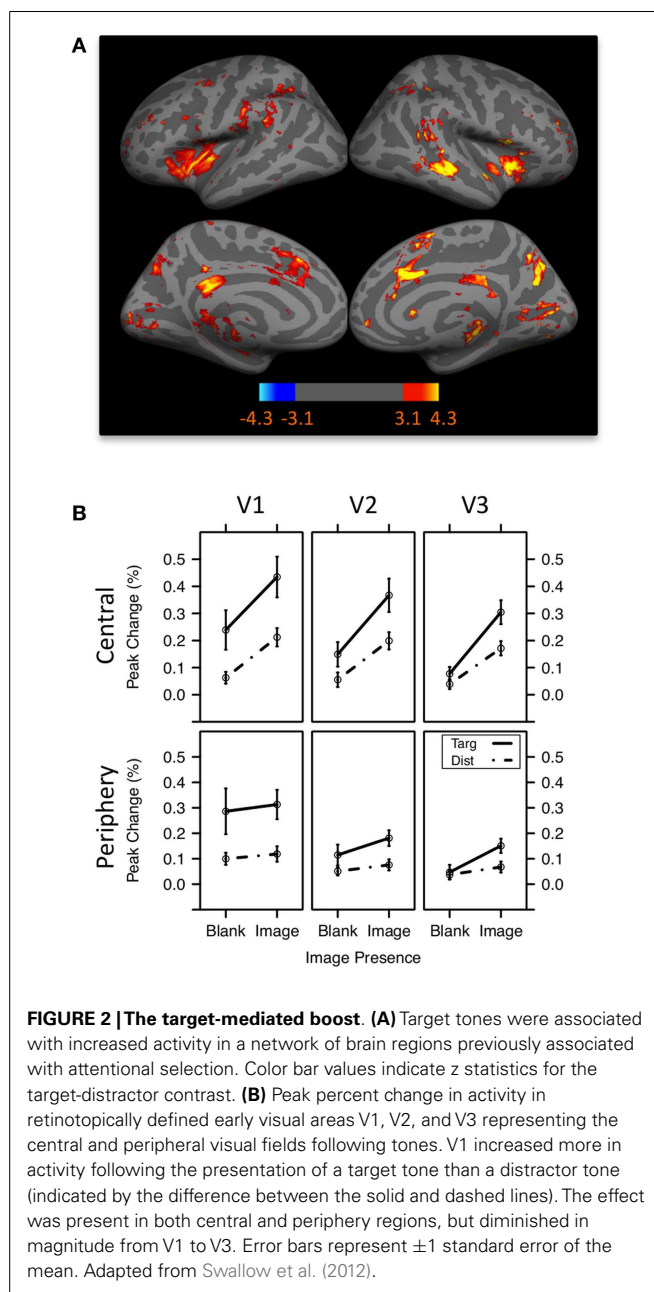
²For consistency, we refer to items that could be targets, but are not, as distractors. Distractors in RSVP tasks may have different effects on task performance than distractors that appear at the same time as a target in flanker tasks. Although they do not divert spatial attention from the target, distractors in RSVP tasks mask the target and could trigger inhibitory processes (e.g., Olivers and Meeter, 2008).

³A memory enhancement for scenes presented with targets has been referred to elsewhere as *fast task-irrelevant perceptual learning* (Leclercq and Seitz, 2012a,b,c).

Lin et al. (2010) first familiarized participants with scenes. In a subsequent task, 16 familiar scenes were presented one at a time (133 ms duration, 367 ms ISI) on each trial. A letter was presented in the center of each scene, and participants reported the identity of the gray letter at the end of each trial. They were also shown a scene and asked to indicate whether it was presented during the trial. Thus, this and similar experiments (e.g., Leclercq and Seitz, 2012a) examined how detecting a target letter influenced memory for whether a familiar image was recently presented. Consistent with the effects of targets on long-term visual memory, target detection enhanced short-term source memory for scenes.

Target detection also enhances short-term memory for semantically impoverished stimuli (Makovski et al., 2011). Participants performed a change detection task on color arrays separated by a 1500 ms delay. A letter was presented at fixation and participants quickly pressed a button when the letter was a T. The letter could appear at the same time as the first color array, during the 1500 ms retention interval, or at the same time as the second color array. Participants were better able to detect a color change when a target letter was presented than when a distractor letter was presented. Importantly, this benefit occurred only when the target letter coincided with the first color array, suggesting that target detection facilitated the encoding of the color patches into memory, but not their retention or comparison to current perceptual input. Interestingly, these data might help account for an earlier report of enhanced change detection in scenes when targets are present (Beck et al., 2001). Although no statistical analyses were reported, performance on the change detection task was better when a target letter was present (41%) than when it was absent (51%). These data offer initial evidence that the selection of behaviorally relevant events enhances the encoding of information into short-term memory.

Other evidence that target detection produces broad encoding enhancements comes from a recent fMRI study (Swallow et al., 2012). Participants pressed a button as quickly as possible whenever a tone of a pre-defined pitch was presented over headphones. If increasing attention to an auditory target pulls perceptual resources away from visual regions of the brain (Shomstein and Yantis, 2004; Johnson and Zatorre, 2006), then activity in visual areas should decrease when an auditory target is presented. If, however, temporal selective attention leads to widespread perceptual enhancements, then activity in visual areas should increase more when an auditory target is presented, rather than a distractor. The data confirmed the latter prediction. Activity in early visual cortex increased when an auditory target was presented, rather than a distractor (**Figure 2**). These data indicate that the response of early visual areas to goal-relevant events (Jack et al., 2006) is mediated by attention. In addition, unlike spatial selective attention (e.g., Kastner et al., 1998; Silver et al., 2007), temporal selection of an auditory target produced effects that were not spatially localized and that decreased in magnitude from early to late visual areas. This effect was present when auditory tones were presented on their own and when they were presented at the same time as a face, scene, or scrambled image. Moreover, the same pattern occurred when visual targets were presented with visual scenes. Under these conditions, detecting a target in the central visual field led to enhanced activity in regions representing the



visual periphery and in early auditory cortex. These data rule out the possibility that the increase in early visual cortical activity in response to target tones reflects purely multi-modal processing in a region that is traditionally considered unisensory (Brosch et al., 2005; Baier et al., 2006; Ghazanfar and Schroeder, 2006; Driver and Noesselt, 2008; Kayser et al., 2008). Rather, temporal selection of a target, but not distractor rejection, boosts activity in perceptual regions of the brain that are not involved in its processing (*target-mediated boost*).

The effects of target detection on perceptual processing are not limited to tasks involving visual stimuli, or to situations in which the background image and the target overlap in space. As just reviewed, the target-mediated boost is observed even in a purely auditory task (Swallow et al., 2012). Furthermore, both

long-term and short-term memory for scenes is enhanced when they coincide with the presentation of an auditory target, such as a high-pitched tone presented in a stream of low-pitched tones (Lin et al., 2010; Swallow and Jiang, 2010). Spatial overlap is also unnecessary. Short-term memory for color patches presented several degrees from fixation is enhanced by the presence of a target letter during encoding (Makovski et al., 2011), and scenes presented in an unattended location also benefit from target detection (Leclercq and Seitz, 2012a). Combined, these data suggest that target detection produces enhancements that are not specific to the spatial location or modality of the target.

Finally, perceptual learning data further support the claim that target detection results in widespread perceptual enhancements (Watanabe et al., 2001; Seitz and Watanabe, 2003). For these studies, participants identified gray letters in a stream of black letters. Each letter was presented in the center of an irrelevant random dot motion display (RDM). Motion coherence in these displays was below threshold, so learning was unconscious. Importantly, one direction was always paired with the gray target letters. Following nearly 20,000 trials, perceptual learning was obtained only for the direction of motion paired with the target letter, but not for motion directions paired with a distractor letter. Detecting the target letter increased sensitivity to concurrently presented, task-irrelevant, and unattended, perceptual information (Seitz and Watanabe, 2003). Interestingly, *task-irrelevant perceptual learning* (TIPL) is strongest for motion features processed in primary visual cortex (V1) and located near the target (Watanabe et al., 2002; Nishina et al., 2007). TIPL is clear evidence that behaviorally relevant events can influence context processing. However, it is slow to develop and restricted entirely to information that slips past attentional filters. In fact, no learning occurs when participants are able to detect the dominant direction of motion in the RDM displays and presumably suppress it (Tsushima et al., 2008; see also Dewald et al., 2011). Although there are similarities between TIPL and the attentional boost effect, inconsistencies such as these require further investigation.

Together these data indicate that selectively attending to behaviorally relevant events can enhance the processing of, and memory for, concurrently presented information. These effects are immediate and long lasting, influencing activity in perceptual regions of the brain (Swallow et al., 2012), short-term memory for color arrays and scenes (Lin et al., 2010; Makovski et al., 2011), long-term memory for visual stimuli (Swallow and Jiang, 2010), implicit memory for words (Spataro et al., 2013), and perceptual sensitivity to orientations and directions of motion (Seitz and Watanabe, 2003; Seitz et al., 2009). The fact that many of these effects occur cross-modally suggests that detecting goal-relevant events such as a target has broad effects on perceptual processing.

The attentional boost effect can be distinguished from previous demonstrations of enhancements that occur across tasks. Previous observations that two tasks and stimuli can interact have been limited to situations in which the tasks and items are semantically congruent. For example, masked images (e.g., a dog) are more easily identified when they are presented at the same time as a semantically congruent sound (e.g., barking), rather than an incongruent sound (e.g., hammering; Chen and Spence, 2010; see also Griffin, 2004). Furthermore, holding a word or image

in memory increases the likelihood that semantically congruent stimuli will be attended (Soto and Humphreys, 2007). In contrast to these findings, the attentional boost effect is unique in demonstrating that cross-task enhancements can occur for stimuli that are unrelated but concurrently presented. The targets and distractors are completely unrelated to the background images.

TEMPORAL SELECTION DRIVES THE ATTENTIONAL BOOST EFFECT

The experiments just reviewed point to a robust and broad processing advantage for information that coincides with targets. These data contradict the near ubiquitous finding that increasing attention to one task impairs performance on another (Kinchla, 1992). The availability of attentional resources appears to vary rapidly over time and is greater in some moments (when targets are detected) than in others. This fluctuation creates difficulties for limited-capacity theories such as the load theory. As a result, it is of critical importance to address whether alternative explanations can account for the attentional boost effect.

An immediate concern is that detecting a target may not have required more attention than did rejecting a distractor. Although target detection demands attention (Duncan, 1980; Chun and Potter, 1995), it is possible that the target square was too easily distinguished from the distractor squares and did not sufficiently tax perceptual resources. To address this concern, in one study we changed the simple color-detection task to a task that involved conjunction search (Swallow and Jiang, 2010). For this task, participants pressed a button for a target letter (e.g., a Red-X) that differed from distractor letters (e.g., Red-Y's and Blue-X's) in the combination of color and shape. Under these conditions, the target was perceptually similar to distractors, so perceptual load should have been high (Lavie and Tsai, 1994). In addition, distinguishing targets from distractors when they are defined by the conjunction of two features requires selective attention (Treisman and Gelade, 1980). The attentional boost effect was found under these conditions, indicating that it occurs even when targets are difficult to distinguish from distractors.

Another class of potential explanations for the attentional boost effect stem from the possibility that it reflects attentional phenomena that have already been well characterized in the literature. In particular, targets may have alerted participants and increased arousal, effectively increasing the amount of attention available to perform the two tasks (Posner and Boies, 1971). However, an inspection of **Figure 1B** makes it clear that there was no memory advantage for scenes that were presented immediately after the target, when the effects of alerting and arousal should have been greatest. Memory for scenes that followed a target was no better than memory for scenes that preceded it (Swallow and Jiang, 2010, 2011). Moreover, temporal selective attention produces a pattern of brain activity in early visual cortex that is distinct from the effects of alerting and arousal. Unlike alerting, detecting an auditory or visual target increases activity more strongly in primary visual cortex (Swallow et al., 2012), than in late visual areas (Anderson et al., 2003; Thiel et al., 2004; Fan et al., 2005).

Another possibility is that the target could have cued attention to the background scene. Attentional orienting in response to a cue has its largest effects 100–200 ms later (Nakayama and MacKeben,

1989; Egeth and Yantis, 1997). If the target acts as an attentional cue, then images that are presented during this brief time window should be better encoded into memory than those presented at the same time as a target. However, this is not the case. In one experiment (Swallow and Jiang, 2011) faces were presented for 100 ms and then masked for 400 ms (**Figure 3**). In different blocks of trials the target and distractor squares either onset at the same time as the face, or onset over the mask 100 ms before the face was presented. A memory advantage was observed only for faces that onset at the same time as the target. Moreover, another experiment found no evidence of enhanced memory for a face when it preceded a target (Swallow and Jiang, 2011), suggesting that the effects of target detection are temporally constrained.

Alternatively, it is possible that the effects of target detection on learning and memory are due to their distinctiveness. Items that are semantically or perceptually distinct from other items in a study list are better remembered than those that are not (Schmidt, 1991; Fabiani and Donchin, 1995; Hunt, 1995). However, recent data indicate that the attentional boost effect in short- and long-term memory is just as strong when target squares are as common as distractors (a 1:1 target to distractor ratio) and when they are relatively rare (a 1:6 ratio; Makovski et al., 2011; Swallow and Jiang, 2012). The target-mediated boost in fMRI is also observed when targets and distractors are equally frequent (Swallow et al., 2012). Moreover, poorer memory is observed for images that coincide with infrequent distractors rather than with distractors that are common (Swallow and Jiang, 2012). Distinctiveness is neither necessary nor sufficient for the attentional boost effect.

A final consideration is the nature of the attentional boost effect itself. Rather than an enhancement due to target detection, the attentional boost effect could reflect poorer memory for images presented with distractors. Several lines of evidence argue against this possibility. First, TIPL represents an increase in sensitivity for visual features that coincide with a target following training, and no change in sensitivity for those that coincide with distractors (Seitz and Watanabe, 2009). Second, in a study examining short-term memory for familiar scenes, scene memory was significantly above chance only when it was paired with a target, but not when the scene appeared on its own or with a distractor (Lin et al., 2010). Third, when task demands were held constant, long-term memory for faces that were presented at the same time as a distractor was similar to that for faces that were presented on their own (**Figure 3**; Swallow and Jiang, 2011). Finally, priming is enhanced for words presented with a target circle and unaffected for words presented with a distractor circle, relative to a condition in which the circles were task-irrelevant (Spataro et al., 2013). It therefore appears that the relative advantage for visual information that coincides with a target, rather than a distractor, reflects an enhancement due to target detection.

RECONCILING THE ATTENTIONAL BOOST WITH LOAD

The available data support the contention that, despite requiring attention, detecting a target can boost the processing of concurrently presented information. This finding challenges the notion that all perceptual resources are used obligatorily (Lavie and Tsai, 1994): If perceptual processing broadly increases at some

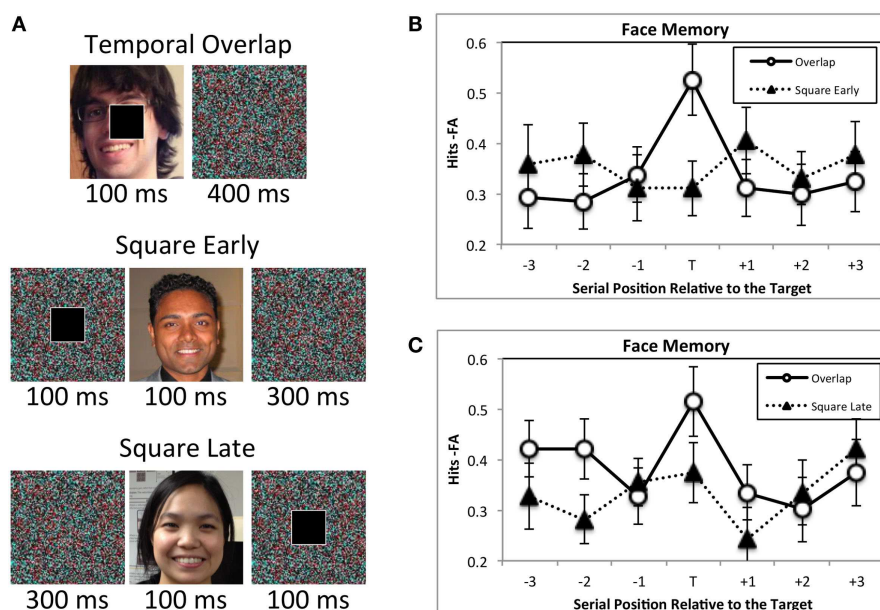


FIGURE 3 | The attentional boost effect occurs only for images that coincide with a target in time. (A) In two experiments participants were asked to memorize faces (100 ms duration, 400 ms mask; faces used in the experiment were famous), and to press a button when a white square, rather than a black square appeared (square duration = 100 ms). For one experiment the square and face onset at the same time in some blocks of trials (Temporal Overlap condition). In the other blocks of trials the square onset 100 ms

before the face onset (Square Early condition). In the second experiment, temporal overlap blocks were interspersed with blocks in which the square onset 100 ms after the face (Square Late condition). **(B,C)** Target detection enhanced memory for faces only when the target and face overlapped in time. It did not facilitate memory for images that occurred 100 ms earlier **(B)** or 100 ms later **(A)**. Error bars represent ± 1 standard error of the mean. Adapted from Swallow and Jiang (2011).

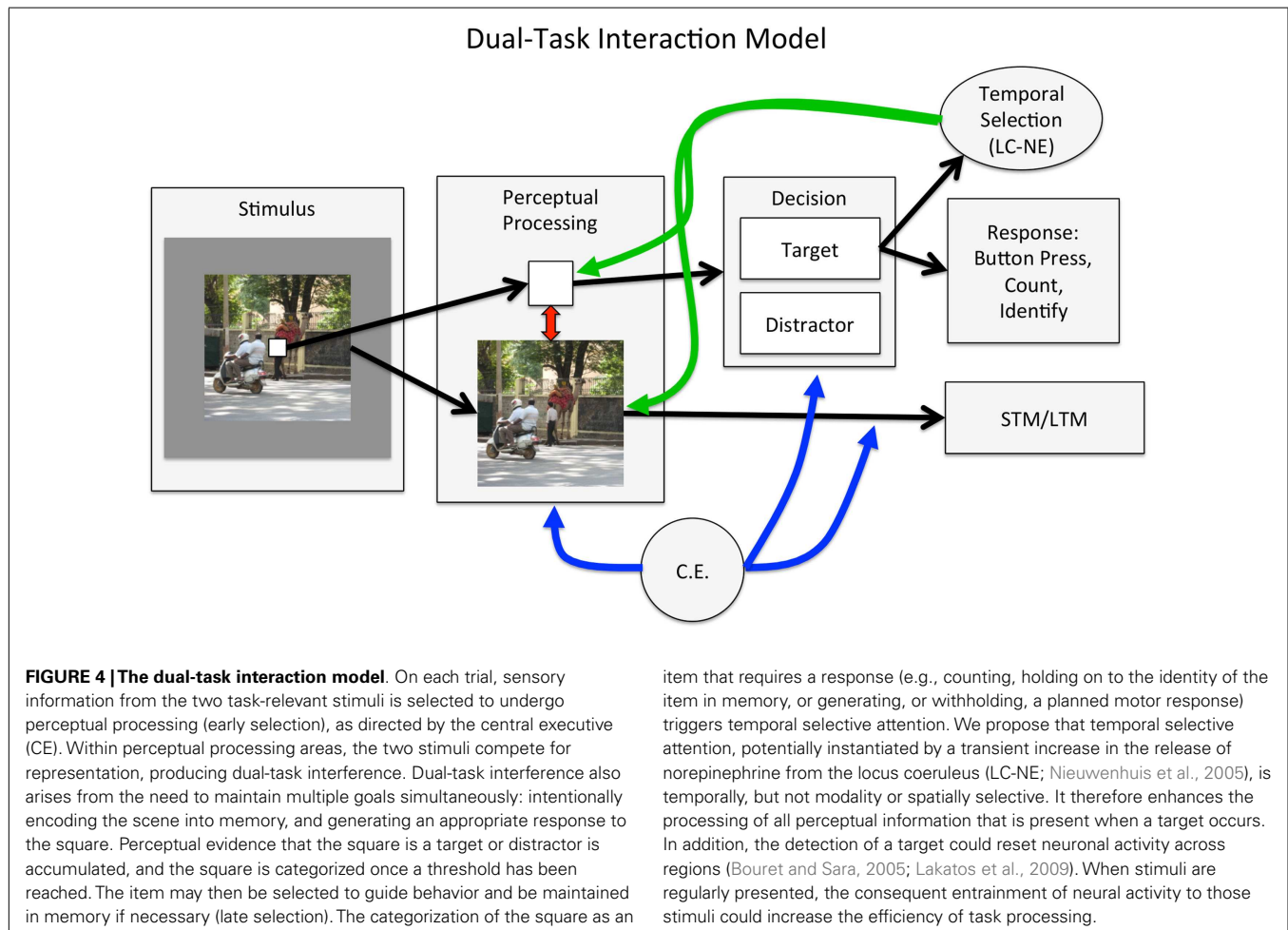
moments in time (e.g., when targets are detected), then it may not have been fully used at other moments in time. The attentional boost effect also represents a significant challenge to the long held view that performance in one task will suffer when another task or item requires more attention. If temporal selective attention of one target impairs the ability to detect a second target that is presented at the same time (Duncan, 1980), or soon after (Raymond et al., 1992), then how does it also enhance the encoding of concurrently presented perceptual information?

This section focuses on accounting for the potential effects of target detection on stimulus encoding. We propose that the encoding enhancement that is captured in the attentional boost effect and related phenomena represents a previously unrecognized feature of temporal selective attention that operates alongside dual-task interference.

Although many questions about the attentional boost effect remain, the available data provide a basis for proposing an extension to what is currently understood about temporal attention and selection. As in most models of attentional selection (e.g., Lavie and Tsai, 1994; Desimone and Duncan, 1995), the *dual-task interaction model* (Figure 4) proposes that task goals, maintained by a cognitive control mechanism like the central executive (Baddeley, 2003), prioritize the perceptual processing of goal-relevant

stimuli. Goal-based attentional prioritization occurs early in perception, ensuring that relevant stimuli are perceptually processed. It also occurs post-perceptually, ensuring that those stimuli are maintained in memory if necessary and lead to task-appropriate responses. The dual-task interaction model is entirely consistent with load theory's claims that selection occurs at multiple stages, and that cognitive control plays a critical role in ensuring that relevant information is used to guide task performance (Lavie, 2005).

The dual-task interaction model extends load theory and other theories of dual-task performance with two components. The first is a broad attentional enhancement that is triggered by the appearance of a target in a stream of distractors. This enhancement roughly corresponds to temporal selective attention mechanisms described by others (e.g., Bowman and Wyble, 2007; Olivers and Meeter, 2008) and is closest conceptually to a model of the attentional blink that is based on the locus coeruleus–norepinephrine (LC-NE) system (Nieuwenhuis et al., 2005). However, the dual-task interaction model emphasizes the broad and spatially unconstrained perceptual enhancements that result from temporal selection. The second component is the coupling of task processes when stimuli are rhythmically presented. Although we propose that detecting a target always triggers an attentional



enhancement, this effect may be more easily observed when the stimuli are rhythmically presented. Rhythmic stimulus presentation promotes efficient processing (Jones et al., 2002; Schroeder and Lakatos, 2009; Mathewson et al., 2010) and the temporal coupling of task processes.

TEMPORAL SELECTION BROADLY ENHANCES PERCEPTUAL PROCESSING

Within the dual-task interaction model, the decision that an item is a target leads to response selection and production, which are determined by the current goal set. It also leads to temporal selection, which enhances perceptual processing (Figure 4). To account for the finding that detecting a target results in the enhanced processing of the target and its context, the dual-task interaction model proposes that temporal selection is selective for time, but not for space or modality.

The target-mediated boost, makes it clear that temporal selective attention is not simply the brief application of spatial selective mechanisms (Swallow et al., 2012) (although the effects of both types of selection are likely to overlap and could interact; Coull and Nobre, 1998; Nishina et al., 2007; Leclercq and Seitz, 2012a). Indeed, the challenges facing temporal selection are distinct from those facing spatial selection. Rather than resolving competition in neural receptive fields (Desimone and Duncan, 1995), temporal selection must ensure that sufficient information is acquired about relevant items and their context before their processing is disrupted by new input. One way temporal selection may ensure that information about such items is available for task performance is to prioritize it for maintenance in short-term memory (e.g., Chun and Potter, 1995). However, perceptual processing takes time (Schyns and Oliva, 1994; Ploran et al., 2007) and encoding can be easily disrupted by new input (Breitmeyer and Ganz, 1976; Potter et al., 2004). Temporal selection therefore may also enhance perceptual processing to ensure that information about the relevant item and its context is encoded into memory. Without such an enhancement, perceptual information about behaviorally relevant items and their context could be lost.

The notion that temporal selection ensures that goal-relevant information is available to influence task performance may be best captured by theories that account for the attentional blink. Although they differ in their particulars, most theories of the attentional blink suggest that it reflects the protection of high-level representations of the target from interference (Dux and Marois, 2009). For example, in the Boost and Bounce Theory of temporal attention (Olivers and Meeter, 2008), the recognition of a target triggers an excitatory feedback response to perceptual areas, beginning with those that represent item identity. This response enhances, or boosts, the likelihood that a goal-relevant item will be maintained in working memory and, consequently, influence behavior. To avoid enhancing items that could interfere with task performance, the recognition of a distractor item results in inhibitory feedback to these same areas, reducing the likelihood that subsequent items will reach awareness. Similarly, the simultaneous type, serial token model (ST²) proposed by Bowman and Wyble (2007) claims that the classification of an item as a target triggers an attentional “blaster.” This blaster allows the features of the target item to be bound into an episodic and individuated

representation that is actively maintained in memory until it is needed. In the ST² model, the enhancement is automatically followed by inhibition. In both of these models, the mechanism that produces the attentional blink most closely corresponds to late selection, as its primary function is to determine which stimuli reach awareness and working memory (Vogel et al., 1998), rather than to prevent the perceptual processing of task-irrelevant information.

Like most theories of temporal attention, these two theories focus on explaining how temporal attention protects a target item from interference at the same time that it suppresses the processing of items that soon follow it (Dux and Marois, 2009). Like load theory (Lavie and Tsai, 1994; Lavie et al., 2004) however, their focus is almost exclusively on how a single relevant item is prioritized. In contrast, the dual-task interaction model proposes that temporal selection also enhances perceptual processing in regions that are not involved in representing the target. Although it is not an explicit component of most theories of temporal selection, the LC-NE model (Nieuwenhuis et al., 2005) does suggest that the effects of temporal attention may in fact be widespread. The LC-NE account of the attentional blink proposes that it reflects the dynamics of the LC-NE response to targets. In monkeys, a behavioral response to targets is reliably preceded by a phasic increase in the release of norepinephrine from the LC (Aston-Jones et al., 1994). NE increases the responsivity of target neurons to their input (Servan-Schreiber et al., 1990; Aston-Jones and Cohen, 2005). As a result, it could provide the neurophysiological basis for temporal selection as well as the attentional blink (Aston-Jones and Cohen, 2005; Nieuwenhuis et al., 2005). Of importance to the dual-task interaction model, the LC projects widely throughout neocortex. The effects of the phasic LC-NE response to targets therefore are likely to be widespread, spanning different sensory modalities and representing different spatial locations (Aston-Jones and Cohen, 2005).

The neurophysiological mechanisms that underlie the attentional boost effect and related phenomena are unknown. However, the broad perceptual enhancements that result from target detection (Seitz and Watanabe, 2009; Lin et al., 2010; Swallow and Jiang, 2010, 2011; Makovski et al., 2012; Swallow et al., 2012; Spataro et al., 2013) are a plausible consequence of phasic LC-NE signaling.

One potential effect of temporal selective attention on neural processing could be to reset the phase of neural oscillations in a diverse network of cortical areas (Schroeder and Lakatos, 2009). This, combined with work suggesting that the phasic LC-NE response to goal-relevant events can reset neuronal activity (Bouret and Sara, 2005) reinforces the proposal that the effects of targets on neural activity are widespread. They may also provide an explanation for one of the more surprising aspects of the target-mediated boost (Swallow et al., 2012): Detecting an auditory tone increases activity in early visual areas, even when no visual stimuli were presented. It is possible that these data reflect the resetting of neuronal activity in these areas, modulating their sensitivity to new input (Lakatos et al., 2009). The next section discusses the consequences of phase resets in greater detail.

As with the phasic LC-NE response to targets (Aston-Jones and Cohen, 2005), we propose that the perceptual enhancements resulting from temporal selection occur whenever a target is

detected. However, the ability to detect these enhancements is likely to be a function of many different factors. One factor is the presence of interference effects later in processing. Performance of even the simplest tasks involves multiple mechanisms, some that are parallel (e.g., perception) and some that are serial (e.g., response selection; Pashler, 1994). Although two stimulus streams may be perceptually processed in parallel, their encoding into working memory, and the generation of appropriate responses are likely to be limited by serial mechanisms (Pashler, 1994). Therefore, enhancements in perceptual processing may not translate into better performance when the consolidation or maintenance of perceptual information in long-term and short-term memory is disrupted. Indeed, increasing the difficulty of response selection by asking participants to make different, arbitrary responses to different targets eliminates (but does not reverse) the memory advantage for scenes presented at the same time as targets (Swallow and Jiang, 2010). Load theory (Lavie et al., 2004) also suggests that increasing cognitive load might interfere with the ability to observe the broad effects of temporal selection. Reducing the availability of cognitive resources to maintain or consolidate perceptual information into memory should reduce the utility of perceptual processing enhancements produced by temporal selection.

RHYTHMIC STIMULI PROMOTE THE COUPLING OF TASK PROCESSES

A second component of the dual-task interaction model is the proposal that the temporal structure of the stimulus streams may play a critical role in how much temporal selection for one task influences performance in another. Attentional boost effect experiments that irregularly presented task stimuli tended to show a weaker memory advantage for information that coincided with targets than experiments with regularly presented stimuli (e.g., 3–5% effects in Makovski et al., 2011 and Swallow et al., 2012 vs. 10–20% effects in Swallow and Jiang, 2010, 2011, 2012). This difference across studies could be explained by recent research that examines how rhythmic stimuli influence one's attentional state. Visual neural activity can entrain both to rhythmically presented stimuli and to activity in other sensory areas, enhancing the effects of temporal selection and integrating information across modalities (Large and Jones, 1999; Jones et al., 2002; Lakatos et al., 2007, 2008; Schroeder and Lakatos, 2009; Busch and VanRullen, 2010; Mathewson et al., 2010).

Neuronal oscillations correlate with how easily input can drive the activity of neural populations. In one influential study, Lakatos et al. (2008) trained monkeys to attend to either visual or auditory stimuli that were alternately presented in a continuous stream. Occasionally an oddball stimulus was presented, signaling the monkey to make a motor response. Two findings that are particularly relevant to the attentional boost effect were reported. First, activity in supragranular layers of visual cortex entrained to attended stimuli, regardless of whether those stimuli were presented in the auditory or visual modality. This entrainment could reflect the phase resetting of activity in visual cortex in response to an attended event (Lakatos et al., 2007). The second relevant finding was that the speed with which the monkeys responded to an oddball stimulus was influenced by when it occurred relative to the phase of low frequency (delta) neuronal oscillations. Faster

responses were generated to stimuli presented when the neurons were most excitable (Lakatos et al., 2008; Schroeder and Lakatos, 2009).

Oscillatory activity in EEG recordings also appear to influence attention and perception in humans (Mathewson et al., 2009, 2010; Busch and VanRullen, 2010). Visual stimuli are more easily detected when they are presented at the peak of an alpha wave in EEG recordings (Mathewson et al., 2009). Moreover, behavioral data further indicate that the entrainment of cortical activity across visual and auditory regions has widespread effects on attention. Attention to an item is enhanced when it occurs at a moment in time that is predicted by the rhythm of stimuli that precede it, regardless of whether they were in the same or different modalities (Klein and Jones, 1996; Jones et al., 2002; Miller et al., 2013). It therefore appears that attention to rhythmic stimuli can encourage synchronous activity across a network of cortical areas (including those involved in higher-order cognitive processes, Besle et al., 2011), which in turn makes them maximally sensitive to input at similar points in time.

This possibility is captured in the proposal that attention to perceptual information operates in two different modes (Schroeder and Lakatos, 2009). In the *rhythmic* mode perceptual regions of the brain are maximally sensitive to input at the moment in time that input is expected (see also Large and Jones, 1999; Baier et al., 2006). The rhythmic mode is therefore advantageous when stimuli are presented in simple regular sequences. However, it comes with the cost of introducing long periods of time in which perceptual regions are less responsive to their input; periods of high excitability are interspersed with periods of low excitability. If stimuli appear irregularly or in isolation, then adopting a rhythmic processing mode could be maladaptive. In these situations, attention may shift into what Schroeder and Lakatos (2009) refer to as the *continuous* mode of processing. This processing mode is less efficient, but is also better able to maintain neural excitability over long periods of time.

In the dual-task interaction model we propose that the regular presentation of stimuli for both tasks encourages the adoption of a rhythmic processing mode. This, in turn, allows for greater apparent interaction between areas and processes that are involved in performing the detection task and the encoding task. In this situation, the broad effects of temporal selective attention may more efficiently influence multiple tasks and stimuli when regions involved in performing them are optimally excitable at the same time. As a result, the effects of temporal selection should be more easily detected when stimuli are presented regularly, rather than irregularly. In the latter condition, the attentional boost effect may be small and more difficult to detect.

LOAD THEORY AND THE DUAL-TASK INTERACTION MODEL

As reviewed previously, load theory (Lavie, 2005) proposes that limits in perceptual and cognitive processing are accommodated by both early and late selection mechanisms. Early selection ensures that perceptual resources are directed to goal-relevant items. Late selection ensures that goal-relevant items reach awareness and influence behavior once they have been perceptually processed. To account for the late selection data, load theory asserts that all perceptual resources are used: attended items are processed,

but any perceptual capacity that remains spills over to irrelevant items (Lavie and Tsal, 1994).

The dual-task interaction model does not contradict the claim that selection can happen both early and late in processing. It is also consistent with dual-task interference and limitations in post-perceptual processing more generally (Pashler, 1994). According to the dual-task interaction model, responding to a target should increase demands on control processes. However, a corresponding reduction in control resources devoted to the encoding task can be offset by enhancements to perceptual processing that result from temporal selection. Thus, the dual-task interaction model reconciles the attentional boost effect with several aspects of load theory and the broader dual-task interference literature (e.g., Kinchla, 1992; Pashler, 1994).

The dual-task interaction model's suggestion that perceptual processing varies as a function of temporal selection, however, is difficult to reconcile with load theory's claim that all perceptual resources are obligatorily used (Lavie and Tsal, 1994). Although alerting and arousal are thought to influence the amount of available perceptual resources (Lavie and Tsal, 1994), the attentional boost effect conforms to neither of these (Swallow and Jiang, 2012; Swallow et al., 2012). In fact, the attentional boost effect lasts no more than 100 ms and is constrained to information presented concurrently with, rather than after, a target (Swallow and Jiang, 2011). If all available perceptual resources are used all the time, then it is not clear how such short-term variability in perceptual processing would occur, even in dual-task situations.

These inconsistencies suggest several possibilities. One is that this aspect of load theory is wrong – perceptual resources can be held in a reserve that is tapped when goal-relevant items appear. However, one could argue that we are comparing apples to oranges. Perceptual load theory describes attentional selection in space. In addition, whereas dual-task interference is important for explaining the effects of cognitive load on spatial selection, the effects of perceptual load can be observed in single tasks (Lavie, 2005). In contrast, the attentional boost effect involves selection over time and is usually observed in dual-task situations. However, the effects of target detection on early visual cortical activity occur even in single task situations (Swallow et al., 2012). Although one could argue that load theory accurately describes spatial selection processes, adhering to load theory's claim that all perceptual resources are used requires asserting that perceptual capacity rapidly increases when task-relevant events occur. It is not clear how such a claim could be falsified.

Another possibility is that the dual-task interaction model is wrong, and that temporal selective attention of a target item does not broadly enhance perceptual processing. Enhanced memory for a scene that coincides with a target could reflect post-perceptual effects of temporal selection. However, the data strongly suggest that target detection influences perceptual processing, even if it also influences post-perceptual processing. Target detection increases activity in early perceptual areas that are uninvolved in target processing (Swallow et al., 2012), enhances perceptual, but not conceptual priming (Spataro et al., 2013), and facilitates perceptual learning (Seitz and Watanabe, 2003). Although additional research is needed to clarify which stages of processing temporal selective attention enhances, the evidence points to perception.

A final possibility is that broad enhancements in perceptual processing produce unrecognized costs. Most studies of the attentional boost effect use recognition tests that do not capture differences in memory for perceptual details. Image encoding takes place at multiple scales, with coarser, more conceptual information extracted more rapidly than fine-grained perceptual details (Schyns and Oliva, 1994). Although memory for scene orientation was examined in one study (Swallow and Jiang, 2010), the data were noisy and inconclusive. Future research will need to determine whether temporal selection broadly enhances the processing of fine, as well as coarse, perceptual information.

IMPLICATIONS AND OPEN QUESTIONS

In its current form, the dual-task interaction model represents an initial attempt to account for the facilitatory effects of target detection on a concurrent encoding task, despite the increased demands on attention. Like the attentional boost effect itself, this model raises questions about the nature of temporal selective attention, its spatial characteristics, and the roles that load, reinforcement learning, and different attentional states may play in the ability to perform multiple tasks at once.

The dual-task interaction model proposes that temporal selection is broad and not constrained to particular locations or modalities. Although this claim is consistent with the available data, there is only one published study that attempts to address the spatial distribution of the effect (Leclercq and Seitz, 2012a). Additional research investigating both the spatial distribution and time course of temporal selective attention is needed. Moreover, the degree to which these effects are modulated by spatial attention and the relevance of the background information is also unclear. Most studies that have shown an effect of target detection on memory, rather than on perceptual learning, have done so by asking participants to attend to the background images (e.g., Lin et al., 2010; Swallow and Jiang, 2010; Spataro et al., 2013). In one study that examined incidental memory for the background scenes, no advantage for the scenes presented with targets was observed (Swallow and Jiang, 2011). Another recent study found that making targets difficult to perceive may eliminate the memory advantage for concurrently presented scenes (Huang and Watanabe, 2012). Along these lines, it will be important for future research to better characterize how different types of load influence the attentional boost effect. In its current form, the dual-task interaction model suggests that perceptual load and cognitive load may have very different effects on the ability of temporal selection to enhance perceptual processing. A better understanding of how attention and task relevance influence the attentional boost effect will be critical for the development of the dual-task interaction model and its reconciliation with load theory.

The close correspondence between the attentional boost effect and TIPL raises the question of whether they reflect the same mechanism operating on different time scales (Leclercq and Seitz, 2012a). In this and other papers we have proposed that this mechanism is temporal selection. However, TIPL has been explained by appealing to reinforcement learning in the attention-gated reinforcement learning model (AGREL; Seitz and Watanabe, 2009; Roelfsema et al., 2010). According to this perspective, detecting a

target is intrinsically rewarding, and therefore triggers the release of neuromodulators that reinforce neural activity in perceptual areas. As a result, the visual system slowly becomes more sensitive to perceptual features that are present when a target occurs. This is consistent with the finding that external rewards, such as the delivery of water, also produce similar perceptual learning effects (Seitz et al., 2009). The dual-task interaction model, in contrast, suggests that the effects that are captured in short- and long-term memory reflect temporal selection rather than reinforcement learning. Although similar, the dual-task interaction and AGREL models differ in what they propose is happening in perceptual areas. Whereas the dual-task interaction model emphasizes that a boost in activity occurs, AGREL emphasizes that the underlying neural structures (e.g., connection strengths) are being altered. This likely reflects a difference in the phenomenon that is the focus of investigation – memory for scenes or perceptual learning – and it is certainly possible that target detection results in both temporal selection and reinforcement learning. Attention and reward are closely related (Anderson et al., 2011), and their effects are difficult to disentangle (Maunsell, 2004). It will therefore be important to reconcile the AGREL and dual-task interaction models in the future.

Finally, additional research exploring the attentional boost effect in neuropsychological populations and in development could be invaluable for testing several claims of the dual-task interaction model. For example, examining whether the attentional boost effect is observed throughout the visual field in spatial neglect patients would provide a new test of how temporal selective attention and spatial selection interact (Robertson et al., 1998). Similarly, studying whether the attentional boost

effect is present or impaired when the dopamine system is compromised, as in Parkinson's disease and schizophrenia (Schultz, 1998), could shed light on the role of reinforcement learning in the effect. In addition, a recent account of autism suggests that it could reflect dysregulation of the LC-NE system (Mehler and Purpura, 2009). It is therefore possible that examining the attentional boost effect in this population could provide valuable insight into the nature of the attentional boost effect, as well as into the role of the LC-NE system in autism. Finally, because the enhancements that result from target detection are observable in memory only when demands on control processes are relatively low, it may also be useful to look at how changes in the development of multi-tasking ability and control (Luciana et al., 2005) influence the effect of target detection in behavioral and in brain activity.

CONCLUSION

For decades research on attention and dual-task processing has been based on the notion that attention and cognition are limited in capacity, and research on these processes has consistently supported this claim. Recent data from the attentional boost effect, the target-mediated boost, and TIPL, however, suggest that there is more to attention than mitigating capacity limits in space. Rather, attending to a target can enhance the perceptual processing of concurrently presented information. Although not predicted by current theories of attention, these data can be accounted for by the proposal that temporal selective attention is broad in space, but selective in time. Additional research is needed to reconcile the dual-task interaction model with load theory's claim that all perceptual resources are obligatorily used.

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Rhythm and Attention: Does the Beat Position of a Visual or Auditory Regular Pulse Modulate T2 Detection in the Attentional Blink?

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The attentional blink (AB) is one impressive demonstration of limited attentional capacities in time: a second target (T2) is often missed when it should be detected within 200–600 ms after a first target. According to the dynamic attending theory, attention cycles oscillatory. Regular rhythms (i.e., pulses) should evoke expectations regarding the point of the next occurrence of a tone/element in the rhythm. At this point, more attentional resources should be provided. Thus, if rhythmic information can be used to optimize attentional release, we assume a modulation of the AB when an additional rhythm is given. We tested this idea in two experiments with a visual (Experiment 1) or an auditory (Experiment 2) rhythm. We found large AB effects. However, the rhythm did not modulate the AB. If the rhythm had an influence at all, then Experiment 2 showed that an auditory rhythm (or stimulus) falling on T2 might generally boost visual processing, irrespective of attentional resources as indexed by the AB paradigm. Our experiments suggest that oscillatory cycling attention does not affect temporal selection as tapped in the AB paradigm.

Keywords: attentional blink, temporal attention, rhythm, pulse, alerting signals, audition and vision, multisensory processing

INTRODUCTION

A fundamental function of attention is the ability to select information in space or time given the limited capacities of the cognitive system. One impressive demonstration of limited attentional capacities in time is the attentional blink (AB) (for reviews see e.g., Shapiro et al., 1997; Dux and Marois, 2009; Martens and Wyble, 2010): within a rapid stream of irrelevant stimuli, a second relevant stimulus (target 2, T2) is often missed when it should be detected within 200–600 ms after a first relevant stimulus (target 1, T1; see below for more details). To optimize attentional precision, it would be beneficial if resources are provided at the right time. To determine when attentional resources should be provided, it might be helpful to use additional information such as previous knowledge, cues, primes, or context stimuli. In general, it is assumed that the incoming stream of events is partitioned by help of anticipated as well as actually presented stimuli (e.g., Klauer and Dittrich, 2010) to optimize the distribution of processing and response resources.

According to Barnes, Jones and colleagues (e.g., Large and Jones, 1999; Barnes and Jones, 2000; Jones et al., 2002), attention cycles oscillatory (see also e.g., Klimesch, 2012) when a rhythm is given. When the cognitive system is adapted to a given (auditory) regular rhythm (i.e., a pulse), the largest

“attentional energy” is provided at that point in time at which the next rhythmic stimulus (i.e., a beat given by a tone) is expected. In other words, the rhythm is used to optimize the release of attentional resources. The experiments of Barnes and Jones (2000) investigated time perception. In several experiments, the authors presented isochronous auditory rhythms/pulses. The stimulus onset asynchrony (SOA) between two tones of the rhythm was always 600 ms. At the end of the rhythm, a standard interval was presented which was varied between 524 and 676 ms. Thereafter a comparison interval was presented, which was equally often shorter, equal to, or longer than the standard interval. Participants had to decide whether the comparison interval was shorter, equal to, or longer than the standard interval of the rhythm. Accuracy in categorizing the comparison interval was greatest for the expected SOA, that is, if the standard interval was exactly the same as the intervals in the preceding rhythm (600 ms). Accuracy was worst for very long or very short (i.e., very unexpected) standard intervals. The authors interpreted their results in the context of their dynamic attending theory.

Evidence for their theory of attentional deployment in time comes from neurophysiological studies in monkeys and humans as well as from behavioral studies (for reviews see e.g., Schroeder and Lakatos, 2009; Calderone et al., 2014). For example, in macaque monkeys, it was shown first, that neural oscillations modulate responses to stimuli and second, respond to external rhythmic stimuli. In the last case, intrinsic rhythms are entrained and shifted by extrinsic rhythms, resulting in optimization of neural responses when task-relevant events are expected (e.g., Lakatos et al., 2008). Predictable rhythmic beats are more easily perceived and faster detected than unpredictable (non-rhythmic) stimuli (e.g., Rohenkohl et al., 2012). Further, selective attention seems also closely related to entrainment to rhythms (Calderone et al., 2014). There are some recent studies showing that rhythm can drive the temporal allocation of attention and that orienting of attention is not modality dependent but even cross-modal (for uni-modal evidence see, for example, Doherty et al., 2005; Sanabria et al., 2011).

First, Bolger et al. (2013) used simple auditory and visual detection and discrimination tasks. They introduced a rhythm sequence (either with simple isochronous meter or with complex musical stimuli) prior to the occurrence of the stimuli which had to be detected. Reaction times depended on the metrical positions at which the stimuli were presented. The authors interpreted their results as evidence that metrical entrainment can enhance stimulus processing. Second, Miller et al. (2013) also found cross-modal influences of an auditory rhythm on the temporal attentional allocation to visual stimuli. These authors used regular or irregular tone sequences either synchronous or asynchronous to visual targets. Results showed faster saccadic detection responses (Experiments 1, 2) and improved accuracy in a discrimination task (Experiment 3) to visual targets coinciding with a tone of a regular rhythm compared to asynchronous (i.e., tone preceded or followed the visual target) as well as irregular rhythms.

Previous studies in which the influence of rhythms on attention and perception was investigated, focused on simple reaction time tasks (and sometimes accuracy tasks) to target

stimuli. That is, one central aspect of attention—its limited capacity which is thought to be changing over time depending on stimuli which had to be processed—is not sufficiently touched by previous research on entrainment and/or rhythmic influences on attention. As already mentioned above, the AB paradigm is a suitable tool to investigate limitations of attention. In the visual domain, the AB reflects a robust deficit to correctly detect a second target (T2) appearing approximately 200–600 ms after a correctly identified first target (T1; e.g., Raymond et al., 1992). As a paradigm, the AB is most often studied by use of rapid serial visual presentation (RSVP) of shortly presented (distracting) stimuli, most often (strings of) letters, and varying the lag or SOA between the first and the second target. Typically, the first target has to be identified and the second target has to be detected or both targets have to be identified. Several theories might explain the AB (for an integration see e.g., Hommel et al., 2006). Whereas, early theories suggested a perceptual locus of the phenomenon (Raymond et al., 1992), later theories explained the AB at later, postperceptual stages of processing (e.g., Vogel et al., 1998; Jolicoeur and Dell’Acqua, 2000). The core element of most theories on the AB is based on capacity limitations of short-term memory or working memory. It is supposed that there are problems transferring and consolidating new information into working memory as long as preceding information is not processed to a certain level and that these processes related to the working memory draw on attentional resources (Hommel et al., 2006). Most likely, several mechanisms work together to result in an AB (Chun and Potter, 2001).

There are two studies in which entrainment and the AB were related. First, it was found that alpha entrainment (without an additional external rhythm except the RSVP rhythm) is larger for trials in which T2 cannot be reported than for trials in which T2 can be reported (Zauner et al., 2012). The authors argue that for stimuli presented with a frequency of about 10 Hz (i.e., approximately like the alpha frequency) those processes that underlie the generation of the P1 of the visual event related potential in the EEG (and that are related to alpha) interfere with those processes that enable the encoding of stimuli, specifically of T2. Second, there is recent work by Ronconi et al. (2015) who studied the influence of an acoustic or visual rhythmic stream before the RSVP stream, but with the same frequency. The authors presented entraining stimuli before the RSVP stream either with a regular rhythm, that is with the same frequency as the RSVP stimuli, or with an irregular rhythm, that is with variable interstimulus intervals between the entraining stimuli. Their results showed reduced AB effects with a regular (compared to an irregular) rhythm.

However, until now, there is no study in which the dependence of the AB effect on an additional rhythm like that used by Barnes and Jones (2000; see above) is studied. If other information, especially rhythmic information, can be used to optimize attentional release, we assume there should be a modulation of the AB when an additional rhythm is given. Specifically, we assume that the AB could be diminished by introducing a rhythm which peaks at the point in time when T2 is presented. In this case, the rhythm should evoke expectations regarding the point of T2 and more attentional resources should

be provided at this point. All current theories concerning AB lead to the prediction that a peak of additional attentional resources corresponding to the onset of T2 should diminish the AB. That is, when a tone is expected at position T2, this should lead to a simultaneous release of attentional resources which in turn would lead to a diminished AB effect—given that a rhythm is able to release additional attentional resources. The general aim of the present experiments is to examine whether the assumed cyclical

oscillating nature of attention in the presence of a rhythm can be manipulated to release attentional resources at peak times in the RSVP cycle, as would be shown by a reduction of the AB effect (for the general idea and procedure see also **Figure 1**).

In Experiment 1, we tested this prediction by using a visual rhythm before and during the RSVP stream. In Experiment 2, we used an auditory rhythm (Please note, in contrast to Ronconi et al., 2015, we did not investigate the question whether a regular

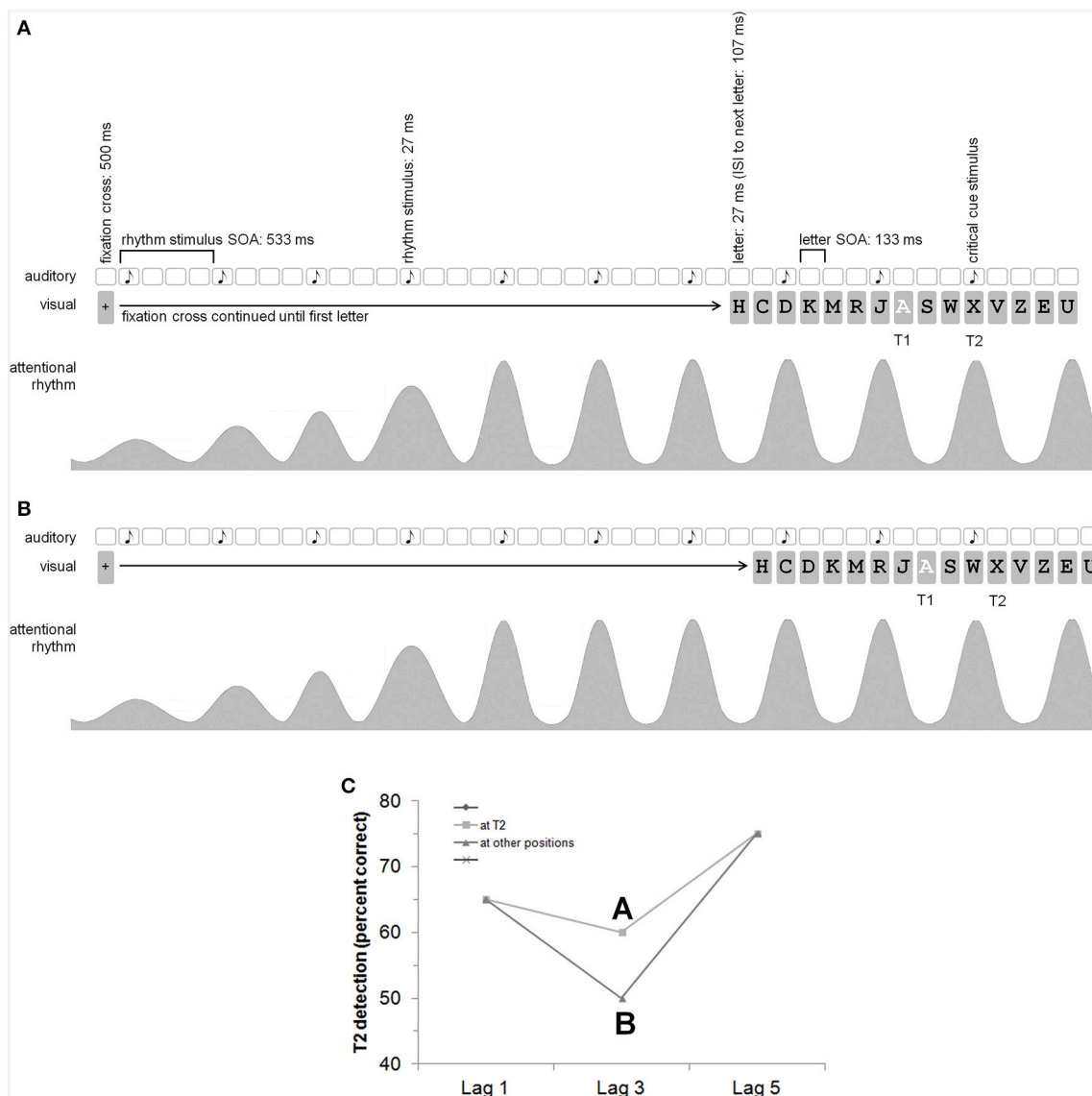


FIGURE 1 | General idea and procedure (with an auditory rhythm, i.e., Experiment 2). Please note that the time information is given with rounded values. With a refresh rate of 75 Hz, the exact timing is 26.66..., 106.66..., 133.33..., 506.66..., 533.33... (A,B) show the auditory rhythm presentation (the white squares indicate that there is no acoustic event at this time), the visual presentation (especially the RSVP with letters) with T2 at lag 3, as well as the attending/attentional rhythm. According to Barnes and Jones (2000), “an expected point in time corresponds to the peak of the attentional pulse carried by the oscillator” (p. 262). It is assumed that the oscillator adapts to stimulus time structure. (A) The auditory critical cue stimulus appears together with T2 which should result in a reduction of the AB (i.e., better T2 detection rates at lag 3; cf. C). (B) The auditory critical cue stimulus appears one position before T2. (C) Shown is our hypothesis for the AB effect depending on the rhythm and critical cue stimulus (which is either at T2 or at another position). The picture shows a reduction of the AB for T2s appearing together with the auditory critical cue stimulus (A better than B). We did not explicitly predict a general modulation of T2 detection by a rhythm—there might be a general enhancement or reduction of T2 detection also at lags 1 and 5. The main prediction, however, refers to the AB effect.

or irregular rhythm—induced by entraining stimuli before the RSVP stream—enhances T2 performance. In their experiments and due to their research question, attention to each stimulus should be enhanced with a regular rhythm. In contrast, we tested the specific effect of rhythms falling at T2 vs. rhythms falling at stimuli surrounding T2).

EXPERIMENT 1 (VISUAL RHYTHM)

In Experiment 1, we used a visual rhythm (red symbols or letters) which was presented before the RSVP stream and continued during the RSVP stream. The last rhythm stimulus (=critical cue stimulus) appeared either one position before T2, at T2, one position after T2, or two positions after T2. Participants had no task regarding the rhythm. Their task was to indicate T1 identity and detect T2.

Methods

Participants

The sample consisted of 29 students from Saarland University. Participants had normal or corrected-to-normal vision. They were paid for their participation or participated in exchange for course credit and gave informed written consent before participation. We excluded two participants as they made overall more than 60% errors in either the T1 or the T2 task. Of the remaining participants, 8 were male and 19 were female. Their median age was 24 years, ranging from 20 to 33 years.

The experiment was run in conformity with the ethical standards of our field and the AB task was approved by the ethical committee of the University of Hildesheim.

Design

Essentially, we used a 4 (position of the critical cue stimulus: one position before T2, at T2, one position after T2, two positions after T2) \times 3 (lag: 1, 3, 5) design. Note that the factor Lag also determined the position of T1 (10, 8, 6) in the RSVP stream. Additionally, it was varied whether a T2 probe was presented or not. All factors were varied within participants. In the tradition of AB experiments, we used correct T2 probe detections when a T2 probe was presented (after correct T1 responses) as the dependent variable.

Material

Attentional blink task

The stimuli in the RSVP stream consisted of the letters of the alphabet except the letters I, O, and Q. Each letter except the X could appear at each position of the stream. X served exclusively as T2 probe letter and was presented in half of the trials. Stimuli were written in Courier New font (pt. 18, bold). Most of the letters were presented in black. T1 was presented in white. In Experiment 1, some letters were presented in red according to the rhythm. All letters were presented at the center of a gray background.

Critical cue stimulus and rhythm stimuli

The critical cue stimulus was embedded in a visually presented rhythm. For the visual rhythm, the critical cue stimulus, and the

other rhythm stimuli were realized by colored letters or symbols. Before the RSVP stream began, participants saw rarely used symbols (e.g., ¥, Ø) written in red and with the same font and size as the letters in the RSVP stream. The symbols appeared in the same manner as the AB stimuli (i.e., at the center of the gray background; written in Courier New font, pt. 18, bold) and one after the other, to realize the rhythm. Overall, we used 14 different symbols. Seven randomly chosen symbols were presented in each trial. With the beginning of the RSVP stream, the rhythm continued by coloring the respective letters of the RSVP stream in red (or in white in the cases in which the rhythm coincides with T1). When the rhythm appeared together with T2, T2 was colored in red.

Procedure

Participants were individually tested in sound-attenuated chambers. The experiment was run using E-Prime software (version 1.3) with standard PCs connected to 17" CRT monitors with a refresh rate of 75 Hz and standard QWERTZ-keyboards. Stimulus presentation was synchronized with the vertical retrace signal of the monitor. Viewing distance was about 60 cm. Instructions were given on the CRT screen. Participants had two tasks which were to be answered after each RSVP stream. First, participants answered the question (T1 identification): Which one was the white letter? They used the standard keyboard and entered the corresponding key. Second, participants answered the question (T2 detection): Was there an X after the white letter? Participants pressed the M-key (marked with JA = yes) or the C-key (marked with NEIN = no).

The sequence of each trial was as follows (see **Figure 1** for an auditory variant): Participants started each trial self-paced by pressing the space-key. Then, a fixation stimulus (+) appeared at the center of the screen for 506.66...ms. Next, the first rhythm stimulus appeared for 26.66...ms. With a SOA of 533.33...ms, the next rhythm stimulus appeared. In each trial, seven rhythm stimuli were presented before the RSVP stream. After the seventh rhythm stimulus, there was an interval of 106.66... (critical cue stimulus one position after T2), 240 (critical cue stimulus at T2), 373.33... (critical cue stimulus one position before T2), or 506.66... (critical cue stimulus two positions before = after T2) ms. Then, the first letter of the RSVP stream appeared for 26.6...ms, followed by a blank screen for 106.66...ms. Thereafter, the next letter appeared (letter-to-letter SOA = 133.33...ms). Each RSVP stream contained 15 letters. The rhythm was continued during the RSVP stream with an SOA of 533.33...ms between two successive rhythm stimuli until the critical cue stimulus. The rhythm stimulus appeared simultaneously with a letter of the RSVP stream. There were three letters between two succeeding rhythm stimuli. T2 was always presented at position 11 of the RSVP stream. T1 was presented at position 10 (lag 1), 8 (lag 3), or 6 (lag 5) of the stream. There were 9, 7, or 5 distractor letters before T1, respectively, and 4 distractor letters after T2.

Each participant worked through five experimental blocks with 48 trials each. There was a short pause after each block. Before the first experimental block, there was a practice phase with 14 trials. Each experimental block consisted of 16 trials in

which T2 was at lag 1 (i.e., directly after T1), 16 trials in which T2 was at lag 3, and 16 trials in which T2 was at lag 5. At position T2, half of the trials contained an X and the other half of the trials did not contain an X. Additionally, the critical cue stimulus appeared equally often one position before T2, at T2, one position after T2, and two positions after T2 in each lag (1, 3, 5) \times T2 probe present (yes/no) condition. Within each block, conditions were presented in random order. Participants' task was to indicate first, which letter the white letter was and second, whether there was an X after the white letter or not.

Results

Mean error rates were 11.9% ($SD = 10.1$) in the T1 task and 25.3% ($SD = 12.2$) in the T2 task. We first excluded trials with incorrect T1 responses. For the remaining trials (for each lag \times position of critical cue stimulus there were between $M = 8.3$ and $M = 9.3$ observations after removal of trials with inaccurate T1 responses), we calculated mean correct T2 probe detections (in percent) when a T2 probe was presented. These mean correct T2 probe detections were subjected to a 4 (position of the critical cue stimulus) \times 3 (lag) repeated measures ANOVA. The main effect of lag was significant, $F_{(2, 52)} = 9.60$, $MSE = 1073.05$, $p < 0.001$, $\eta_p^2 = 0.27$. This main effect reflected the AB: Repeated contrasts showed that there was a significant difference in correct T2 detections between lag 5 and lag 3, $F_{(1, 26)} = 14.07$, $p = 0.001$, but no difference between lag 3 and lag 1, $F_{(1, 26)} < 1$, $p > 0.44$.

Neither the main effect of "position of critical cue stimulus," $F < 1$, $p > 0.65$, nor the interaction effect, $F < 1$, $p > 0.94$, were significant. That is, there was no evidence for an influence of the rhythm on the general T2 detection rate or the AB. As shown in **Figure 2**, there was no better (but also no worse) T2 detection performance if the critical cue stimulus appeared simultaneously with T2.

As we only used trials with correct T1 performance for further analysis, of course, T1 performance in these trials was the same across conditions.

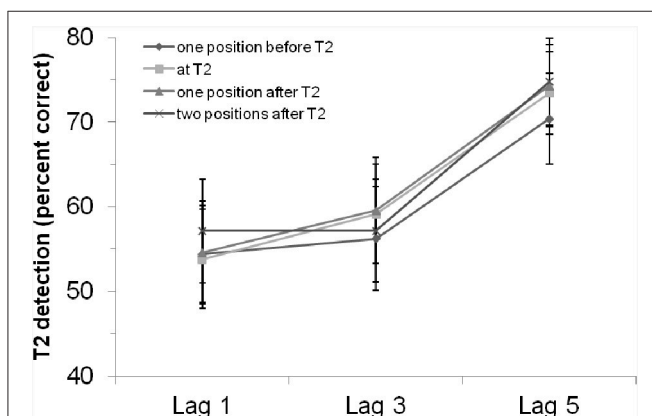


FIGURE 2 | T2 detection rate (in %, for trials with correct T1 identification and when the T2 probe was present) in Experiment 1 with a visual rhythm, depending on lag and position of the critical cue stimulus. Bars indicate the standard error of the mean.

Discussion

Using rhythmically and repeatedly presented colored visual stimuli before and during an RSVP—in which a critical stimulus could appear either at the position of T2, one position before T2, one position after T2 or two positions after T2—we found a significant visual AB with better detection rates at lag 5 than lag 3 (or lag 1). However, there were no significant influences of the rhythm, neither in general nor in interaction with the AB. That is, the visual rhythm did not induce specific expectations or act as a general alerting signal. However, our results also show that the position of the critical cue stimulus does not *hamper* T2 detection, as there were no differences between the different positions of the critical cue stimulus.

EXPERIMENT 2 (AUDITORY RHYTHM)

In Experiment 2, we attempted to make the rhythm more salient/relevant and to approximate the rhythm to that of the experiments by Barnes and Jones (2000). Therefore, we used an auditory instead of a visual rhythm and added a task regarding the rhythm, to ensure that participants could not fully ignore the rhythm.

Methods

Participants

The sample consisted of 43 students (9 male) from Saarland University with a median age of 22 years (ranging from 19 to 28). Participants had normal or corrected-to-normal vision. They were paid for their participation or participated in exchange for course credit and gave informed written consent before participation.

The experiment was run in conformity with the ethical standards of our field and the AB task was approved by the ethical committee of the University of Hildesheim.

Design, Material, and Procedure

The experiment was equal to Experiment 1 with the following exceptions. First, the rhythm was now realized auditorily with 1000 Hz tones presented via headphones for 27 ms each. The fixation cross remained on the screen until the onset of the first letter of the RSVP stream. Second, at the end of each trial and after the T1 and T2 response, participants indicated whether the rhythm was regular or not (note that each rhythm was actually regular); again, the answer was given by the M- or C-key. For this task, participants worked through a second practice phase directly after the first practice phase (with T1/T2 task) in which they practiced all three tasks (T1/T2/rhythm task). Third, each participant worked through five experimental blocks with only 24 trials each. Each block consisted of 8 trials in which T2 was at lag 1 (i.e., directly after T1), 8 trials in which T2 was at lag 3, and 8 trials in which T2 was at lag 5.

Results

Mean error rates were 22.3% ($SD = 11.4$) in the T1 task and 30.0% ($SD = 11.0$) in the T2 task. Again, we first excluded trials with incorrect T1 responses. For the remaining trials (for each lag \times position of critical cue stimulus there were between $M = 3.7$ and

$M = 4.0$ observations after removal of trials with inaccurate T1 responses), we calculated mean correct T2 probe detections (in percent) when a T2 probe was presented. These mean correct T2 probe detections were subjected to a 4 (position of the critical cue stimulus) \times 3 (lag) repeated measures ANOVA. If necessary, the Greenhouse-Geisser correction was applied, and corrected values are reported. The main effect of lag was significant, $F_{(1.48, 61.94)} = 5.27$, $MSE = 2805.62$, $p = 0.01$, $\eta_p^2 = 0.11$. This main effect reflected the AB: Repeated contrasts showed that there was a significant difference in correct T2 detections between lag 5 and lag 3, $F_{(1, 42)} = 22.08$, $p < 0.001$, but no significant difference between lag 3 and lag 1, $F_{(1, 42)} = 1.88$, $p = 0.18$.

The main effect of “position of critical cue stimulus” was not significant, $F_{(3, 126)} = 1.64$, $p = 0.18$. However, the planned contrast showed that T2 detection was marginally better if the critical cue stimulus appeared at T2 position compared to the other positions, $F_{(1, 42)} = 3.77$, $p = 0.059$. This revealed a tendency for enhanced attention when the critical cue stimulus appeared at T2. The interaction effect was not significant, $F < 1$, $p > 0.54$. That is, the rhythm had—if at all—a general effect on T2 detection, but was not able to modulate the AB. **Figure 3** clearly shows that, especially at lag 3, there was no difference between the positions at which the critical cue stimulus appeared.

Discussion

By use of an auditory rhythm before the critical auditory stimulus (again either coinciding with T2, or preceding or following T2), we again found a significant AB. Although the main effect of “position of critical cue stimulus” was again not significant, planned contrast revealed slight evidence for enhanced attention when the critical cue stimulus appeared at the point in time at which T2 was presented (compared to the other possible positions of the critical cue stimulus). Most interesting seems to be that there was no difference between the positions at which the critical cue stimulus appeared at lag 3 (which is the position with the largest AB). That is, the AB was again not modulated by the rhythm; if at all, the rhythm and the critical

cue stimulus improved T2 detection irrespective of lag. This result might be interpreted as visual boosting due to an auditory stimulus. For example, better detection rates of visual stimuli were found with simultaneous presentation of an irrelevant auditory accessory stimulus (Frassinetti et al., 2002). Chen and Yeh (2009) could reduce or even reverse repetition blindness in a visual RSVP stream by presenting an auditory stimulus together with the stimuli of interest. We hasten to add that we created a cross-modal situation by using a visual AB task and an auditory rhythm. Perhaps, this might be a crucial difference to the experiments by Barnes and Jones (2000). However, when comparing the results of Experiment 1 (only visual) and 2 (visual and auditory), there were no large differences (see also below).

GENERAL DISCUSSION

We analyzed the possible influence of oscillatory cycling attention on the AB. In particular, following Jones and colleagues (e.g., Barnes and Jones, 2000), we presented visual and auditory rhythms in a typical AB task. If attention adapts to the presented rhythm, the AB should depend on whether T2 is presented at a point in time when the attentional resources are at a maximum (due to the rhythm). However, although we found clear and large AB effects, we found not even the slightest hint of modulation of the AB effect by rhythm. If the rhythm had an influence at all, then Experiment 2 showed that an auditory rhythm (or stimulus) might generally boost visual processing at this particular point in time—irrespective of attentional resources as indexed by the AB paradigm.

Thus, the idea of oscillatory cycling attention as a model for the allocation of attentional resources in temporal selection (like in the AB task) does not hold. Participants obviously did not “use” (which is not necessarily meant in the controlled and/or conscious sense) the rhythm as a cue for increasing the allocation of attention although our rhythms were always perfectly reliable. In addition, note that we used two different variations of presenting the rhythm (visual and auditory) and also followed the procedures used by Jones and colleagues. This is important, because one may argue that it matters whether the rhythm is presented in the same modality as the to be attended stimuli (see Arend et al., 2006, who also concluded that the same AB attenuation effects resulted when additional stimuli were presented in the same or in another modality than the AB stimuli) or whether the modality in which the rhythm is presented “fits” to rhythm-processing in general (Welch et al., 1986)—of course it still might be the case that a particular combination of the modality in which the rhythm is presented and the modalities of rhythm and the RSVP stimuli might be a precondition for an effect of oscillatory cycling attention on the AB (e.g., maybe only rapid serial auditory streams are affected by auditory rhythms?). In addition, we must admit two possible caveats. First, we did not check in the same experiment whether our rhythm actually manipulated attention, but just failed to manipulate the AB (in other words, some kind of manipulation check concerning the effect of the rhythm would have been desirable). Second, the experiments conducted by Barnes, Jones, and colleagues (e.g., Large and Jones, 1999; Barnes and Jones, 2000; Jones et al., 2002)

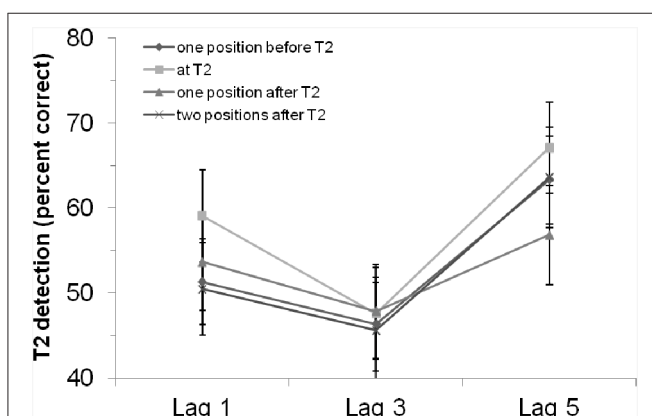


FIGURE 3 | T2 detection rate (in %, for trials with correct T1 identification and when the T2 probe was present) in Experiment 2 with an auditory rhythm, depending on lag and position of the critical cue stimulus. Bars indicate the standard error of the mean.

focused mainly on time perception or pitch judgments, which surely taps different attentional resources as compared to the AB. Thus, our data do not speak against these previous findings but only suggest that the model of oscillatory cycling attention is not easily applied to other tasks like the AB. It is clear that more research in different paradigms is needed to analyze whether the oscillatory cycling attention model could be applied to other domains than time perception and pitch judgments.

The fact that we observed—if any—generally slightly better T2 detection when an auditory stimulus coincided with the visual T2 fits to previous observations in RSVP streams which found visual boosting due to auditory stimuli (Frassinetti et al., 2002; Olivers and Van der Burg, 2008; Chen and Yeh, 2009). In particular, Olivers and Van der Burg (2008) found better T2 detection when an irrelevant bleep was presented together with T2 but not when it was presented directly before T2. This pattern suggests that the visual boosting is not due to alerting (because one might expect to find better detection performance if the auditory signal is presented shortly before T2) but due to multisensory enhancement. In fact, Busse et al. (2005) investigated whether neurophysiological signals to an irrelevant auditory stimulus were altered by a simultaneously presented, spatially (mis-)aligned visual stimulus. They found the strongest neurophysiological response to the irrelevant tone when the simultaneously presented visual stimulus was attended—suggesting some kind of multisensory enhancement of visual processing due to auditory stimulation (see Vroomen and de Gelder, 2000 for a discussion when auditory signals enhance or decrease visual processing).

There are a few papers in which a general enhancing effect of music/rhythm was found on T2 detection rates. Olivers and Nieuwenhuis (2005) found better T2 detection rates when participants listened simultaneously to a continuous rhythmic tune compared to the standard condition without music. The beat was not synchronized to the presentation of the stimuli in the RSVP stream. Better T2 detection rates were also found when participants should think about their holidays or their shopping plans for a dinner with friends simultaneously to the AB task. Also task irrelevant visual motion and flicker attenuates the AB (Arend et al., 2006). The authors suggested that a more diffuse attentional state causes better T2 detection rates, either via arousal or via positive affective state (see also Olivers and Nieuwenhuis, 2006). Ronconi et al. (2015) also found reduced AB effects when an auditory (but not when a visual) rhythm preceded the RSVP stream in the same frequency as the RSVP items. In general, however, there are also single reports, that the effect of music could not be replicated (Spalek and Di Lollo, unpublished data, as cited by Colzato et al., 2014). Further, differences between studies on entrainment and the AB (Zauner et al., 2012; Ronconi et al., 2015) used rhythms touching alpha. This also might explain differences in results. In this context, it also might be that the items of the RSVP stream themselves induce a rhythm, too, which could generally enhance performance (in our experiments and all experiments using fixed time intervals between items in an RSVP stream).

We ran a control experiment of Experiment 2 in which we removed the rhythm and presented only the critical cue

stimulus. The experiment was a replication of Experiment 2 except that we did not present any rhythm but only single tones as critical cue stimuli. (Please find the detailed description of the control experiment in the Appendix in Supplementary Material.) The critical cue stimuli were tones between 750 and 1250 Hz and participants had to compare (same/different decision) the tone pitch of the critical cue stimulus with a 1000 Hz standard tone presented at the beginning of each trial. With 24 student participants, we again found a significant main effect of lag, i.e., an AB effect, $F_{(2, 46)} = 9.30$, $MSE = 1050.33$, $p < 0.001$, $\eta_p^2 = 0.29$. The main effect of “position of critical cue stimulus” as well as the interaction of both factors were not significant ($ps > 0.40$; for the results see also Figure 4). In addition, comparing the control experiment and Experiment 2, we did not find statistical evidence for a general enhancement or impairment by the rhythm (i.e., there was no main effect of experiment/rhythm, $F < 1$, $p = 0.85$), and the interaction of experiment/rhythm and lag also missed the criterion for being significant, $F_{(2, 128)} = 1.99$, $p = 0.14$ (all other effects including the factor experiment/rhythm were also not significant, $ps > 0.70$). Thus, we did not find evidence for a general enhancement/influence of the rhythm used in Experiment 2 and a control condition in which no rhythm was used (Of course, the lack of significance does not prove the H_0). We interpret this as evidence that the results in our rhythm experiment(s) are not due a specific entrainment by the rhythm. As long as one does not argue that the presence of a critical cue stimulus effect and the rhythm modulation do interact in a disordinal way, the critical cue stimulus only adds a main effect and as a result the net effect of (any) critical cue stimulus effect and the rhythm modulation would still be usable for testing whether rhythms modulate the AB.

Why did we find no attenuation of the AB as it was found by Olivers and Nieuwenhuis (2005; 2006; but see Spalek and Di Lollo, unpublished data, as cited by Colzato et al., 2014) or Arend et al. (2006) when introducing a second task or enriching

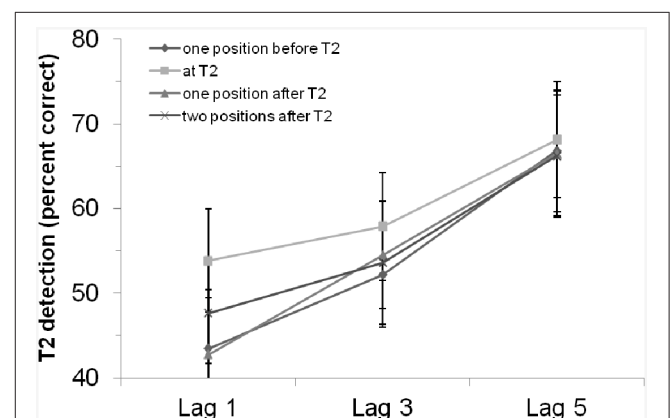


FIGURE 4 | T2 detection rate (in %, for trials with correct T1 identification and when the T2 probe was present) in the control experiment with an auditory critical cue stimulus without a preceding rhythm, depending on lag and position of the critical cue stimulus. Bars indicate the standard error of the mean.

the material by further stimuli? One possible way (besides that some of the effects could not be replicated by Spalek and Di Lollo) to explain the difference between our experiments and that of Olivers and Nieuwenhuis or Arend et al. is that our additional task was not affectively positive (like shopping plans or music) and not as demanding like a flicker task. As a result, attentional resources were not allocated to the rhythm and thus the AB was not attenuated. In contrast to most of the other experiments, in which influences of rhythms/entrainment on perception and attention were found, we used an accuracy measure instead of reaction time measures. This difference might lead to differences in results. However, as Barnes and Jones (2000) also used accuracy measures, we should have found modulations of the AB effect.

Taken together, our experiments suggest that oscillatory cycling attention induced by the rhythms used does not affect temporal selection as tapped in the AB paradigm. Our results might also be interpreted as evidence that the tasks and materials used require different attentional networks with different oscillator frequencies (e.g., Fan et al., 2007; Posner,

2012). Future research could test whether regular and various kinds of irregular rhythms differ in their influence on the AB effect and whether longer/stronger entrainment phases lead to modulations of the AB—also in cases in which no beat is presented at T2 positions.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <http://journal.frontiersin.org/article/10.3389/fpsyg.2015.01847>

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Mechanisms of Choice Behavior Shift Using Cue-approach Training

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Cue-approach training has been shown to effectively shift choices for snack food items by associating a cued button-press motor response to particular food items. Furthermore, attention was biased toward previously cued items, even when the cued item is not chosen for real consumption during a choice phase. However, the exact mechanism by which preferences shift during cue-approach training is not entirely clear. In three experiments, we shed light on the possible underlying mechanisms at play during this novel paradigm: (1) Uncued, wholly predictable motor responses paired with particular food items were not sufficient to elicit a preference shift; (2) Cueing motor responses early – concurrently with food item onset – and thus eliminating the need for heightened top-down attention to the food stimulus in preparation for a motor response also eliminated the shift in food preferences. This finding reinforces our hypothesis that heightened attention at behaviorally relevant points in time is key to changing choice behavior in the cue-approach task; (3) Crucially, indicating choice using eye movements rather than manual button presses preserves the effect, thus demonstrating that the shift in preferences is not governed by a learned motor response but more likely via modulation of subjective value in higher associative regions, consistent with previous neuroimaging results. Cue-approach training drives attention at behaviorally relevant points in time to modulate the subjective value of individual items, providing a mechanism for behavior change that does not rely on external reinforcement and that holds great promise for developing real world behavioral interventions.

Keywords: cue-approach training, behavioral change, value-based decision making, attention, eyetracking

INTRODUCTION

Monetary and food reinforcements have traditionally been employed to influence behavior (Thorndike, 1911; O'Doherty et al., 2004), but targeting automatic processes is likely more effective at attaining lasting behavioral change (Marteau et al., 2012). Previous research has established the cue-approach task as a reliable means to influence snack food choices for real consumption following a relatively short training period that does not employ external reinforcement or framing of the decision problem (Schonberg et al., 2014a). During cue-approach training, participants press a button on the keyboard in response to a neutral auditory tone that is consistently paired with approximately 25% of food stimuli. These “Go” food items that were paired with the tone and

button press during training were later chosen for real consumption more often than other food items with equal pre-experimental preferences. Thus, after just an hour of training that involved no external reinforcements, we saw a shift in choice behavior. Several candidate mechanisms were put forth to account for this shift in preferences following non-reinforced cue-approach training, several of which we test in the current experiments: (1) cued attention alone modulates preferences (addressed in previous publication); (2) approach behavior alone modulates value for the trained action (Experiment 1); (3) internal reinforcement for correctly performing the training task modulates choice (Experiment 2); (4) cueing sustained top-down attention in anticipation of performing a motor approach response modulates item-specific subjective value (Experiment 3).

Development of the cue-approach task was largely inspired by the attentional boost effect (Lin et al., 2010; Swallow and Jiang, 2010), which refers to the counterintuitive finding that participants have better memory for images that were viewed concurrently with a behaviorally relevant target stimulus compared to images that were viewed concurrently with a distractor. The attentional boost effect is counterintuitive because most previous research described a memory deficit – rather than a benefit – for information learned under divided attention conditions (as is the case for the target condition in attentional boost paradigms, for review, see Mulligan, 2008). The cue-approach effect shares many commonalities with the attentional boost effect, but is distinct in several important ways. Most importantly, the effect is measured in value-based choice for cue-approach vs. episodic memory for attentional boost. Although episodic memories bias value-based decisions (for review, see Delgado and Dickerson, 2012; Shohamy and Turk-Browne, 2013; Palombo et al., 2015), the value of foods that govern choice in the cue-approach task are thought to be largely learned through non-declarative memory processes. The association between the food and tone cue during training does not fully explain choice behavior because participants do not choose those items any more than they choose non-associated items when foods are of relatively lower value in the stimulus set as is evident in studies 1 through 4 in Schonberg et al. (2014a). Thus the shift in preferences following cue-approach training is not explained solely by an attentional boost effect on memory for cue-associated foods. Furthermore, the attentional boost effect has typically been studied using rapid serial presentations of stimuli (non-word stimuli typically remained on the screen 100–500 ms). In contrast, during the cue-approach training task, food images remain on the screen for one second and trials are separated by an intertrial interval lasting between one and twelve seconds and averaging three seconds. These main differences, along with others discussed below, we believe make the cue-approach effect unique from the attentional boost effect. It is important to draw parallels between the two effects in terms of the importance of attention and behavioral relevance of attention orienting cues (Gottlieb et al., 2014), but to also appreciate the contribution of the cue-approach effect to understanding how values may be modulated to help more effectively change behavior. To better assist with the development of real-world behavioral

change interventions based on cue-approach, we aim to better understand the cognitive mechanism by which preferences are modulated during training of the cue approach effect.

Development of the cue-approach training task was also heavily influenced by work on trained inhibition using the go/nogo or stop-signal training paradigms (for review, see Verbruggen and Logan, 2008b). In fact, the cue-approach task is the functional mirror of the cue-avoidance task in Studies 5 and 6 in Schonberg et al. (2014a). The cue-avoidance task we developed is highly similar to the ‘automated inhibition’ version of the stop-signal task (Verbruggen and Logan, 2008a; Lenartowicz et al., 2011). The cue-avoidance procedure was identical to cue-approach, except for the training phase. While during cue-approach training, participants responded with a key press only when they heard a tone cue, participants pressed a key on all trials *except* when they heard a tone cue in the cue-avoidance task. In our original published cue-avoidance studies and two additional unpublished studies, we did not see significant avoidance of stop-cue-associated food items during a choice phase identical to that used in the cue-approach studies. However, several other researchers have demonstrated a shift in preferences away from stop- or nogo-associated stimuli (Veling et al., 2013a,b; Houben and Jansen, 2015; Lawrence et al., 2015) or devaluation of stop-associated stimuli (Wessel et al., 2014), highlighting the potential of trained inhibition for development of real-world behavioral change paradigms. The cognitive mechanism underlying the shift in preferences following trained inhibition is under active investigation and the extensive literature that has thus far ensued offers some possibilities and some conundrums for understanding the mechanism underlying the cue-approach effect. In particular, recent work on the role of attention and expectancies in mediating response slowing to previously nogo-associated stimuli following modified go/nogo training revealed that stimulus-stop learning had a stronger effect on subsequent go performance when attention was higher to both task-relevant and task-irrelevant stimulus features (Best et al., 2015). In the present experiments, we focus on possible attentional mechanisms that may modulate the shift in preferences following cue-approach training.

Previous research has highlighted the importance of viewing time on choice preferences (Krajchich and Rangel, 2011). Additionally, manipulating visual attention during decisions influences choice behavior (Shimojo et al., 2003; Armel et al., 2008). Therefore, a simple mechanism of action during cue-approach training could be the modulation of preferences by attention captured when the auditory cue to particular items sounds. This mechanism does not rely on motor output, and eliminating the approach response should not affect the expected behavior change. However, in previous work, we showed that associating foods with a neutral tone without requiring a motor output did not result in a change in choice preferences (Schonberg et al., 2014a). This result is at odds with findings that the attentional boost effect does not require overt motor responses (Swallow and Jiang, 2012). More research on the parameters under which the cue-approach effect requires a motor response is necessary (e.g. covertly counting the cues without executing a motor response), however, we can rule out automated

attention orienting due to an auditory cue on its own as a mechanism for modulating preferences in the cue-approach task.

Having shown that a motor response during cue-approach training is likely key to the shift in choice behavior, we posit that the combination of an auditory cue with a motoric approach response is necessary to induce the cue-approach choice effect. However, we have not tested the possibility that a motor response alone, paired with particular food items, is sufficient to measure a later change in choice preferences. In cue-approach studies, participants use the index finger of the right hand during the training phase, and then use the index and middle fingers to indicate left and right item choices, respectively, during the probe phase. In previous studies, we did not find a bias for left item choices (Schonberg et al., 2014a), suggesting that a simple stimulus-specific action (i.e., index finger-button press) association is not formed. This does not, however, preclude the possibility of a generalized approach behavior toward stimuli that had previously been associated with an approach response. To test the hypothesis that approach behavior alone modulates preferences, we eliminated the auditory cue to press a button and paired button presses with foods in blocks of trials in Experiment 1. Participants were instructed at the beginning of each block of trials to either press a button on every trial or to simply view items on the screen without pressing any buttons. In Experiment 1 presented here, maintaining attention on a trial-by-trial basis was not necessary, but we ensured that participants were viewing items equally between Go and NoGo blocks using eye-tracking (see exclusion criteria for Experiment 1 below). If approach behavior alone modulates preferences and attentional mechanisms are minimally at play, we would expect a shift in preferences following blocked training in Experiment 1. However, we believe that participants generate expectancies for the Go signal and subsequently increase top-down attention to Go items during standard cue-approach training. Thus, if attention plays an important role in the shift in preferences following cue-approach training, we expect that eliminating the need for participant-generated top-down attention during blocked training would eliminate the shift in preferences in Experiment 1.

An alternative mechanism responsible for a shift in choice behavior during cue-approach training is internal reinforcement for the subjective evaluation of correctly pressing a button when cued. To test this hypothesis, we presented the tone cue with the snack food item and instructed participants to press a button on the keyboard as fast as possible only when they heard an infrequent tone, but before the food item disappeared from the screen, a fixed second after onset in Experiment 2. Participants were told that they would not obtain feedback on button press successes, but that they would receive a small monetary bonus commensurate to their performance on the task and determined at the end of the experiment. We suspect that internal reinforcement, or the positive subjective feeling of having correctly pressed the button in time during training, does not rely on increased top-down attention. Thus, we presented the tone cue at the same time as the snack food appeared on the screen with no delay. In the standard version of the cue-approach task, the tone appears on average 750 ms after the

onset of the food image on the screen. This go-signal-delay was titrated using a staircase procedure that ensured success (defined as pressing the button after the tone sounds, but before the image disappears from the screen a fixed one second after onset) on only 75% of all trials. Because the task in Experiment 2 is easier (since they have a full second rather than ~250 ms to press a button), participants should have higher success rates. If the cue-approach effect relies on internal reinforcement for the subjective feeling of correctly pressing a button, we would expect a more dramatic shift in preferences following training in Experiment 2 than in the standard delayed cue design due to the higher success rate for pressing the button in time. However, our main hypothesis is that cue-approach training relies on heightened attention at behaviorally relevant points in time rather than internal reinforcement. We hypothesize that participants learn to expect a cue when a Go food item appears on the screen. We expect that heightened attention to detect the cue to perform an action modulates preferences. In Experiment 2, the tone sounds at the same time as the food image appears, thus no expectancies can be formed. Thus, we expect that eliminating the need for heightened attention to detect the cue in Experiment 2 yields no shift in preferences.

Whereas Experiments 1 and 2 address the relevance of behaviorally important cues and their timing to the cue-approach effect, neither address what type of values (values for the possible actions vs. intrinsic item-specific values) are being modulated during training. Decision-making in the cue-approach task involves choices between two food stimuli, each involving a different physical action (i.e., press a button with the index finger or press another button with the middle finger). Although we hypothesized that cue-approach training perturbs the value of stimuli directly, it remains possible that cue-approach training instead modulates values of the possible actions to indicate choice. If the latter is true, then the choice effect would be motor effector specific and we would see a shift in preferences when choices are executed using the trained motor effector (i.e., the finger), but not if the choice is executed using a different motor effector (e.g., eyes). The first indication that cue-approach training may not modulate action values lies in the fact that we found no bias for choosing the food item on the left of the screen using the index finger (the finger used to press the button when cued during training) in any of studies 1 through 4 in Schonberg et al. (2014a). We wanted to follow this observation up with a stronger test of our main hypothesis. We hypothesize that subjective value of individual items is modulated by heightened top-down attention to particular foods at behaviorally relevant points in time. We tested this hypothesis by training one motor effector (the hand) and tested choice using a different effector (the eyes) in Experiment 3. These two motor effectors were chosen because they each recruit distinct and dissociable networks of motor regions. The presence of two different networks for the hands vs. eyes can be used to test hypotheses about the motor responses required during the choice phase of the cue-approach task. It is possible that cue-approach training modulates value signals of possible actions at the supplemental motor area (SMA)/pre-SMA level (Wunderlich et al., 2009), but does not perturb the Go items' intrinsic value at a higher level.

In this case, cue-approach effects would not be present when participants choose using eye movements at the probe choice phase. Conversely, if value change in this task is achieved at a level independent of specific motor circuits, we should observe a standard cue-approach effect regardless of choice motor effector. To test this, in Experiment 3, participants were trained on a standard cue-approach training phase using their finger to press a button when they heard the cue tone that sounded after a variable delay following the onset of the food stimulus on the screen. In the probe choice for real consumption phase, participants were required to fixate on the item they would like to choose for 750 consecutive milliseconds to indicate their choice.

The set of experiments presented here test three main hypotheses and narrow the field of possible mechanisms responsible for the cue-approach effect. These findings help to better understand which automatic cognitive processes are targeted during the cue-approach task to achieve lasting behavioral change. The mechanism underlying the shift in preferences following cue-approach training is not yet fully understood. In the three experiments reported here, we address three questions: (1) Is a non-cued motor response sufficient to induce a shift in preferences? (2) Is the delay in cue appearance after the food stimulus onset required for a shift in preference? and (3) Is the shift in preferences motor effector specific?

MATERIALS AND METHODS

In the experiments reported here, we modified the standard cue-approach task to better understand the mechanisms responsible for a shift in preferences for appetitive junk food items. The standard cue-approach task implemented in studies 1 through 4 in Schonberg et al. (2014a) consisted of three phases: an auction (Figure 1A), a training phase (Figure 1B), and a probe phase (Figure 1C). For details of the procedures used, please refer to Schonberg et al. (2014a), but we will summarize them here then describe the differences in the procedure for each of the three new experiments.

Stimuli and Procedure

Color photographs of 60 appetitive junk food items were used in this experiment. The same stimuli were used in previous experiments (Plassmann et al., 2007; Schonberg et al., 2014b,a). Stimulus presentation and behavioral data acquisition were implemented in python using Pygame (Shinners, 2011) for the auction, and in Matlab (Mathworks, Inc. Natick, MA, USA) using Psychtoolbox (Brainard, 1997; Kleiner et al., 2007) for the training and probe phases.

Procedure for Standard Cue-approach Training

Auction

Upon arrival at the laboratory, participants were endowed with \$3 and told that they would take part in an auction (Figure 1A). The auction followed the procedure outlined by Becker et al. (1964, BDM). Single pictures of food items appeared on the screen one at a time and participants placed their bid for each individual

item by selecting a value on a visual analog scale at the bottom of the screen using a mouse. Participants were explicitly told that their best strategy for the auction was to bid exactly what the item was worth to them to buy from the experimenter at the end of the session. At the end of the experiment a single trial was selected at random and played out such that the computer generated a counter bid, which was a random number between 0 and 3 in 25 cent increments. This number was compared to the participant's bid on the randomly selected trial and if the computer bid was higher than or equal to the participant's, the participant could not buy that item. If, however, the computer bid was lower than the participant's, then the latter was offered that item at the computer's bid lower price. This auction provided us a measure of willingness-to-pay (WTP) for all 60 food items per participant.

Item Selection

We used WTP to rank order the foods for each participant from most preferred (highest WTP, rank order number 1) to least preferred (lowest WTP, rank order number 60). Items were split into high-value (rank order numbers 1–30) and low-value items (rank order numbers 31–60). Items were then placed into one of two training conditions; Go items required a button press during training and NoGo items required no response from the participant. Eight items were designated as Go items to later be paired with NoGo items matched for WTP in comparisons of interest during probe (see below): 4 high-value Go items (e.g., rank order numbers 8, 11, 12, and 15) each to be paired with 4 high-value NoGo items (e.g. rank order numbers 9, 10, 13, and 14) to yield sixteen unique high-value pairs, 4 low-value Go items (e.g., rank order numbers 46, 49, 50, and 53) each to be paired with 4 low-value NoGo items (e.g., rank order numbers 47, 48, 51, and 52) to yield sixteen low-value pairs of interest. This pairing procedure ensured that pairs of items presented during probe would be matched for WTP but differed on Go status, such that participants should a priori be indifferent in a choice between a Go and a NoGo item. To maintain ~25% cue frequency as is common in stop-signal tasks (Logan and Cowan, 1984), we selected eight additional items to be paired with a Go cue during training: 4 high-value Go items (e.g., rank order numbers 16, 19, 20 and 23) to be paired with 4 low-value Go items (e.g., rank order numbers 38, 41, 42 and 45). These items will later be paired and used for high-value Go vs. low-value Go comparisons during probe. Full details of the pairing procedure can be found in Schonberg et al. (2014b).

Training

Participants viewed one food item at a time appear on the screen for 1 s followed by an inter trial interval (ITI) that lasted between 1 and 12 s and generated from an exponential distribution with mean 3 s (Figure 1B). Sixteen stimuli consistently required the participant make a button press on the keyboard (Go items, ~25% of trials), while the rest (44 items) required no motor response (NoGo items). The order of Go and NoGo trials was randomized per block of 60 trials. Participants were told to press a button on the keyboard as quickly as possible only when they heard a tone. The auditory Go cue sounded

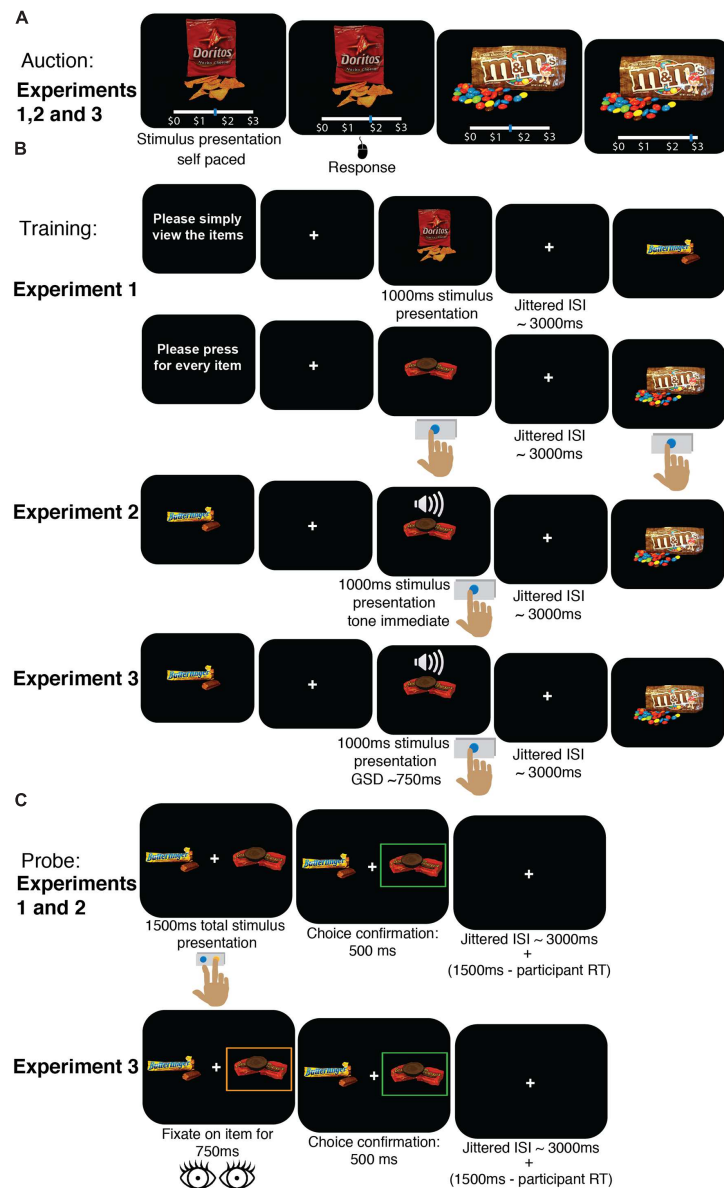


FIGURE 1 | Task procedure. (A) Auction to obtain WTP for each item. This procedure was identical in all three experiments. **(B)** Training phase. In Experiment 1, participants were instructed at the beginning of each block to either press a button every time an item appeared on the screen or to simply view the items without pressing any buttons. In Experiment 2, participants were instructed to press a button when they heard a tone (that appeared concurrently with food onset, with no delay) but before the image disappeared from the screen (1 s after it appeared). In Experiment 3, training was standard, i.e., participants were instructed to press a button when they heard a tone (occurring after a variable delay based on a staircase) but before the image disappeared from the screen (1 s after it appeared). Images appeared on the screen one at a time, and ~25% of items were associated with a tone. Trials were separated by a jittered intertrial interval (ITI) with a mean duration of 3 s. GSD, Go-signal delay. **(C)** Probe phase. Participants were instructed to choose one of two items that appeared on the screen to the right and left of a central fixation cross. Participants were told that a single trial would be selected and honored for real consumption, meaning they would receive the food item they chose on that particular trial to eat. Participants had 1.5 s to make their choice, and trials were separated by a variable intertrial interval with a mean duration of 3 s. In Experiments 1 and 2, participants made their choice using button presses, whereas in Experiment 3, participants were asked to fixate for 750 ms with their eyes on one of the items to indicate choice. RT, reaction time.

a variable time averaging 750 ms after food stimulus onset and was adjusted using a 1-up/3-down staircase procedure that ensured that participants would successfully press the button in time on only 75% of Go trials. If the participant successfully pressed the button in time, go-signal-delay (GSD) was increased

by 17 ms, making it harder to press the button in time on the next Go trial. If the participant failed to press the button in time after the tone, GSD was reduced by 50 ms, making it easier to press the button in time on the next Go trial.

Probe

After filling out a computer adapted version of the Barratt Impulsiveness Scale questionnaire (BIS-11, Patton et al., 1995) and on average 4 min after the end of training, participants were presented trials in which they chose between two items on the screen for real consumption (**Figure 1C**). On each trial, two food items appeared immediately to the right and left of a central fixation cross, and the participant was told to choose one item. They were told that a single trial would be selected at random at the end of the experiment and their choice on that trial would be honored for real, meaning they would receive the item they chose on that trial to eat at the end of the experiment. Each pair of interest was made up of two items with similar WTP; one was a Go and the other a NoGo item such that participants' a priori preference for either item should be equal given their stated pre-experimental preferences measured by the auction. Full details of the pairing procedure are described in Supplementary Figure 1 of Schonberg et al. (2014a). Right-left item placement and pair presentation was randomized across trials and participants. Each of 32 unique pairs of interest and 32 unique pairs used for sanity checks (high- vs. low-value items) was presented twice for a total of 128 probe trials.

Differences in Procedures for Current Experiments

Experiment 1

The auction was identical to the procedure described above. Training, however, was different. Participants viewed food items on the screen one at a time in blocks of Go or NoGo trials (**Figure 1B**, Experiment 1). At the beginning of each block participants were told to either press a button on the keyboard every time an item appears on the screen, but before it disappears in Go blocks or are told to passively view the items on the screen without pressing any buttons in NoGo blocks. Go items only appeared in Go blocks and NoGo items always appeared only in NoGo blocks. Stimuli appeared in random order per block. The order in which blocks appeared was counterbalanced across participants. Each of the 30 training items was repeated 15 times in different blocks for a total of 450 training trials. The probe task in Experiment 1 was identical to that described above; participants used the index and middle finger of their right hand to make choices (**Figure 1C**, Experiment 1).

Experiment 2

The auction was identical to the standard procedure described above. The training phase was very similar to the standard training procedure, but differed in the timing of the tone cue. Participants were instructed to view food stimuli appearing on the screen one at a time. They were instructed to press a button on the keyboard as quickly as possible and before the food stimulus disappeared from the screen only when they heard an auditory tone. In Experiment 2, the auditory cue always sounded immediately and concurrently with Go food stimuli presentation onsets (i.e., GSD = 0 ms, **Figure 1B**, Experiment 2). This contrasts with the cue-approach task in the original studies, in which the Go cue sounded after a variable delay (mean

GSD = 750 ms) following the food stimulus onset. Each of the 60 items was presented 16 times for a total of 960 training trials. The probe task in Experiment 2 was identical to that described in Schonberg et al. (2014a); participants used the index and middle finger of their right hand to make choices.

Experiment 3

The auction was identical to the standard procedure. Participants also underwent standard cue-approach training identical to that described above. Each of the 60 items was presented 16 times for a total of 960 training trials. The probe phase was different from the standard procedure, however. It differed in the actions required to make a choice. Participants were required to make eye movements rather than manual button presses to indicate choice. Participants were asked to fixate on one of the two items on the screen for 750 ms continuously in order to confirm their choice for that item on each trial rather than press one of two buttons on the keyboard to indicate choice (**Figure 1C**, Experiment 3).

Participants

Demographic details of the participant samples for the three experiments are described in **Table 1**. Briefly, Experiment 1 included 21 participants (15 female, mean age 21.2 ± 2.3), Experiment 2 included 25 participants (21 female, mean age 20.8 ± 2.3) and Experiment 3 included 25 participants (15 female, mean age 21.4 ± 2.8). Exclusion criteria are described below. Participants in the three experiments did not differ in age or BMI (p 's > 0.4). Sample sizes are similar to previously published studies (Schonberg et al., 2014b,a). All participants had normal or corrected-to-normal vision, no history of psychiatric, neurologic or metabolic illness, no history of eating disorders, no food restrictions and were not taking any medication that would interfere with the experiment. Participants were informed that the goal of the experiment was to study food preferences and were asked to refrain from eating or drinking anything besides water for four hours prior to their visit to the laboratory. All participants gave informed consent. The study was approved by the institutional review board (IRB) at the University of Texas at Austin.

Participant Exclusion Criteria

Auction Exclusion

Participants who consistently bid low on items during the initial auction did not provide us with enough range in bids to form pairs using the pairing procedure detailed in Schonberg et al. (2014a) and that matched items in pairs of foods to be used during the choice phase on stated subjective value. Thus we excluded one participant from Experiment 1 and two participants from Experiment 3 who bid less than 25 cents on 40 items or more during the initial auction.

Viewing Time Exclusion

Participants in Experiment 1 passively viewed items in blocks of NoGo trials and pressed a button on the keyboard every time a food appeared on the screen in blocks of Go items. Any observed shift in choice preferences that are due to differences in viewing time between Go and NoGo blocks would be explained

TABLE 1 | Participant demographic characteristics.

Expt	N	Gender (F/M)	Age		BMI		Excluded participants	Purpose of experiment
			M	SD	M	SD		
1	21	15/6	21.2	2.3	23.1	3.8	1 for auction 21 for viewing time	Effect of removing auditory cue
2	25	21/4	20.8	2.3	23.6	5.1	1 left handed	Effect of removing go-signal-delay
3	25	15/10	21.4	2.8	23.0	3.9	2 for auction 1 for training ladders	Effect of requiring a different motor effector during training and probe

Participants who bid less than \$0.25 on over 40 items during the auction were excluded. Participants who did not view the items as instructed during training were excluded. Participants whose training ladders (which govern the go-signal-delay) did not converge (indicating erratic behavior) were excluded.

by the mere exposure effect (Zajonc, 1968, 2001). We recorded participants' gaze location on the screen using an infrared eyetracker during training in Experiment 1. The cue-approach effect is not explained by the mere exposure effect given that participants do not show differences in viewing time for Go vs. NoGo items during training in our original studies and that there were no differences in preference-related brain activation for Go vs. NoGo items at the end of training in our original imaging study (given that participants do not show differences in viewing time during training and that there were no differences in preference-related brain activation for Go vs. NoGo items at the end of training, Schonberg et al., 2014a). In order to eliminate the mere exposure effect as a potential explanation for any changes in preferences following modified cue-approach training in Experiment 1, we excluded 21 participants that viewed items during Go blocks (when they were pressing a button) more than when they were instructed to passively view items during NoGo blocks, but didn't follow instructions and didn't maintain their gaze on the food during NoGo blocks. Thus, the exclusion criterion was a significant difference in item viewing time (i.e. time spent fixating on the food) within subject for Go and NoGo blocks in Experiment 1. The unusually large number of excluded participants in Experiment 1 is due to the fact that this version is inherently different from the standard cue-approach task. In the standard set up, cue trials are presented randomly during training and thus participants need to maintain their vigilance to press the button on time before the items disappears from the screen. However, in Experiment 1, Go and NoGo items are presented in blocks and thus participants know they will not have to do anything during the NoGo block and potentially shifted their gaze and visual attention away from the images in NoGo blocks.

Training Ladder Exclusion

Participants in Experiment 3 underwent standard cue-approach training. The cue initially sounded 750 ms after the onset of a Go food on the screen. This GSD was adjusted on every Go trial using a staircase procedure. When participants pressed the button on time after the cue sounded, but before the image disappeared from the screen (a fixed one second after onset), GSD was increased by 17 ms on the next Go trial, making it more difficult to press the button on time. But if the participant failed to press the button in time, GSD was decreased by 50 ms on

the next Go trial, making it easier to press the button on time. This 3:1 ratio ensured that participants would be accurate on about 75% of Go trials. Most participants' GSD ladders converged around 750 ms. One participant in Experiment 3 was excluded from analysis because their ladders did not converge (i.e., GSD fluctuated throughout the training phase and did not asymptote as is typical), indicating that they were not following instructions and were behaving erratically during training.

Eye Tracking

During training and probe in Experiments 1 and 3, we recorded participants' eye movements using an Eyelink-1000 by SR Research (Mississauga, Ontario, Canada). We obtained coordinates for eye position on the computer screen at a rate of 250 Hz. Additionally, we used eye position data in real time in Experiment 3 by providing feedback to facilitate participants' choices during the probe phase. Participants in Experiment 3 were required to fixate on one of the two items on the screen for 750 ms in order to confirm their choice of that item on each trial.

Data Analysis

To test whether different forms of cue-approach training induced a preference change or whether using a different modality during choice reveals a preference shift, we performed repeated-measures logistic regression to compare the odds of choosing Go to NoGo items against equal odds for high-value and low-value pairs separately. To test any differences in reaction time (RT) or stimulus viewing time, we performed repeated-measures linear regression to compare these measures when participants chose Go vs. when they chose NoGo items.

RESULTS

Experiment 1

We conducted this experiment to test the hypothesis that approach behavior alone modulates action values. To test this hypothesis, we eliminated the auditory cue and presented approach (Go) and no-approach (NoGo) item trials in blocks of trials. Each block was preceded by instructions indicating which block the participant was about to start.

Choice

Eliminating the auditory cue to press a button during cue-approach training, and thus rendering button presses completely predictable, eliminated the shift in preferences toward Go items. **Figure 2** summarizes the probe behavioral results in Experiment 1. Participants chose Go over NoGo items on 48% of high-value pair trials [odds ratio = 0.90, 95% CI = [0.65 1.24], $p = 0.5$ for odds of choosing high-value Go to NoGo items, Bayes Factor in favor of the null (BF_n) = 5.06] and 50% of low-value trials (odds ratio = 0.97, 95% CI = [0.62 1.52], $p = 0.9$ for odds of choosing low-value Go to NoGo items, BF_n = 10.15). The high-value pair choice effect in Experiment 1 are significantly different than the effect in the four original studies that employed the standard cue-approach design in Schonberg et al. (2014a), odds ratio = 2.05, 95% CI = [1.34 3.15], $p = 0.001$ for choices of high-value Go items in Experiment 1 compared to the four original studies). The low-value pair effect in Experiment 1 did not differ from the effect in the four original studies (odds ratio = 1.32, 95% CI = [0.78 2.23], $p = 0.3$, BF_n = 3 for choices of low-value Go items in Experiment 1 compared to the four original studies).

Eyetracking

In line with previous findings (Shimojo et al., 2003; Armel et al., 2008; Schonberg et al., 2014a), there was a main effect for chosen items (regardless of Go/NoGo status) on the proportion of choice time spent viewing an item (**Figure 3**, mean proportion for chosen item = 0.41, mean proportion for unchosen item = 0.32, $\beta = 0.09$, 95% CI = [0.08 0.10], $p < 0.0001$). However, unlike previous findings using the standard cue-approach task, there was no main effect of Go status on the proportion of time participants viewed the item (mean proportion of choice time viewing Go items = 0.36, NoGo = 0.36, $\beta = 0.002$, 95% CI = [-0.01 0.01], $p = 0.8$, BF_n = 22.02). There was no

interaction between item chosen/unchosen and Go/NoGo status on proportion of time spent viewing the item. These results suggest that training with no auditory cue did not bias attention toward Go items. Previous findings showed that participants tended to look at the Go item longer, even when that Go item was not chosen (Schonberg et al., 2014a).

Reaction Time

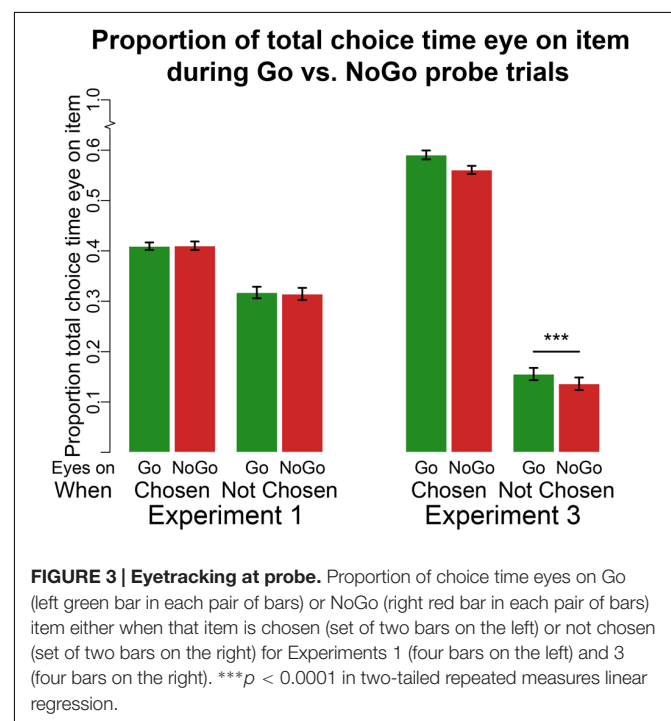
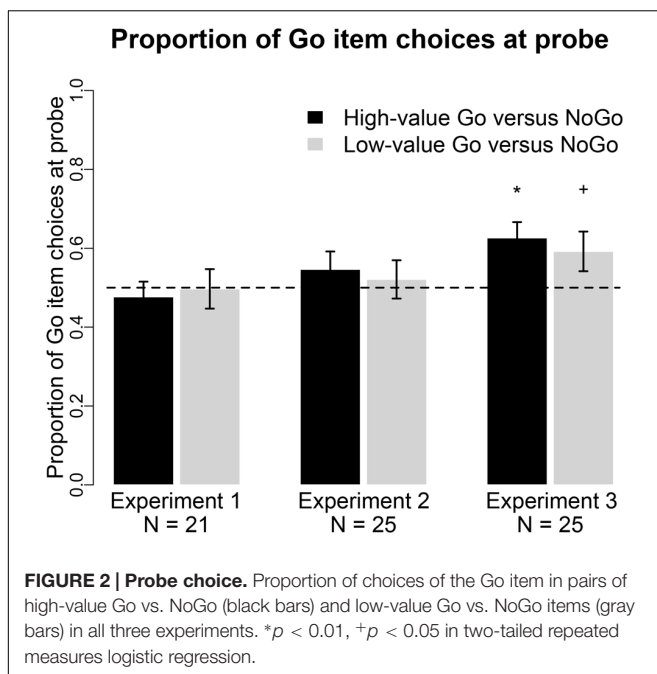
Participants were on average slower at choosing between low-value items than they were choosing between high-value pair items (low-value choice mean RT = 871.4 ms, high-value choice mean RT = 839.1 ms, $\beta = 33.75$, 95% CI = [13.1 54.4], $p = 0.001$). There was no interaction between pair type (high- or low-value pairs) and choice of Go or NoGo on RT ($\beta = 8.9$, 95% CI = [-34.2 52.2], $p = 0.7$, BF_n = 14.03). RT also did not differ for choices of Go or NoGo ($\beta = 5.95$, 95% CI = [-15.7 27.6], $p = 0.6$, BF_n = 14.21).

Experiment 2

We conducted Experiment 2 to test the hypothesis that internal reinforcement for correctly performing the training task modulates choice. This hypothesis posits that vigilance, or heightened top-down attention is not required during the cue-approach training. We test this hypothesis by eliminating the Go signal delay (GSD) – i.e., the delay to sound the auditory cue to press a button after food stimulus onset – during cue-approach training.

Choice

Eliminating the delay between food stimulus onset and auditory cue onset during cue-approach training eliminated the shift in preferences toward Go items. **Figure 2** summarizes the probe



behavioral results in Experiment 2. Participants chose Go over NoGo items on 55% of high-value pair trials (odds ratio = 1.27, 95% CI = [0.83 1.93], $p = 0.3$ for odds of choosing high-value Go to NoGo items, $BFn = 0.39$) and 52% of low-value trials (odds ratio = 1.08, 95% CI = [0.69 1.71], $p = 0.7$ for odds of choosing low-value Go to NoGo items, $BFn = 5.66$). The choice effect for the high-value pairs was marginally lower than in the four previous studies in Schonberg et al. (2014a), odds ratio = 1.47, 95% CI = [0.96 2.25], $p = 0.08$, for choices of high-value Go items in Experiment 2 compared to the four original studies). The choice effect in the low-value pairs did not differ from the effect in the previous samples (odds ratio = 1.17, 95% CI = [0.71 1.93], $p = 0.5$, $BFn = 3.84$ for choices of low-value Go items in Experiment 2 compared to the four original studies). These choice effects do not differ between Experiments 1 and 2 (p 's > 0.2, BFn 's > 1.89).

Reaction Time

Reaction times did not differ between low-value and high-value pair choices. RTs were also the same for choices of Go and NoGo items (all p 's > 0.2, β 's < 12.5, and BFn 's > 7).

Experiment 3

We conducted Experiment 3 to test the hypothesis that cueing sustained top-down attention in anticipation of performing a motor approach response modulates item-specific subjective value. If item-specific values rather than action values are being modulated, the choice effect should not be motor effector specific. To test this hypothesis, participants were trained using manual button presses but were asked to indicate choice during probe using eye movements.

Choice

Using a different motor effector (eye rather than hand) during the probe phase revealed a choice preference for Go items following standard cue-approach training. Cue-approach training likely affects item valuation/processing rather than simpler action values. **Figure 2** summarizes the probe results in Experiment 3. Participants chose Go over NoGo items using eye movements on 63% of high-value pair trials (odds ratio = 1.83, 95% CI = [1.25 2.68], $p = 0.002$ for odds of choosing high-value Go to NoGo items) and 59% of low-value trials (odds ratio = 1.59, 95% CI = [1.04 2.42], $p = 0.03$ for odds of choosing low-value Go to NoGo items). The choice effects in Experiment 3 did not differ from those in the previous four studies in Schonberg et al. (2014a), p 's > 0.4, BFn 's > 2.93). Choices of high-value Go items were significantly higher in Experiment 3 when compared to choices in Experiment 1 (odds ratio = 2.02, 95% CI = [1.22 3.35], $p = 0.006$ for choices of high-value Go items more prevalent in Experiment 3 compared to Experiment 1), but not significantly different than in Experiment 2 (odds ratio = 1.46, 95% CI = [0.83 2.57], $p = 0.2$, $BFn = 1.87$ for choices of high-value Go items in Experiment 3 compared to Experiment 2). Choices of low-value Go items were not different between any of the experiments (odds ratios < 1.64, p 's > 0.1, BFn 's > 1.43).

Eyetracking

Participants were instructed to fixate on the item they would like to choose for 750 ms in order to execute their choice. Thus, the main effect of choice on the proportion of choice time the eyes are fixated on a particular item is artificial (see **Figure 3**). However, we ran a mixed effects linear regression model examining the effect of Go status (two levels: Go and NoGo) on proportion of choice time viewing a particular food with participant as a grouping factor. We found a main effect of Go status on viewing time (mean proportion of choice time viewing Go items = 0.42, NoGo = 0.30, $\beta = 0.12$, 95% CI = [0.10 0.12], $p < 0.0001$). This finding replicates previous results using eyetracking during the standard cue-approach task when participants chose between the two items using button presses (i.e. using the same motor effector that was trained). Moreover, using the same mixed-effects model above on data for times participants were fixated on unchosen items only, we found a simple effect of Go status on viewing time within unchosen items (mean proportion of time spent viewing unchosen Go = 0.16 and viewing unchosen NoGo = 0.14, $\beta = 0.02$, 95% CI = [0.01 0.04], $p < 0.0001$). Participants viewed Go items longer than they viewed NoGo items even when the item was not ultimately chosen.

DISCUSSION

We have recently shown that choices can be influenced using the novel cue-approach paradigm that does not rely on external reinforcement or re-framing of the decision problem (Schonberg et al., 2014a). The findings of the experiments described here shed light on the mechanism by which preferences shift during cue-approach training. This was achieved by manipulating several aspects of the basic cue-approach task design. In Experiment 1, we eliminated the tone that cues participants to perform a motor action, instead presented food items in blocks of trials and instructed participants to passively view items or to press a button every time a food appears on the screen. In this experiment, we found no evidence of a shift in choice preferences following blocked training, consistent with our view that motor approach alone is not sufficient to elicit a change in preferences. In Experiment 2, we eliminated the delay between the onset of the food image and the tone cue to press a button. This made the task easier for participants to perform and did not allow for anticipation of the tone when a Go food item appeared on the screen. We found no evidence of a change in preferences following modified training that omitted the delay, consistent with our hypothesis that top-down attention directed at the foods during anticipation of the tone is key to a shift in preferences. Finally, in Experiment 3, we required a different motor effector during standard cue-approach training and choice phases. When participants used eye movements to make choices, we found evidence of a significant shift in preferences on par with findings in our original studies where participants used their fingers during both training and choice phases.

Cueing a motor response during training appears to be important for the shift in choice preference. In the standard cue-approach training task, the food stimulus is presented first,

followed by the cue to perform a motor response. Performing an uncued motor response during blocks of training trials at the beginning of which the participant receives instructions to follow for the whole block of trials (press a button or passively view items), does not lead to a shift in choice behavior (**Figure 2**, Experiment 1). This finding, in combination with our previous finding that an auditory cue in the absence of a motor response is also not sufficient to induce a change in choice preferences, reinforces our claim that attentional as well as motor mechanisms are likely at play during cue-approach training. It should be noted that the design of this version is also different from the original task as the presses are entirely predictable and do not involve heightened anticipation. Due to this fact we also incurred a very high percentage of excluded participants as they were not watching the items that were not associated with a button press. However, in a post hoc analysis of the probe phase data including all participants did not change the pattern of results. Excluding participants that did not view the Go and NoGo items equally ensured that mere exposure was not a factor in this experiment and that participants were indeed maintaining visual attention on the foods equally in both task conditions. An alternative task design was considered where participants are instructed to press the button when they wanted to without a cue as was implemented in Swallow et al. (2012). However, this design would have required only a single participant-determined button press-food pairing whereas food-cue-button press pairings were repeated (8, 12, or 16 times per item) in previous standard cue-approach training phases. The block design in Experiment 1 here also allowed us to maintain the same controlled food pairing procedure that matched values in choice pairs of items based on the initial auction used in previous standard versions of the task. The absence of an auditory cue in the version of the cue-approach task implemented in Experiment 1 eliminates the need for focusing attention at behaviorally relevant points in time. The absence of a need for sustained top-down attention usually initiated by an expectation of the forthcoming cue to make a motor response once the block of training trials commences, despite maintenance of visual fixation on the foods, is likely responsible for the lack of a behavioral or eyetracking effects in Experiment 1. These findings are consistent with the view that an auditory cue along with a motor response during training are essential to elicit a shift in preferences in this task. However, future research should investigate different types of cues that may affect cue-approach training differentially. To date, only neutral tones have been employed as the cue to perform a motor action. Additionally, although Experiment 1 results are consistent with the view that an approach response alone is not sufficient to lead to a change in preferences, the response in this version of the cue-approach task is instructed. Perhaps agency is important for the inherently valenced approach response to have an effect on value of foods. Future research should employ a task design similar to the alternative design described above to test this possibility and provide fuller understanding of the contributions of motor and attentional mechanisms in the cue-approach task.

External reinforcement on a trial-by-trial basis has been shown to be effective at influencing behavior (Thorndike, 1911; O'Doherty et al., 2004; Tricomi et al., 2009; Schonberg et al.,

2014b). However, the effectiveness of this strategy on long-term behavioral change has been questioned (Marteau et al., 2012). Thus, we were inspired to develop a paradigm that did not rely on external reinforcement and showed that cue-approach training had an effect on preferences that lasted longer than a month (Schonberg et al., 2014a). We could not however control participants' subjective feelings during the training task and wanted to test the possibility that internal reinforcement for correctly pressing the button when cued was responsible for a shift in preferences. This form of reinforcement would presumably be equally vulnerable on the long-term as external reinforcement. In Experiment 2, we eliminated the delay between onset of the food image on the screen and the sounding of the tone cue. In this version of the task, participants achieved a higher rate of success than in the standard version as they had more time to press the button in time after the cue sounded, thus would presumably receive more internal reinforcement. If internal reinforcement played a role during cue-approach training, we would expect a larger effect on preferences at the choice phase in Experiment 2. We found no evidence of change in preferences following training that yielded more correct responses, suggesting no role for internal reinforcement. This version of the task however is significantly easier for the participants to perform than the standard version, given that the tone sounds concurrently with the food stimulus onset in Experiment 2. The original studies employ a staircase procedure that ensures that participants are successful at pressing the button after the tone sounds and before the food image disappears from the screen on only three quarters of all trials. Given the discrepancy in task difficulty, a limitation of the design in Experiment 2 is the possibility that participants do not receive as much internal reinforcement in this easier task compared to the standard design. Future studies should measure the subjective value of being correct in this task to ascertain its role in modulating food value during cue-approach training.

Attention has been shown to significantly modulate value. When participants view items longer they tend to later choose them (Krajchich and Rangel, 2011) and experimentally biasing visual attention influences choice (Shimojo et al., 2003; Armel et al., 2008). However, in the standard cue-approach task, viewing times for the Go and NoGo items did not differ during the training phase (Schonberg et al., 2014a). This suggests that mere exposure did not play a significant role in this task and cannot account for the choice phase findings. Automated attention capture on its own also does not appear to be sufficient to induce a shift in preference since a tone cue that does not require a motor response does not lead to a bias in choice for cued items (Schonberg et al., 2014a). It remains unknown, however, whether requiring a covert task such as counting without an overt motor response would lead to a shift in choice preferences. However, attention clearly plays a significant role in this task. Eliminating the delay between the onset of food stimulus and the auditory cue to press a button during the training phase in Experiment 2 weakened the choice effect at the later probe phase (**Figure 2**, Experiment 2). Choices for Go over NoGo items were not significant, but were only marginally lower than in previous studies. This suggests that sustained attention toward particular

Go items enhances the modulation of preferences during the cue-approach task. After participants learn to anticipate the tone once a Go item appears on the screen in the standard cue-approach design, they focus more intently on that item in anticipation of the cued motor response. However, the tone onset time in the standard version of the task is not perfectly predictable since it sounds at a variable time after the food stimulus onset to ensure 75% Go success. The timing of the cue during the cue-approach task seems to play a more central role than in the attentional boost task, where overlap in time between the to-be-remembered image and the target is crucial, but the timing of the overlap has been shown to matter little (Swallow and Jiang, 2011). Further research is needed to elucidate whether the uncertainty in the timing of the cue is key to the cue-approach choice effect, or if anticipation of the cue, even if onset time is perfectly predictable, is sufficient. By eliminating GSD, we reduced the time during which top-down attention is potentially sustained toward Go items before a behavioral response is executed. Eliminating the need for sustained attention has potentially reduced its modulatory effect on the value of Go items. Not only is a cued motor response apparently necessary for the cue-approach effect, but also the cue must appear some time after the food stimulus onset. The findings from Experiment 1 and 2, however, do not preclude the possibility that lower-level attentional mechanisms rather than higher-level top-down attention is engaged during cue-approach training. This possibility could be resolved by future research examining the explicit awareness of participants for the food-Go contingencies. We have some unpublished data from a recognition memory test that suggests that participants were aware of these contingencies, but better tests of explicit awareness are needed for more conclusive evidence. We suspect that greater awareness of the contingencies will lead to greater shifts in preferences following cue-approach training, analogous to findings by Wessel et al. (2015) that show greater stimulus devaluation following a stop-signal task when the value representation for those stimuli is explicit.

Experiments 1 and 2 yielded expected null results consistent with our main hypothesis, suggesting that approach responses along with an expectancy for the cue may play important roles in modulating value of foods during cue-approach training. However, the nature of the values modulated in this task remained untested. It remained possible that during cue-approach training, value for the action (pressing a button with the index finger) rather than item-specific intrinsic value was being modulated. If action value was being modulated and played a role in the cue-approach effect, we would expect there to be a bias toward choices executed using the index finger (which is the trained effector). However, we found no bias toward choices made with the index finger in our previous studies employing standard cue-approach training (Schonberg et al., 2014a). Furthermore, in Experiment 3 here, participants used a different motor effector (eyes) than the trained motor effector (finger) to make choices. Although non-saccadic decisions remain dependent on the visual network when stimuli are presented visually, the actual motor responses in value-based decisions made with the eyes vs. the hands recruit dissociable

motor networks. Participants in Experiment 3 exhibited a choice bias in favor of Go items previously associated with a cued manual button press during the training phase. These findings suggest that intrinsic item-specific value rather than action value is being modulated during the training phase to lead to a choice preference at the choice phase. Requiring participants to choose between two items that were equated for pre-experimental preferences but differed on Go status using eye movements rather than button presses (i.e., a different motor effector than the trained effector) did not eliminate the Go choice effect. Given these findings, cued button presses seem to focus attention at behaviorally relevant points in time during cue-approach training, which likely modulates intrinsic item value rather than the value assigned to the action of pressing a button with the index finger. However, more research on the nature of values modulated during cue-approach is warranted. Although we did not find an effect on value as measured by a second auction *in lieu* of binary choice following standard cue-approach training in Study 9 in Schonberg et al. (2014a), we were likely underpowered to detect a subtle effect in that study, especially considering that the measurement of willingness-to-pay is susceptible to regression-to-the-mean during the second auction. Future studies that employ a method of measuring item-specific value that does not rely on binary choice or a BDM auction could shed more light on the nature of the values modulated during non-reinforced training in the cue-approach task.

CONCLUSION

Further evidence is consistent with our hypothesis that the cue-approach task works at the level of modulating individual items' intrinsic value by driving attention toward those items at behaviorally relevant points in time. Thus far, we have only shown that the value of initially already high-value stimuli (appetitive snack foods) can be boosted following cue-approach training. For compelling relevance of the cue-approach task for real-world applications, future work should investigate the effectiveness of this training in shifting preferences toward initially lower-valued stimuli such as less palatable but healthier foods, for example. However, this research has already modestly improved our understanding of how value can be modulated and holds great promise in the development of novel real-world behavioral change interventions.

AUTHOR CONTRIBUTIONS

AB, RP, and TS designed the studies. AB, AH, and NG programmed the tasks. CL, AH, and NG collected the data. AB, CL, and TS analyzed the data. AB, RP, and TS wrote the paper.

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Does the Attentional Boost Effect Depend on the Intentionality of Encoding? Investigating the Mechanisms Underlying Memory for Visual Objects Presented at Behaviorally Relevant Moments in Time

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Pictures in a rapid serial visual presentation (RSVP) stream are better remembered when they are simultaneously presented with targets of an unrelated detection task than when they are presented with distractors. However, it is unclear whether this so-called “attentional boost effect” depends on the intentionality of encoding. While there are studies suggesting that the attentional boost effect even occurs when encoding is incidental, there are several methodological issues with these studies, which may have undermined the incidental encoding instructions. The present study ($N = 141$) investigated the role of the intentionality of encoding with an improved experimental design. Specifically, to prevent a spill-over of intentional resources to the pictures in the RSVP stream, the speed of the stream was increased (to four pictures per second) and each picture was presented only once during the course of the experiment. An attentional boost effect was only found when encoding was intentional but not when encoding was incidental. Interestingly, memory performance for incidentally encoded pictures was nevertheless substantially above chance, independently of whether images were presented with search-relevant targets or distractors. These results suggest that the attentional boost effect is a memory advantage that occurs only under intentional encoding conditions, and that perceptual long-term memory representations are formed as a natural product of perception, independently of the presence of behaviorally relevant events.

Keywords: attentional boost effect, visual long-term memory, incidental encoding, intentional encoding, perceptual long-term memory

INTRODUCTION

Based on the observation that only a fraction of our visual field is represented in high resolution, while non-foveated, peripheral information is represented in reduced fidelity (see, e.g., Rosenholtz, 2011; Cohen et al., 2016) as well as based on phenomena such as change blindness (e.g., Rensink et al., 1997) or inattention blindness (e.g., Simons and Chabris, 1999), it has become

a widely accepted idea that most perceptual information is rapidly forgotten or never stored at all (for a critical review of this perspective, see, e.g., Dudai, 1997; Brady et al., 2011; Hutmacher, 2020). However, this assumption has been challenged by various studies published in the last decade, demonstrating that detailed and durable long-term memory representations are formed as a natural product of perception. While most studies have investigated visual long-term memory (Vogt and Magnussen, 2007; Brady et al., 2008; Konkle et al., 2010; Kuhbandner et al., 2017), similar results have been obtained for auditory (Hutmacher and Kuhbandner, 2020) and haptic (Hutmacher and Kuhbandner, 2018) long-term memory (for the reasons behind the dominance of vision in research, see Hutmacher, 2019). In short, performance in these studies indicated that much more of the incoming perceptual information is stored in long-term memory than previously believed. However, the participants' memory was not perfect, that is, the participants did not remember *all* of the presented stimuli. Thus, an interesting question remains: What are the mechanisms that select whether a stimulus is stored in long-term memory?

One possible answer to this question is provided by the idea that the encoding of perceptual information is enhanced at behaviorally relevant moments in time: When something important happens in our environment, it seems adaptive to store not only the stimulus to which we react but also the seemingly unrelated surroundings. The existence of such a selection mechanism is demonstrated by the so-called "attentional boost effect" (for a review, see Swallow and Jiang, 2013). In the typical attentional boost paradigm, participants perform two concurrent but unrelated tasks. One task is to view a series of pictures and to remember them for a later memory test. The other, concurrently executed task is to press a button when a target (e.g., a white square) appears in a series of distractors (e.g., a black square). Typically, the targets and distractors are superimposed on the pictures. Although the two tasks are completely unrelated, memory performance for pictures that are paired with a target in the concurrent task are remembered better in a subsequent memory test than those that are paired with a distractor (see, e.g., Lin et al., 2010; Swallow and Jiang, 2010, 2011, 2012, 2014a; Leclercq and Seitz, 2012a,c; Leclercq et al., 2014b). The attentional boost effect has been replicated under different levels of uncertainty (Leclercq et al., 2014a), using pupillometry (Hoffing and Seitz, 2015) and implicit memory tests (Spataro et al., 2013), as well as for verbal material (Mulligan et al., 2014; Protopapas et al., 2017; but see Walker et al., 2017) and emotional stimuli (Rossi-Arnaud et al., 2018).

As described above, the standard procedure for investigating the attentional boost effect is based on a dual-task paradigm in which both streams of information are relevant for the participants: They are asked to detect target squares *and* to remember the pictures presented in the background for a later memory test. Thus, a crucial question arises: Does the presentation of the target lead to a general enhancement in perceptual processing, as hypothesized by Swallow and Jiang (2013, 2014a), or is this advantage limited to settings in which the visual stimuli in the background are encoded intentionally?

A straightforward way of answering this question is to compare performance when participants are instructed to remember the pictures in the background for a later memory test (*intentional encoding*) with performance when participants are instructed to ignore the pictures in the background, as they are irrelevant to the current task (*incidental encoding*). In fact, the question whether the attentional boost effect can also be found when encoding is incidental has been investigated in several studies, albeit with mixed results. While some studies (Dewald et al., 2011; Swallow and Jiang, 2011; Leclercq and Seitz, 2012b, Experiment 4) found no attentional boost effect when encoding was incidental, other studies did (Dewald et al., 2013; Swallow and Jiang, 2014b; Broitman and Swallow, 2019, Experiments 2 and 3). It has consequently been argued that the attentional boost effect can occur when encoding is incidental, although the magnitude of the effect may be reduced under such conditions (see Swallow and Jiang, 2014b; see Choi et al., 2009 as well as Tsushima et al., 2008, for possible explanations).

Before accepting this conclusion, however, it seems important to take a closer look at the way the intentionality of encoding was manipulated in the studies that found an attentional boost effect under incidental encoding instructions. As described above, participants were instructed to ignore the pictures in the background to ensure that encoding is incidental. Although this is likely to rule out intentional memorization strategies in preparation for a later memory test, the overall effectiveness of such an instruction also depends on the specific characteristics of the task. For instance, when the demands in the detection task are relatively low, the remaining attentional resources may spill over to task-irrelevant items (see, e.g., Lavie, 1995, 2010). In particular, participants may choose to encode the background pictures although they have been deemed irrelevant when performing the detection task is not experienced as challenging enough or when the background pictures attract their attention.

In fact, this may potentially have been the case in the studies that found an attentional boost effect under incidental encoding instructions for several reasons. First, in all of these studies, the same pictures were presented several times, ranging from three (Swallow and Jiang, 2014b) to eight (Broitman and Swallow, 2019) and 120 times (Dewald et al., 2013).¹ Second, the pictures were presented at a rate of one picture every 500 ms (i.e., with an SOA of 500 ms). As it takes no longer than about 150 ms to process even a complex natural image (Thorpe et al., 1996), and as the concurrent detection task requires relatively simple decisions, one could hypothesize that the remaining time and attentional resources were used to encode the pictures. Third, while the pictures in the background were visible for 500 ms, the search target and distractor stimuli were presented for only 100 ms in two of the three aforementioned studies (Swallow and Jiang, 2014b; Broitman and Swallow, 2019). In other words, the supposedly irrelevant pictures were visible

¹Note, that Broitman and Swallow (2019) have demonstrated that the attentional boost effect can occur even when the stimuli are presented only once (Experiments 2A,B). However, this experimental setup was not combined with different encoding instructions (Experiment 1).

on the screen for further 400 ms after the relevant target had already disappeared, leaving ample room for encoding.

In short, while encoding was incidental in these studies in the sense that participants did not know that their memory for the background images would be tested later, encoding may still have been intentional in the sense that participants may have chosen to encode the background stimuli for various reasons, as they had sufficient time and attentional resources for doing so. The present study was set up to account for this possibility, and to provide a clear test for determining whether the attentional boost effect depends on the intentionality of encoding.

Specifically, compared to the previous studies that found an attentional boost effect under incidental encoding instructions, we made three adjustments. First, each picture (the image of an everyday object) was presented only once during the course of the experiment. Second, the presentation speed of the pictures was increased (to four pictures per second, i.e., an SOA of 250 ms). Third, the search target and distractor stimuli (squares) in the foreground were presented for the same amount of time as the pictures. To examine the role of the intentionality of encoding, encoding was incidental for half of the participants and intentional for the other half. If an attentional boost effect occurs in both conditions, the attentional boost effect would stem from a general enhancement in perceptual processing. If no attentional boost effect occurs in the incidental encoding condition, the attentional boost effect should better be viewed as a memory advantage that occurs only when stimuli are encoded intentionally.

MATERIALS AND METHODS

Participants

We decided to collect data from at least 27 participants per group in order to have sufficient power (0.95, $\alpha = 0.05$, two-tailed) to detect medium sized effects in a between-subjects design ($f = 0.25$; G*Power 3.1.9.7, Faul et al., 2007), and to continue data collection until the end of the semester. In total, we recruited 143 undergraduate students. Due to a computer crash, two participants could not finish the experiment. Thus, the data of 141 participants (106 female, 34 male, 1 diverse; age: $M = 20.94$ years, $SD = 1.73$, 18–29 years) were included in the analysis. Half of them ($N = 70$) performed the experiment under incidental encoding instructions, the other half ($N = 71$) under intentional encoding instructions. Participants received five euros and an additional amount of money based on their performance (see below for details). All participants provided written informed consent and reported normal or corrected-to-normal vision. During recruitment, potential participants were asked not to take part in the study when suffering from defective color vision. The study was conducted in accordance with the Helsinki Declaration and the University Research Ethics Standards. In Germany, these types of psychological studies do not require ethical approval of an Ethics Committee.²

²https://www.dfg.de/foerderung/faq/geistes_sozialwissenschaften/

All data exclusions, manipulations, and measures in the experiment are reported. Data can be downloaded at <https://osf.io/6fej2/>.

Apparatus

The stimuli were presented on a 23 inch LG 23ET63V monitor with a resolution of 1,920 by 1,080 pixel and a vertical refresh rate of 60 Hz. Viewing distance was about 50 cm. The experiment was programmed using the E-Prime 2.0 software (Psychology Software Tools, Inc., 2012). Participants sat unconstrained in a normally lit interior room. Room lighting was kept constant by closing the window shutters.

Materials

Prior to the experiment, 840 pictures of everyday objects were randomly chosen from a database containing pictures of 2,400 unique objects (Brady et al., 2008). The same 840 pictures were used for all participants.

A fraction of these pictures was used as *filler objects* to separate trials during the detection task ($n = 240$). The filler objects were the same across participants. As memory for the pictures was tested using a two-alternative-forced-choice recognition test (2AFC; see below), the remaining pictures were divided into two picture sets, which served either as *old objects* (shown in the detection task; $n = 300$) or *new objects* (not shown in the detection task; $n = 300$) in the recognition test. Which of the picture sets served as old and new objects was counterbalanced across participants. During the detection task, two colored squares (pink and green) were used as targets and distractors, respectively. Whether the pink or the green square was the target square was counterbalanced across participants. The colors were chosen so that the squares were clearly distinguishable from the objects presented in the background.

Design and Procedure

Following the typical paradigm of studies on the attentional boost effect (see, e.g., Swallow and Jiang, 2010), the experiment consisted of two parts: a detection task and a recognition test. During the initial detection task, participants viewed a rapid stream of pictures ($8.5^\circ \times 8.5^\circ$) presented at the center of the screen and overlapped by a colored square ($0.9^\circ \times 0.9^\circ$; for an illustration of the trial procedure, see **Figure 1A**). Both the picture and the square were shown for 200 ms, followed by a 50 ms blank interstimulus interval. Participants were asked to press the spacebar as quickly as possible whenever they saw a target square and to make no response whenever the distractor square appeared. As the squares and pictures were visible for 200 ms only, it was difficult for participants to press the spacebar, while the target square was still visible on the screen. Thus, participants were instructed to press the spacebar whenever they had seen a target square, even if it had already been replaced by the next trial. In total, 30 target squares were presented during the detection task.

In order to examine the attentional boost effect, serial positions in the detection task have to be fixed. Thus, trials

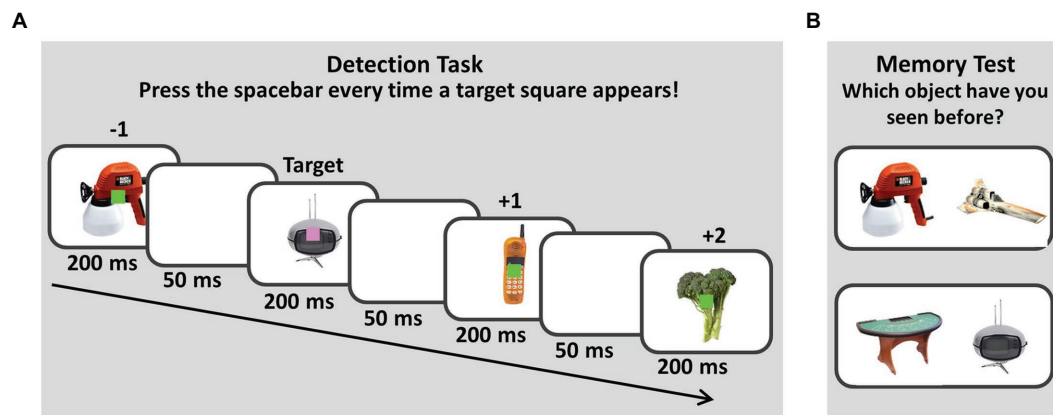


FIGURE 1 | Memory paradigm. The experiment consisted of two phases. In an initial detection task depicted in **(A)** participants viewed a rapid stream of pictures presented at the center of the screen, overlapped by a colored square. Participants were asked to press the spacebar as quickly as possible whenever they saw a target square (here: pink) and to make no response whenever the distractor square appeared (here: green). Half of the participants knew that their memory for the pictures would be tested later (*intentional encoding*), while the other half of the participants was asked to ignore the pictures as good as possible (*incidental encoding*). After completing the detection task, participants performed a two-alternative-forced-choice recognition test, depicted in **(B)**. On each trial, a previously presented picture was paired with a new picture. Participants were asked to indicate which of the two pictures they had seen before by pressing one of two keys.

were grouped into blocks of 10 trials. A block of trials started with the presentation of two pictures paired with a distractor square (serial positions -2 and -1, relative to the target), followed by the presentation of a picture paired with a target square (serial position 0) and the presentation of seven pictures paired with a distractor square (serial positions +1 to +7, relative to the target). Each picture was presented only once in the detection task. In which serial position a picture was presented was counterbalanced across participants. To minimize potential effects of temporal regularity, zero to eight filler pictures (all presented with the distractor square) separated the blocks of 10 trials, following the procedure by Swallow and Jiang (2010). The number of filler pictures (zero to eight) that was presented between two blocks of trials was determined randomly after each block of trials.

The crucial manipulation in the present experiment was the way participants were instructed. In the *incidental encoding condition*, participants were asked to ignore the pictures as good as possible. Participants were told that the pictures are irrelevant to the task and that the experiment was designed to investigate how well humans can ignore irrelevant information while performing another task. No mention was made that memory for any of the pictures would be tested later. In the *intentional encoding condition*, we followed the instructions typically used in studies on the attentional boost effect. That is, participants were instructed to remember the pictures presented during the detection task for a later memory test. The exact nature of the memory test was not explained.

After completing the detection task, participants performed a 2AFC recognition test (for an illustration, see **Figure 1B**). On each trial, an old picture, which had been presented in the detection task was paired with a new picture. Participants were asked to indicate which of the two pictures they had seen before by pressing one of two keys. Participants were

asked to follow their “gut feelings” when not knowing the answer and proceeded at their own pace. Participants received feedback whether their response was correct or incorrect (750 ms). For each correct answer, participants received 5 cents. For each wrong answer, 5 cents were subtracted. The total amount of money participants received in addition to the fixed amount of 5 euros was shown on the screen after completing the experiment. Except from the filler pictures, all pictures from the detection task were tested in the 2AFC recognition test (300 memory test trials). Whether the novel picture or the previously presented old picture was shown on the left or on the right was counterbalanced within participants. The order of testing was random.

RESULTS

Detection Task

The first key press after the presentation of a target was counted as a correct response as long as it was made during the same block of trials. Participants reliably detected the target square, both when encoding was incidental ($M_{\text{Accuracy}} = 89.48\%$, $SD = 10.27$) and when encoding was intentional ($M_{\text{Accuracy}} = 83.43\%$, $SD = 10.88$). Target detection performance was significantly better under incidental encoding instructions, $t(139) = 3.39$, $p = 0.001$, $d = 0.57$. In addition, reaction times were lower under incidental encoding instructions ($M_{\text{incidental}} = 384$ ms, $SD = 63$; $M_{\text{intentional}} = 412$ ms, $SD = 70$), $t(139) = 2.52$, $p = 0.013$, $d = 0.42$. The distribution of the key presses across the serial positions in response to the target was highly similar across the two conditions. Most responses were either given while the target was still present (i.e., at serial position 0; incidental: 10.43%, intentional: 8.16%) or one trial after the target had disappeared (i.e., serial position 1;

incidental: 83.08%, intentional: 82.22%). Some responses were also given two trials after the target had disappeared (i.e., serial position 2; incidental: 3.99%, intentional: 5.40%), while later responses (i.e., serial positions 3–7) were extremely rare (incidental: 2.50%, intentional: 4.22%).

Memory Performance

A detailed depiction of the memory performance for the pictures presented at the different serial positions can be found in **Figure 2**. For the statistical analysis, the nine non-target positions (-2 and -1 as well as +1 to +7) were integrated into one estimate (see e.g., Swallow and Jiang, 2010). Next, we ran a 2×2 ANOVA with the between-subjects factor instruction (*incidental* vs. *intentional encoding*) and the within-subjects factor position (*target* vs. *non-target*). The main effect for instruction was significant, $F(1,139) = 12.24$, $p = 0.001$, $\eta^2 = 0.08$, indicating that overall memory performance was better when the pictures were encoded intentionally ($M = 63.81\%$, $SD = 6.58$) than when they were encoded incidentally ($M = 60.47\%$, $SD = 6.97$). The main effect for position was not significant, $F(1,139) = 0.22$, $p = 0.642$, $\eta^2 = 0.002$. However, there was a significant instruction by position interaction, $F(1,139) = 5.16$, $p = 0.025$, $\eta^2 = 0.04$.

In order to better understand the significant interaction, we took a closer look at performance in the different conditions (see **Table 1**). When encoding was intentional, performance

for the target position was better than performance for the non-target positions, that is, there was an attentional boost effect [$M_{\text{Difference}} = 2.24\%$, $SD = 9.34$, 95% CI (0.03; 4.45)]. However, when encoding was incidental, performance was numerically worse for the target position than for the non-target positions, that is, there was no attentional boost effect [$M_{\text{Difference}} = -1.48\%$, $SD = 10.08$, 95% CI (-3.88; 0.93)]. In addition, participants performed better when encoding was intentional than when encoding was incidental, both for the target position [$M_{\text{Difference}} = 6.68\%$, $SD = 11.65$, 95% CI (2.80; 10.56)], and the non-target positions [$M_{\text{Difference}} = 2.97\%$, $SD = 6.74$, 95% CI (0.72; 5.21)].

DISCUSSION

The present study was designed to answer the question whether the attentional boost effect depends on the intentionality of encoding. Previous research has reported mixed results (Dewald et al., 2011, 2013; Swallow and Jiang, 2011, 2014b; Leclercq and Seitz, 2012b; Broitman and Swallow, 2019). However, a closer look at the studies that found an attentional boost effect under incidental encoding instructions indicates that encoding may not have been completely incidental as the to-be-ignored pictures were presented several times with a relatively long presentation duration. In the present study, to ensure that encoding was truly incidental, presentation speed was increased to four pictures per second and each picture was presented only once during the course of the detection task. Under such conditions, an attentional boost effect was only found when encoding was intentional but not when encoding was incidental.

Performance in the target detection task indicated that the intentionality of encoding was manipulated successfully. Participants' target detection performance was lower and their reaction time was longer when they were instructed to remember the pictures in the background in addition to searching for presented targets, compared to when they were instructed to ignore the background pictures. That is, participants followed the instructions and paid more attention to the target detection task in the incidental encoding condition compared to the intentional encoding condition. This was also supported by the finding that overall memory performance for the pictures was worse in the incidental encoding condition compared to the intentional encoding condition, replicating the finding that the intention to memorize new information enhances recognition memory (e.g., Neill et al., 1990). In sum, these findings suggest that the methodological adjustments made in the present study have helped to ensure that performance in the incidental encoding condition was not driven by uncontrolled encoding strategies.

In three previous studies, an attentional boost effect was reported even when participants were instructed to focus on the target detection task and to ignore the pictures presented in the background (Dewald et al., 2013; Swallow and Jiang, 2014b; Broitman and Swallow, 2019). However, in these studies, the to-be-ignored pictures were presented several times and

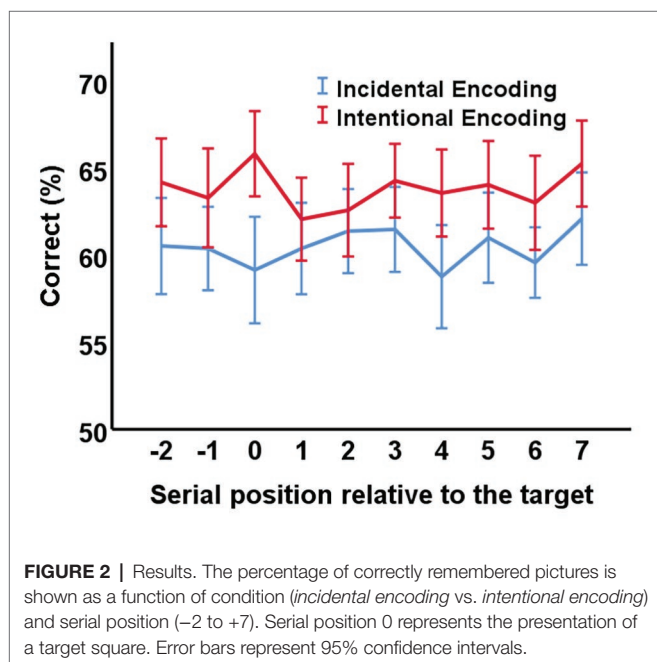


FIGURE 2 | Results. The percentage of correctly remembered pictures is shown as a function of condition (*incidental encoding* vs. *intentional encoding*) and serial position (-2 to +7). Serial position 0 represents the presentation of a target square. Error bars represent 95% confidence intervals.

TABLE 1 | Performance in the different conditions.

	Target		Non-target	
	<i>M</i> (%)	<i>SD</i>	<i>M</i> (%)	<i>SD</i>
Intentional encoding	65.82	10.34	63.58	6.71
Incidental encoding	59.14	12.84	60.62	6.77

for a substantially longer amount of time than necessary to detect the target. Under these conditions, attentional resources may have spilled over to the to-be-ignored pictures (e.g., Lavie, 1995, 2010), which may have undermined the incidental encoding instructions. The fact that no attentional boost effect occurs under incidental encoding instructions when encoding is completely incidental, challenges the assumption that the attentional boost effect mirrors a general enhancement in perceptual processing (see Swallow and Jiang, 2013, 2014a). Rather, it seems that the attentional boost effect is a processing advantage that occurs only when participants try to memorize the background pictures intentionally. In fact, such a finding corroborates the results from other studies that have found no attentional boost effect under incidental encoding instructions (Dewald et al., 2011; Swallow and Jiang, 2011; Leclercq and Seitz, 2012b). Nevertheless, an independent replication of the present findings by other research groups seems desirable.

The present study revealed another intriguing finding: Despite the fact that the pictures were presented very rapidly (four pictures per second) and each of the pictures was presented only once during the course of the detection task, performance was far above chance, even when participants were instructed to ignore the pictures as good as possible. This fits well with several recent studies demonstrating that perceptual long-term memory representations are formed as a natural product of perception, independently of the focus of attention and intention of memorization (e.g., Kuhbandner et al., 2017; Hutmacher and Kuhbandner, 2018, 2020). How astounding this ability actually is, can be illustrated by taking a closer look at the data of the present experiment. In the incidental encoding condition, the observed percentage of correct memory responses was 60.47%. To determine the true percentage of pictures stored in memory (PR_{True}), the observed percentage correct (PC_{Observed}) has to be corrected for fortunate guesses in a 2AFC (formula: $PR_{\text{True}} = 2 * PC_{\text{Observed}} - 100$; see, e.g., Brady et al., 2013), revealing that 20.94% of the pictures were stored in memory in the incidental encoding condition. In effect, this means that about one picture per second was successfully stored in long-term memory – despite the fact that each picture was shown only once for a quarter of a second, and that participants completely focused on the detection task while trying to ignore the pictures as good as possible.

How can this finding be explained? As the present study was not meant to answer this question, future research is needed to unravel the mechanisms underlying performance in the incidental encoding condition. However, one may speculate that a significant fraction of the irrelevant and ignored information is stored simply because it fits with the operating characteristics of human perception and memory. For instance, proponents of predictive coding accounts argue that our current model of the world is constantly refined based on the interplay of sensory inputs and top-down expectations (see, e.g., Friston, 2010; Clark, 2013; Hohwy, 2013). Importantly, this interplay takes place on different hierarchical levels from low-level perception to higher-order cognition. Hence, one could hypothesize that the instruction to focus on the detection task

and to ignore the pictures as good as possible changed higher-order cognitive processes such as the intention to allocate the attention on the detection task, but left low-level processes comparably unchanged, enabling the participants to store a certain amount of information and to retrieve it at the later memory test. Such a perspective fits well with models of long-term memory claiming that incoming information can be processed in multiple independently operating, but also interacting subsystems and that even information we are completely unaware of can be stored in memory and influence our behavior (Johnson, 1983, 2007; Johnson and Hirst, 1993). In fact, recent studies have shown that high-fidelity long-term memory representations are even formed for unattended, irrelevant, and incidentally encoded information (Kuhbandner et al., 2017; Hutmacher and Kuhbandner, 2020).

The methodological adjustments that were made in the present study compared to the previous studies that had found an attentional boost effect under incidental encoding instructions (i.e., presenting each picture only once during the detection task, increasing the presentation speed to four pictures per second, and presenting the search target and distractor stimuli in the foreground for the same amount of time as the pictures in the background) served a common goal: ensuring that encoding was truly incidental under incidental encoding instructions. In other words, the *combination* of these methodological adjustments was a necessary precondition for being able to differentiate between intentional and incidental encoding. Thus, investigating the impact of each adjustment (or a certain combination of adjustments) on the size of the attentional boost effect did not fall into the scope of the present study. Nevertheless, setting up experiments that systematically investigate the impact of various factors (such as the presentation duration or the number of times a certain picture is shown during the detection task) on the size of the attentional boost effect could be a promising avenue for future research. For instance, it has been speculated that the quantity of irrelevant items modulates whether an attentional boost effect is observed under incidental encoding instructions (see Dewald et al., 2013 for an extended discussion). In particular, the authors suggest that one may be more likely to observe an attentional boost effect under incidental encoding instructions when the number of irrelevant items is low and these items are repeated during the initial detection task. Following this line of reasoning, it is no surprise that there was no attentional boost effect under incidental encoding instructions in the present study, in which each picture was presented only once and the number of pictures was relatively large. However, as already mentioned in the introduction, participants may very well notice when a limited number of items is repeated several times during the detection task, which would undermine the incidental encoding instructions. Differently put, it is important to keep in mind that changing a methodological detail can have consequences reaching beyond the manipulation of this very detail.

In conclusion, the present study reveals two interesting findings. First, the encoding of perceptual information is

enhanced at behaviorally relevant moments in time when encoding is intentional but not when encoding is incidental. Second, under incidental encoding conditions, still a relatively large amount of incoming information is stored in memory, independently of behavioral relevance and intention of memorization, indicating that perceptual long-term memory representations are formed as a natural product of perception.

DATA AVAILABILITY STATEMENT

The dataset presented in this study can be found in an online repository. A link can be found in the article.

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ETHICS STATEMENT

Ethical review and approval was not required for the study on human participants in accordance with the local participants and institutional requirements. The participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

FH and CK developed the research idea, analyzed the data, and drafted the manuscript. FH designed the experiment. Both the authors contributed to the article and approved the submitted version.

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Auditory Target Detection Enhances Visual Processing and Hippocampal Functional Connectivity

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Though dividing one's attention between two input streams typically impairs performance, detecting a behaviorally relevant stimulus can sometimes enhance the encoding of unrelated information presented at the same time. Previous research has shown that selection of this kind boosts visual cortical activity and memory for concurrent items. An important unanswered question is whether such effects are reflected in processing quality and functional connectivity in visual regions and in the hippocampus. In this fMRI study, participants were asked to memorize a stream of naturalistic images and press a button only when they heard a predefined target tone (400 or 1,200 Hz, counterbalanced). Images could be presented with a target tone, with a distractor tone, or without a tone. Auditory target detection increased activity throughout the ventral visual cortex but lowered it in the hippocampus. Enhancements in functional connectivity between the ventral visual cortex and the hippocampus were also observed following auditory targets. Multi-voxel pattern classification of image category was more accurate on target tone trials than on distractor and no tone trials in the fusiform gyrus and parahippocampal gyrus. This effect was stronger in visual cortical clusters whose activity was more correlated with the hippocampus on target tone than on distractor tone trials. In agreement with accounts suggesting that subcortical noradrenergic influences play a role in the attentional boost effect, auditory target detection also caused an increase in locus coeruleus activity and phasic pupil responses. These findings outline a network of cortical and subcortical regions that are involved in the selection and processing of information presented at behaviorally relevant moments.

Keywords: attentional boost effect, visual processing, encoding, hippocampus, locus coeruleus, temporal selection

Abbreviations: AC, auditory cortex; ACC, anterior cingulate cortex; AUC, area under the curve; FG, fusiform gyrus; aHPC, anterior hippocampus; pHPC, posterior hippocampus; iFC, intrinsic functional connectivity; IRE, impulse response function; LC, locus coeruleus; MC, motor cortex; ME, multi-echo; ME-ICA, multi-echo independent component analysis; NE, norepinephrine; nmT1, neuromelanin-weighted T1; PG, parahippocampal gyrus; SVM, support vector machine; V1, primary visual cortex; V2, secondary visual cortex.

INTRODUCTION

Attention can be allocated not only to spatial locations or stimulus features (Carrasco, 2011), but also to information presented at particular points in time (Rohenkohl et al., 2011; Nobre and van Ede, 2018). A growing literature shows that perceptual processing is enhanced when events change in meaningful ways (e.g., Jefferies and Di Lollo, 2019) and when they require a response (Swallow and Jiang, 2010; Makovski et al., 2013; Yebra et al., 2019; Clewett et al., 2020). Detecting a behaviorally relevant item, for instance, can improve memory for concurrently presented but otherwise unrelated information (the attentional boost effect, or ABE; Swallow and Jiang, 2010), even when it is task-irrelevant (Swallow and Jiang, 2014; Turker and Swallow, 2019; Broitman and Swallow, 2020). Target detection can also increase visual adaptation, lexical priming, and affective evaluation of concurrently presented items (Pascucci and Turatto, 2013; Spataro et al., 2013; Schonberg et al., 2014; Swallow and Atir, 2019). The beneficial effects of presenting information at the same time as a target can be contrasted with those commonly observed in attention tasks that require participants to select among different sources of information. Under these conditions, competitive interactions within and between regions are associated with reduced processing of unselected information (e.g., in visual cortex when monitoring auditory rather than visual stimuli, Johnson and Zatorre, 2005; of multi-voxel patterns associated with task irrelevant categories when searching for a pre-specified category of objects in natural images, Seidl et al., 2012; in parts of topographically organized visual cortex in uncued regions of a visual display during a search task, Silver et al., 2007). However, despite the extensive evidence that the selection of one item (such as an auditory tone) reliably boosts behavioral indices of background item (such as a visual scene) processing, little is known about its neural basis. Guided by previous empirical work, this project used fMRI to study the neurophysiological basis of the effects of target detection on visual processing and memory in the ABE paradigm. Specifically, we examined whether it enhances the quality of representations in—and communication between—regions involved in episodic encoding.

Consistent with prior work demonstrating that norepinephrine (NE) increases neural gain in response to behaviorally relevant events or task boundaries (Aston-Jones and Cohen, 2005; Bouret and Sara, 2005; Lee et al., 2018), the ABE could reflect the phasic firing of the locus coeruleus (LC) in response to behaviorally relevant events (Swallow and Jiang, 2013). The LC, a brainstem structure whose activity briefly increases in response to changes in a task or in the environment (Sara, 2009; Clewett et al., 2020) and facilitates episodic encoding (Takeuchi et al., 2016), is the main source of NE in the brain. Phasic LC responses correlate with pupil diameter (Murphy et al., 2014; Joshi et al., 2016) and are associated with target detection and orienting (Aston-Jones et al., 1994; Breton-Provencher and Sur, 2019). Though previous studies suggest a relationship between LC activity and the ABE (Swallow et al., 2019; Yebra et al., 2019), they utilized indirect measures (pupil size) or a probabilistic atlas to identify the LC in participants, making it

difficult to pinpoint the source of the modulatory signals (cf. Wang and Munoz, 2015). This is of particular concern because the small size of the LC and its location near the fourth ventricle, a source of physiological noise in fMRI, increase the potential for mislocalization and for the inclusion of spurious signals in estimates of LC activity (Turker et al., 2021). We therefore utilized structural MRI T1 sequences that increase contrast for the high concentrations of neuromelanin in the LC (Keren et al., 2009) to improve our ability to localize the LC in individual participants relative to a probabilistic atlas (Turker et al., 2021). We also employed multi-echo EPI with multi-echo independent components analysis (ME-ICA) and TE-dependent BOLD signal classification (Kundu et al., 2013) to reduce the contributions of noise sources to our data.

The effects of target detection on episodic encoding, visual adaptation, and lexical priming (e.g., Pascucci and Turatto, 2013; Spataro et al., 2013; Turker and Swallow, 2019; Broitman and Swallow, 2020) suggest that it should improve the quality of representations in perceptual and episodic encoding regions. Such effects would also be expected if target detection increases neural gain, enhancing the signal to noise ratio of activity in impacted regions (e.g., Aston-Jones and Cohen, 2005). However, fMRI investigations of the ABE have provided little insight into the mechanisms by which it modulates neural processing. Prior work has shown that target detection broadly increases the BOLD signal in regions not directly involved in processing the target stimulus (e.g., auditory target detection boosts activity in V1; Jack et al., 2006; Swallow et al., 2012). These studies did not include baseline trials, however, making it unclear whether the reported effects reflect target-related facilitation or distractor-related inhibition. Moreover, differences in the magnitude of the hemodynamic response do not, on their own, reflect differences in processing quality (cf. Albers et al., 2018). This study therefore incorporated baseline trials and used multivoxel pattern analysis to test whether target detection enhances the quality of processing (Mahmoudi et al., 2012). Attention-related enhancements in processing quality often coincide with changes in the amount or spread of decodable representational information in perceptual regions (e.g., Zhang et al., 2011); in the medial temporal lobe, increases in BOLD magnitude and decoding accuracy (e.g., Chadwick et al., 2010, 2011) have been linked to episodic encoding and recall. Nonetheless, the relationship between auditory target detection and the quality of visual processing and encoding remains underexplored.

Prior research also leaves the possibility that target detection in the ABE paradigm affects coordination among different brain regions unexplored. Better working memory (Gazzaley et al., 2004) and episodic encoding (Ranganath et al., 2005) are associated with enhanced functional connectivity (Friston, 2011) between the hippocampus (HPC) and visual areas. Findings of enhanced short-term memory (Makovski et al., 2011; Li et al., 2018) and episodic encoding (Leclercq et al., 2014; Turker and Swallow, 2019; Broitman and Swallow, 2020; Mulligan et al., 2021) with the ABE thus suggest that it should increase functional connectivity between these regions. Phasic LC activation also is temporally coordinated with the HPC, anterior cingulate cortex (ACC), and other prefrontal regions (cf. Sara, 2015) and

may lead to the dynamic reconfiguration of cortical functional networks (Bouret and Sara, 2005; Shine et al., 2018; Li et al., 2019). Disruptions to existing population firing patterns created by phasic LC activation could also facilitate the formation of patterns that represent behaviorally relevant information (Moyal and Edelman, 2019). While these findings suggest that auditory target detection should trigger an increase in visuo-hippocampal connectivity, this possibility has yet to be examined directly. It may also be possible that the anterior and posterior hippocampus (aHPC and pHPC, respectively) are differently impacted by target detection. Relative to pHPC, aHPC is more strongly associated with episodic memory encoding (relative to spatial memory encoding), is associated with more generalized (less detailed) representations of events, shows stronger functional connectivity with fusiform gyrus (FG) and medial versus lateral aspects of entorhinal cortex, and may have greater concentrations of NE receptors (Gage and Thompson, 1980; Poppenk et al., 2013; Persson et al., 2018; Frank et al., 2019). However, non-human animal research also suggests that the LC may play a role in modulating episodic memory formation in pHPC (Kempadoo et al., 2016; Wagatsuma et al., 2018). We therefore investigated the effects of auditory target detection in the ABE paradigm on the functional connectivity of aHPC and pHPC to visual areas.

To summarize, we used multi-echo fMRI to characterize the neural correlates of target detection in the ABE, specifically examining responses of the visual cortex, HPC, and LC to images presented on their own or with auditory target or distractor tones (Swallow and Jiang, 2010; Swallow et al., 2012). We expected target detection to increase (1) phasic pupil responses and activity in individually defined LC; (2) the ability to classify patterns of BOLD activity associated with different categories of images; and (3) functional connectivity between visual regions and HPC. We found evidence supporting each of these hypotheses.

MATERIALS AND METHODS

Participants

Twenty-one right-handed individuals (15 female, 6 male, 19–40 years old, $M = 21.48$, $SD = 4.86$) participated in the study. They were screened for non-MRI compatible medical devices or body modifications, claustrophobia, movement disorders, pregnancy, mental illness, use of medication affecting cognition, and color blindness. Consent was obtained at the beginning of the session and participants were debriefed at the end. All procedures were approved by the Cornell University review board. Sample size was based on a previous study examining the effect of auditory target detection on visual cortical activity (Swallow et al., 2012), which reported effect sizes for a peak signal difference following target and distractor auditory tones of $Cohen's f > 1.037$. A sample size of 20 was selected to ensure that smaller effects between conditions and in other measures of connectivity and classification could be detected. With a sample of 20 and false positive rate of 0.05, a traditional one-way (three levels) repeated measures analysis of variance has a power of 0.95 to detect an effect of $Cohen's f > 0.378$ (calculated using G*Power; Faul et al., 2007).

Two participants responded to the wrong tones on some scans so that some images were paired with both target and distractor tones (one of these participants also did not complete the memory test). Because these participants were performing the target detection task (but with the wrong tone) their data for these scans were recoded and included in analyses of detection task performance and in the univariate analyses (which had an N of 21). However, these two participants were excluded from analyses that depended on balancing the number of trials across conditions (image classification and functional connectivity, which fed into an image classification analysis), resulting in an N of 19 for these analyses. They were also excluded from analyses involving the memory test. One additional participant did not complete the memory test due to a fire alarm, leaving 18 participants for all analyses involving memory data.

MRI and Pupillometry Data Acquisition

Magnetic resonance imaging was performed with a 3T GE Discovery MR750 MRI scanner (GE Healthcare, Milwaukee, WI, United States) and a 32-channel head coil at the Cornell Magnetic Resonance Imaging Facility in Ithaca, NY, United States. Participants laid supine on the scanner bed with their head supported and immobilized. Ear plugs and headphones (MR confon GmbH, Germany) were used to reduce scanner noise, allow the participant to communicate with the experimenters, and present auditory stimuli during the tasks. Visual stimuli were presented with a 32" Nordic Neuro Lab liquid crystal display (1,920 pixels \times 1,080 pixels, 60 Hz, 6.5 ms g to g) located at the head of the scanner bore and viewed through a mirror attached to the head coil.

Anatomical data were acquired with a T1-weighted MPRAGE sequence (TR = 7.7 ms; TE = 3.42 ms; 7° flip angle; 1.0 mm isotropic voxels, 176 slices). A second anatomical scan utilized a neuromelanin sensitive T1-weighted partial volume turbo spin echo (TSE) sequence (TR = 700 ms; TE = 13 ms; 120° flip angle; 0.430 mm \times 0.430 mm in-plane voxels, 10 interleaved 3.0 mm thick axial slices; adapted from Keren et al., 2009). Slices for the TSE volume were oriented perpendicular to the long axis of the brain stem to provide high resolution data in the axial plane, where dimensions of the LC are smallest, and positioned to cover the most anterior portion of the pons. Multi-echo echo planar imaging (EPI) sequences were used to acquire functional data during the four task runs (TR = 2,500 ms; TEs = 12.3, 26.0, and 40.0 ms; 80° flip angle; 3.0 mm isotropic voxels; 44 slices). In addition to the task runs, all participants also completed a single resting state scan with their eyes open and the lights on (612 s; TR = 3.0 s; TEs = 13, 30, and 47 ms; 83° flip angle; 3.0 mm isotropic voxels; 46 slices). Resting state data are reported elsewhere (Turker et al., 2021) but were used for this study (see Section "Locus Coeruleus Functional Connectivity").

During the scans, pupil size and gaze location were acquired using an EyeLink 1000 Plus MRI Compatible eye tracker (SR-Research, Canada) for all but two participants (1,000 Hz, right eye). After the participant was positioned in the scanner, mirrors were adjusted to bring the eye into view of the camera. Immediately prior to the resting state scan, thresholds defining pupil and corneal reflectance were automatically adjusted and

a nine-point calibration routine was performed to determine the parameters needed to estimate gaze position. Calibration was validated and adjusted as necessary prior to each scan that included eye data measurement. On task runs, participants were instructed to fixate the central dot and minimize blinking.

MRI Data Preprocessing

All EPI data were denoised and processed using the standard ME-ICA pipeline, except as indicated (meica.py, Version 3.2, beta 1; Kundu et al., 2012, 2013). First, the MPAGE volume was skull stripped using FSL v5.0 BET ($b = 0.25$). After matching the obliquity of the anatomical volume and EPI time series, motion was estimated from the first echo time series using 3dvolreg and the third volume as the target. Third, all EPI data were despiked and slice time acquisition differences were corrected using 3dTshift. Fourth, for each echo time series, the first two volumes were dropped and the remaining EPI data were registered to the third volume. Baseline intensity volume (s_0), the t_2^* map volume (t_2^*), and the optimal combination volume time series were then calculated. Fifth, registration and alignment transforms were applied to the EPI data and the pre-equilibrium volumes dropped in one step to align the data with the individual anatomical volume in its original acquisition space. Sixth, EPI data were denoised to identify and separate BOLD components from non-BOLD components (Kundu et al., 2013). BOLD components were recombined to create the denoised data sets that were used in subsequent analyses. Finally, denoised EPI data were spatially aligned to the MNI N27 atlas for volume-wise group level analyses.

Region of Interest Identification

Individual MPAGE scans were submitted to FreeSurfer's segmentation and surface-based reconstruction software (recon-all v5.3¹; Dale et al., 1999; Fischl et al., 1999) to label voxels according to each individual's anatomy. Labels for the fourth ventricle (4V), hippocampus (HPC), motor cortex (MC), planum temporale for auditory cortex (AC), primary visual cortex (V1), secondary visual cortex (V2), fusiform gyrus (FG), and parahippocampal gyrus (PG) were extracted and converted to volumetric ROIs using FreeSurfer and AFNI tools (Cox, 1996; Cox and Hyde, 1997; Gold et al., 1998). Separate ROIs were created for the left and right hemispheres. In addition, the HPC ROIs were divided into anterior and posterior portions at the anterior-posterior coordinate of their center of mass (aHPC and pHPC), to account for possible differences in their connectivity patterns and function (Fanselow and Dong, 2010; Poppenk et al., 2013). Detailed methods for identifying the LC are described in Turker et al. (2021). Briefly, individual MPAGE scans (including skull) were aligned to the individual normalized T1-weighted neuromelanin scan. After extracting the brainstem from the nmT1, correcting image intensity, and setting the false color palette to the predefined range, candidate LC voxels could be visually distinguished from nearby regions (**Figure 3A** and **Supplementary Figure 3**). Bilateral LC ROIs were then hand-drawn by two tracers (voxel size: $0.43 \text{ mm} \times 0.43 \text{ mm} \times 3.0 \text{ mm}$).

¹surfer.nmr.mgh.harvard.edu

Voxels included as LC by both raters were kept, resampled to 3 mm isotropic voxels, and spatially aligned to the individual EPI and MPAGE. This procedure resulted in an average of 4.5 voxels per participant ($SD = 1.9$). Finally, we also created an ROI for the ACC, based on its connections with the LC (e.g., Ennis et al., 1998). The association test map for the ACC was downloaded from Neurosynth² and thresholded ($z = 6$) to retain an ROI covering only putative ACC.

Experimental Design and Statistical Analysis

Stimuli

Two hundred eighty-eight full color images of faces (48 female and 48 male), objects (48 cars and 48 chairs), and outdoor scenes (48 beaches and 48 forests) were acquired from personal collections and publicly available online databases³ (Huang et al., 2007; Huang and Learned-Miller, 2014; Xiang et al., 2014). 24 images from each subcategory were used in the encoding task (eight in each tone type condition), each presented once per run (four repetitions in total). The rest of the images were used as foils in the recognition test. Scrambled images were generated from these photographs by dividing them into 32×32 tiles and shuffling their locations. The mean and variance of pixel intensity (luminance) was matched across images using the SHINE toolbox (Willenbockel et al., 2010). The presentation of simple auditory stimuli with complex naturalistic images is standard for this paradigm (e.g., Swallow and Jiang, 2010, 2012; Swallow et al., 2012, 2019) and allows for the separation of the effects of selection on processing the target and distractor tones from the impact of auditory target detection on visual stimuli processing.

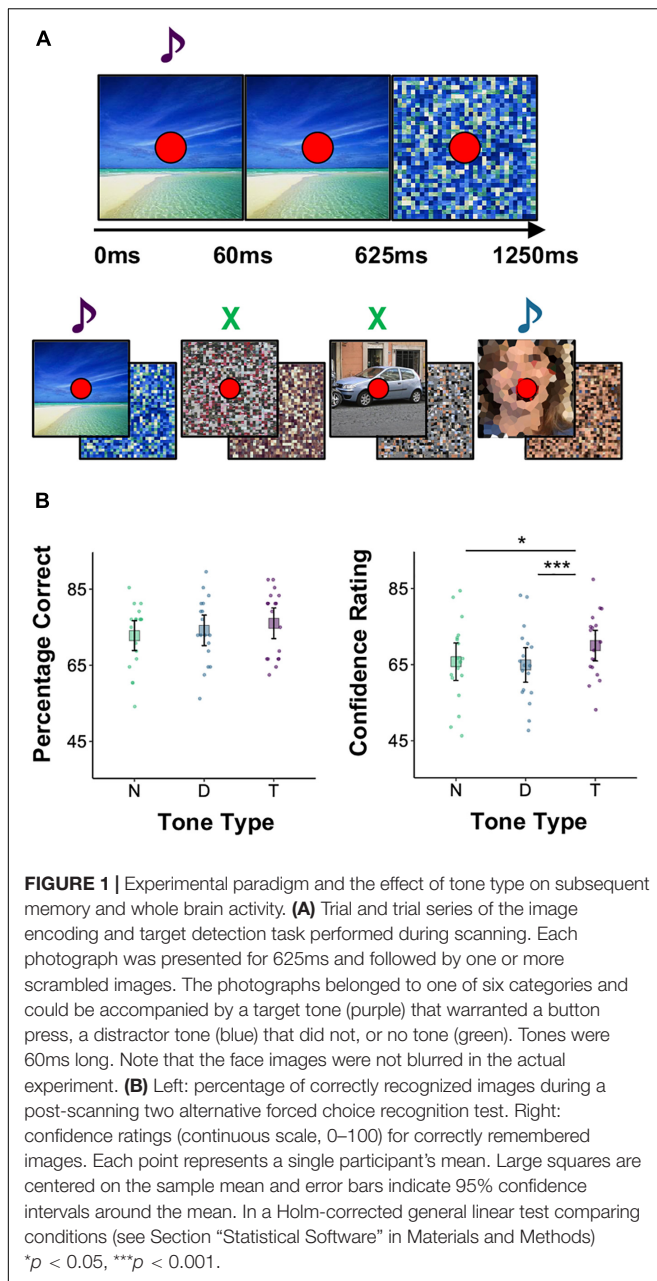
Design and Procedure

In the four functional runs (407.5 s each) participants continuously performed simultaneous image encoding and target detection tasks. On each 1.25 s long trial, one image (7×7 visual degrees; $256 \text{ pixels} \times 256 \text{ pixels}$) was presented for 625 ms and immediately followed by another image for another 625 ms. On most trials, both images were scrambled (no-task trials, 164/run). On task trials (144/run), the first image was a photograph and the second was a scrambled version of that photograph. Participants attempted to memorize the photograph for a later memory test. The inter-trial interval was 0 ms, ensuring that there was an image on the screen throughout the task and that it changed every 625 ms (**Figure 1A**). A red fixation dot (0.25 visual degree diameter) appeared at the center of the screen throughout the task, including 7.5 s of pre-task fixation and 15 s of post-task fixation at the beginning and end of each run, respectively. Scrambled images (alternating every 625 ms) were presented during the pre- and post-task fixation periods as well to avoid large visual transients at the onset and offset of the task.

On some task trials a high (1,200 Hz) or low (400 Hz) pitched auditory tone (60 ms duration) was played over the headphones at the same time an image was presented (0 ms stimulus onset asynchrony). If the tone was the pre-specified target pitch

²neurosynth.org

³vision.stanford.edu/projects/sceneclassification/resources.html



participants pressed a button with their right thumb. Participants made no overt response if the tone was not the pre-specified target pitch (distractor) or if no tone was presented on that trial. The tone assigned to the target condition was counterbalanced within participants by switching it halfway through the encoding task (e.g., high, high, low, and low). Participants were told which tone was the target tone at the beginning of each run. The starting target tone was counterbalanced across participants: Half started with the high tone as the target and half started with the low tone as the target. Tone condition (target, distractor, and no tone) was held constant for each image. Thus, if a high tone was assigned to a given image on the first two runs, it was switched to a low tone on the latter two runs. An equal number of task trials was assigned to each tone type (target, distractor, and no

tone), ensuring that results cannot be attributed to the salience or relative frequency of target occurrences. Tones were never presented on no-task trials. Sound levels were adjusted during the MPRAGE scan to ensure participants could hear both tones during scanning. Participants practiced the task with a different set of images before entering the scanner.

After scanning, participants completed a two alternative forced choice recognition test on the images. On each trial, two images were presented on the screen, one on the left side and one on the right. One of the images was presented during the encoding and detection task and the other was a new image (the location of the old image was pseudo-random and counterbalanced). Participants selected the 'old' photograph by pressing one of two keys (Z or X) on the keyboard. Participants were then prompted to report their confidence by clicking on a line that appeared below the images. Participants were told to click on the far-left side of the line if they were guessing, the far-right side of the line if they were absolutely confident that they were correct, and at points in between to reflect degrees of intermediate levels of confidence. These were coded on a scale from 0 (lowest rating) to 100 (highest rating). A green + or a red – appeared next to indicate their accuracy.

This procedure resulted in a 6×3 design, with *image type* (female face, male face, beach, forest, car, and chair) and *tone type* (no tone, distractor tone, and target tone) as within-participants factors. There were 32 trials per image type-by-tone condition for a total of 576 task trials over four runs. Trial order and spacing were optimized using the AFNI function `make_random_timing` to produce four sequences that minimized the amount of unexplained variance in a simulated task. Task trials were separated by 0–12 non-task trials.

Behavioral Data Analysis

To examine the effect of tone type on memory we fit a binomial generalized linear mixed effects model (Bates et al., 2015) to the recognition accuracy data with tone type as a fixed effect and with random intercepts for participant, old image, and new image [$\text{Accuracy} \sim \text{Tone} + (1|\text{Participant}) + (1|\text{Old}) + (1|\text{New})$]. A linear mixed effects model was fit to participants' recognition confidence ratings for correctly remembered images, with the same variables and random intercepts [$\text{Confidence} \sim \text{Tone} + (1|\text{Participant}) + (1|\text{Old}) + (1|\text{New})$].

Tonic and Phasic Pupil Size Estimation and Analysis

Before estimating tonic and phasic pupil dilation on a trial-by-trial basis, pupil data for each participant and task run were preprocessed using the EyeLink DataViewer application (SR-Research, Canada), the FIRDeconvolution toolbox (Knäpen et al., 2016), and custom routines. In brief, following the procedure outlined in Knäpen et al. (2016), linear interpolation was used to estimate pupil size during blinks flagged by the EyeLink software and extended to include 100 ms margins before and after the blink. High-pass (0.1 Hz) and low-pass (10 Hz) Butterworth filters were applied, after which the data were down-sampled from 1,000 to 100 Hz. Noise associated with the end of blinks and saccades was then removed as follows. For each participant, mean pupil diameter was calculated for every sample during the

6 s time windows following a blink and following a saccade (pupil response). A double gamma impulse response function (IRF) was then fit to the pupil response following a blink. A single gamma IRF was fit to the pupil response following a saccade. The blink and saccade IRFs were convolved with blink and saccade ends to create individually tailored nuisance regressors, and a cleaned data set was then acquired by using the residuals from a linear model describing measured pupil responses as a function of these nuisance regressors. Finally, the previously filtered out slow drift was added back into the data, as this is a meaningful characteristic of pupil size over time.

Tonic pupil size and phasic pupil response were then estimated for each participant and trial of the encoding and detection task. For every trial, tonic pupil size was defined as the mean pupil size in the 500 ms window preceding the trial. In addition, phasic pupil responses were defined as the area under the curve (AUC, using Simpson's rule; Swallow et al., 2019), where the curve was the double gamma IRF that best fit the pupil time series during the 2 s interval following trial onset. Because AUC is the area between the phasic pupil's curve following trial onset relative to the pre-trial mean, trials with pupil dilation result in positive AUCs and trials with pupil contractions result in negative AUCs. AUC values were *z*-scored by subtracting the individual participant's mean AUC and dividing by the standard deviation to produce the *scaled phasic pupil response* (SPPR). A linear mixed effects model with random intercepts for image [SPPR ~ TonicPupilSize + (1| Old)] indicated a significant, negative relationship between the scaled phasic pupil responses and tonic pupil size, $\beta = -0.282$, 95% CI = $[-0.320, -0.244]$, $t(2446) = -14.53$, $p < 0.001$. Due to scaling, random intercepts for participant had near-zero variance and were thus excluded from the model. Residuals from this model were used in subsequent analyses and are referred to as *phasic pupil responses* (PPR) for simplicity.

The effects of tone type on phasic pupil responses during encoding were evaluated by fitting a linear mixed effects model to the phasic pupil responses (averaged over presentations of an image) with tone type as a fixed effect and random intercepts for image [PPR ~ Tone + (1| Old)]. Random intercepts for participant had near-zero variance and were thus removed from the final model.

Univariate Analysis

Following pre-processing, EPI volumes with motion greater than 0.3 mm were excluded and the data were spatially smoothed using a Gaussian kernel until blur reached a full-width-half-maximum of 5.0 mm (3dBlurtoFWHM). To better estimate activity in the LC, voxels in the neighboring fourth ventricle, labeled with FreeSurfer (recon-all), were excluded from smoothing and subsequent analyses. In addition, masks defining the spatial extent of the brain in the aligned anatomical and EPI data sets, excluding the fourth ventricle, were applied to the EPI data. Data were scaled to a mean of 100 and a range of 0–200 to allow interpretation of beta weights as percent change.

Responses to events of different types were estimated for each voxel using 3dDeconvolve. All models included six motion regressors and 3rd order polynomial drift in baseline as nuisance variables. Regressors of interest were created by convolving a

delta function for each event of interest with the two-parameter SPMG2 hemodynamic response function (HRF; Henson et al., 2002). In the univariate encoding and detection task analyses, regressors were included for each combination of tone type and image type, for a total of 18 regressors of interest. When using the SPMG2 HRF, 3dDeconvolve produces two beta estimates for each condition. These were used to estimate the first 5 timepoints (12.5 s) of the hemodynamic response to each of the 18 conditions for subsequent group level analyses.

Univariate analyses of the ROIs were performed by extracting the mean estimated HRF across voxels located within the boundaries of the ROIs for each of the 18 conditions. For each ROI, estimated HRFs were additionally averaged across image type and analyzed in R with a linear mixed effects model that included tone type, time (timepoints 0 – 12.5 s), hemisphere (left and right), and all interactions as fixed effects and random intercepts for participant and image type [HRF ~ Time*Tone*Hem + (1| Participant) + (1| Image Type)]. The one exception was the LC ROI, which was collapsed across hemispheres [HRF ~ Time*Tone + (1| Participant) + (1| Image Type)]. Models were simplified by excluding the interactions with hemisphere for ROIs that did not show a hemisphere by tone type interaction [all but MC; HRF ~ Time*Tone + Hem + (1| Participant) + (1| Image Type)]. To characterize the effects of tone type over time in each ROI, general linear tests comparing activity across encoding conditions were then performed for each time point. Although all time points were tested, we focus on time points 2.5 – 7.5 s in our report. We expected the hemodynamic response to peak within that time frame because the stimuli were brief (cf. Hu et al., 2010) and the ABE, by its nature, should operate quickly.

Whole brain, group-level univariate analyses were performed to characterize the effects of target and distractor tones on activity throughout the brain. Voxels for which there was a significant interaction of tone type and time were identified in an analysis of variance with Type III sums of squares and tone type, image sub-category, and time (timepoints 0 – 12.5 s) as within participants factors, using 3dMVM (Chen et al., 2015). To further characterize the interaction of tone type and time, the statistical map for this interaction was thresholded at a False Discovery Rate of $q < 0.001$ (Genovese et al., 2002) to create a mask of voxels whose hemodynamic response significantly differed across the three tone type conditions. *Post hoc* paired *t*-tests (3dttest++) on voxels within the tone type by time interaction mask were performed on timepoints 2.5–7.5 s of the estimated HRF to target vs. distractor tones, target tones vs. no tones, and distractor tones vs. no tones. Statistical and cluster size thresholds were used to correct for multiple comparisons based on simulations that used spatial auto-correlation functions (using AFNI function 3dClustSim; Cox et al., 2017).

Trial-Specific Activity Estimation

Trial-specific activity was estimated by fitting a separate linear model for each trial of the encoding and detection task using the least square-separate approach (Mumford et al., 2012). The deconvolution was performed using AFNI's 3dDeconvolve with the SPMG2 option, such that each single-trial response was modeled by two regressors (a gamma response function and its

time derivative). Similarly, the combined responses on all other trials were modeled by two nuisance regressors. In addition, the design matrix included the same motion and drift nuisance variables used in the univariate model described above. The single-trial gamma function estimates were then saved, resulting in 576 (4 runs \times 144 trials) beta maps.

Beta Series Correlation Analysis

The effects of tone type on functional connectivity between the HPC and visual ROIs was estimated using beta series correlations (Rissman et al., 2004; Cisler et al., 2014; Geib et al., 2017) generated from the trial-specific activity estimates. To avoid introducing distortions, we did not subtract the mean pattern from each voxel or scale the data prior to computing these values (Garrido et al., 2013).

First, we concatenated the beta weights of trials sharing the same tone type condition (resulting in three series per voxel with 192 elements each). To obtain ROI-to-ROI functional connectivity estimates, separately for each tone type condition, we generated a mean beta series (obtained by averaging the series across voxels) for each ROI and computed pairwise Fisher-transformed Pearson correlations between those. We fit a linear mixed effects model to the correlation coefficients, with tone type and ROI pair as fixed factors and random intercepts for participant [Correlation \sim Tone*ROI + (1| Participant)]. Holm-corrected general linear tests comparing the different levels of tone type were performed.

ROI-to-voxel beta correlation analyses were then performed for each hippocampal ROI to test the hypothesis that communication should increase between the HPC and visual regions following target tones. Fisher-transformed Pearson correlations between the mean beta series of the seed ROI and each voxel in all visual and hippocampal ROIs (including those in the seed ROI) were then calculated for each tone type and participant. Linear mixed effects models (3dLME) with tone type as a fixed effect and random intercepts for participant were then fit to the ROI-to-voxel correlations [Correlation \sim Tone + (1| Participant)]. General linear tests contrasted the target with the distractor and no tone conditions at each voxel. Candidate clusters in the resulting maps were identified after accounting for spatial autocorrelation in the data (estimated with 3dFWHMx) and by thresholding based on a minimal cluster size and maximal p -value (voxel edges must touch, $\alpha = 0.05$, uncorrected $p = 0.05$; 3dClustSim and 3dClusterize; Cox et al., 2017). This was followed by confirmatory analyses in which each cluster was treated as an ROI. The correlation between the average beta series of the ROI and that of the respective hippocampal seed was computed separately for each participant. A linear mixed effects model, with tone type as a fixed effect and random intercepts for participant, was fit to the correlations [Correlation \sim Tone + (1| Participant)]. Follow-up general linear tests contrasting the tone type conditions were then performed. This was done to ensure that the clustering procedure did not produce spurious clusters.

Support Vector Classification

On their own, differences in BOLD magnitude do not necessarily indicate changes in the quality or extent of stimulus processing

(e.g., Ward et al., 2013; Hatfield et al., 2016). We therefore used linear support vector machine (SVM) classification (Suykens and Vandewalle, 1999; Hsu and Lin, 2002) to probe the effects of target tone detection on image category decoding accuracy in the visual and hippocampal ROIs (V1, V2, FG, PG, aHPC, and pHPC). The algorithm estimates a hyperplane that maximizes the margin between it and samples that belong to different classes (Suykens and Vandewalle, 1999; Hsu and Lin, 2002). It is among the most common approaches to multivoxel pattern analysis (Mahmoudi et al., 2012; Haxby et al., 2014; Diedrichsen and Kriegeskorte, 2017). Importantly, it sidesteps many of the interpretability issues inherent to representational similarity analysis (cf. Walther et al., 2016).

Each trial-wise beta map was assigned one of six labels indicating the type of image presented on that trial. Individual beta series maps were standardized across trials such that each voxel had a mean of zero and a standard deviation of one. Classification accuracy was estimated for each tone type and ROI using repeated fourfold cross validation. Balanced training sets of 144 trial-wise beta maps were randomly drawn 30 times (the remaining 48 trials in each iteration were reserved as a test set); on each iteration a new linear SVM ($C = 1$, one-vs.-one multiclass, default implementation in scikit-learn 0.21.2; Pedregosa et al., 2011) was fit to the training set and applied to the test set to obtain a confusion matrix and a classification accuracy estimate for each tone type condition. These were averaged across the 30 iterations to produce one estimate and one confusion matrix for each combination of participant, tone type, and ROI. The effects of tone type on mean classification accuracy were evaluated for each ROI using a linear mixed effects model with tone type as a fixed effect and random intercepts for participant [Accuracy \sim Tone + (1| Participant)].

Locus Coeruleus Functional Connectivity

ROIs that exhibited functional connectivity with LC during rest were identified using resting state data reported in Turker et al. (2021). Briefly, intrinsic functional connectivity (iFC) maps were created for each participant using denoised multi-echo data and the participant's individually defined LC ROI. Data were denoised using ME-ICA (Kundu et al., 2013), bandpass filtered ($0.01 < f < 0.1$), and were not additionally blurred. A group-level iFC map was created using voxel-wise t -tests (3dttest++) and a one-sided clustering procedure at $p = 0.01$ and FDR = 0.018 [3dClusterize; corrected for multiple comparisons using the false discovery rate (FDR = 0.02; Genovese et al., 2002)]. Twenty ranked peaks were extracted from the group iFC map (3dmaxima) with a minimal distance of 18 mm (6 voxels) between peaks. Next, 6 mm spherical ROIs were constructed around those peaks and a final set of 20 ROIs was obtained by intersecting the spheres with the group-level iFC map thresholded at $p < 0.001$, $q < 0.004$, producing the final LC-iFC ROIs (Supplementary Table 1).⁴

⁴Though the regions are similar, the exact coordinates and rank order of ROIs in Supplementary Table 1 differ from those reported in Turker et al. (2021) because of a difference in coordinate systems and a change in how data were compressed during preprocessing.

Statistical Software

All group-level analyses were performed in R v3.6.1 (R Core Team, 2013) or in AFNI v16.2.07 (using 3dLME or 3dMVM). Unless otherwise noted, linear mixed effects models were fit using lme4 v1.1.21 (Bates et al., 2015). Type III (Satterthwaite's method) ANOVA tables were obtained using the 'joint_tests' function in the package emmeans v1.3.5.1 (Length, 2020). General linear tests were performed and uncorrected confidence intervals were obtained using the emmeans functions 'contrasts' and 'confint.' In all analyses, Holm-Bonferroni adjusted p -values were computed separately for each set of tone type comparisons. Confidence intervals, where reported, are uncorrected.

RESULTS

Behavioral Task Performance and Whole Brain Analysis

Participants accurately performed the detection task, pressing the button for $M = 97.5\%$ of the targets, $SD = 0.15$, 95% CI = [0.970, 0.990], $M = 5.1\%$ of the distractors, $SD = 0.22$, 95% CI = [0.023, 0.060] and $M = 0.2\%$ of the no tone trials, $SD = 0.05$, 95% CI = [0.001, 0.003]. Incorrect button presses were more likely to follow a distractor tone than no tone, $t(20) = -4.16$, $p < 0.001$, $d = 1.25$.

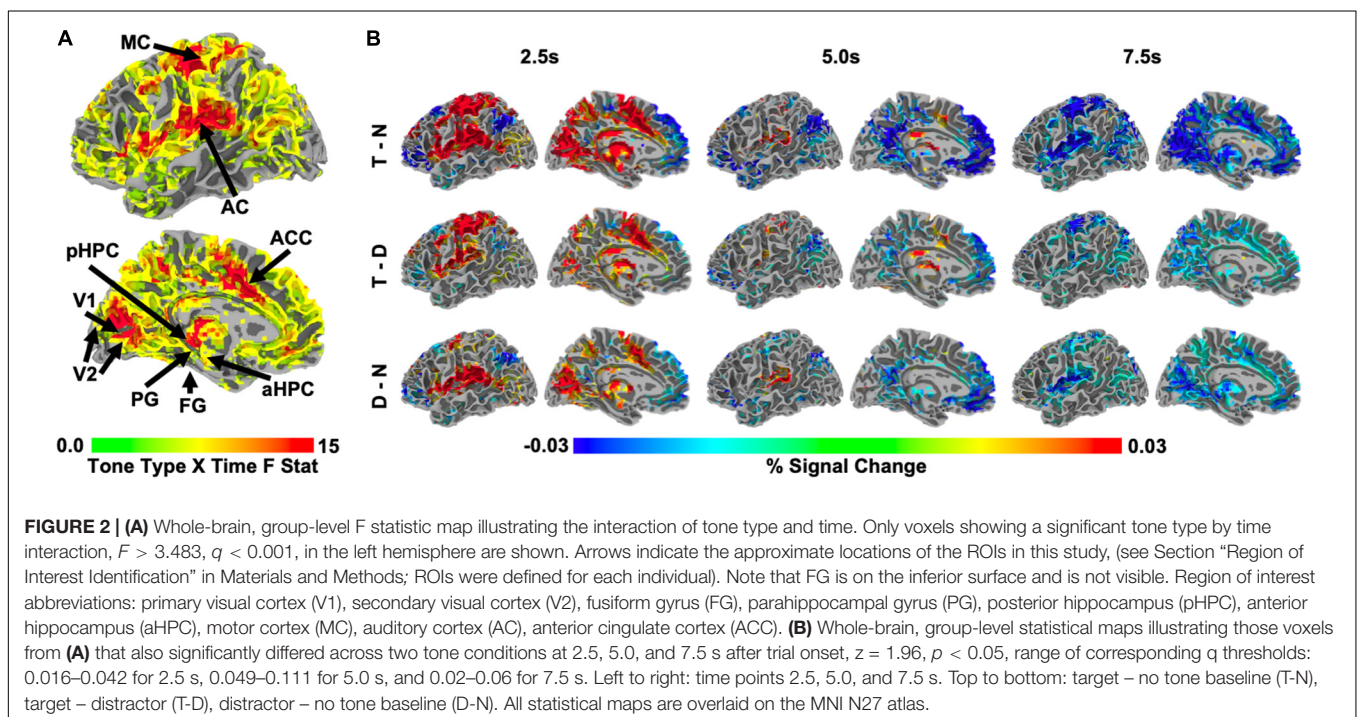
The tone type condition did not significantly influence image recognition accuracy, $F(2, \text{inf}) = 1.08$, $p = 0.34$. However, it did influence the confidence with which images were correctly recognized, $F(2, 1660.8) = 6.81$, $p = 0.001$. Participants reported higher levels of confidence for correctly recognized images paired with a target than for those paired with a distractor ($M_{\text{Diff}} = 5.58$),

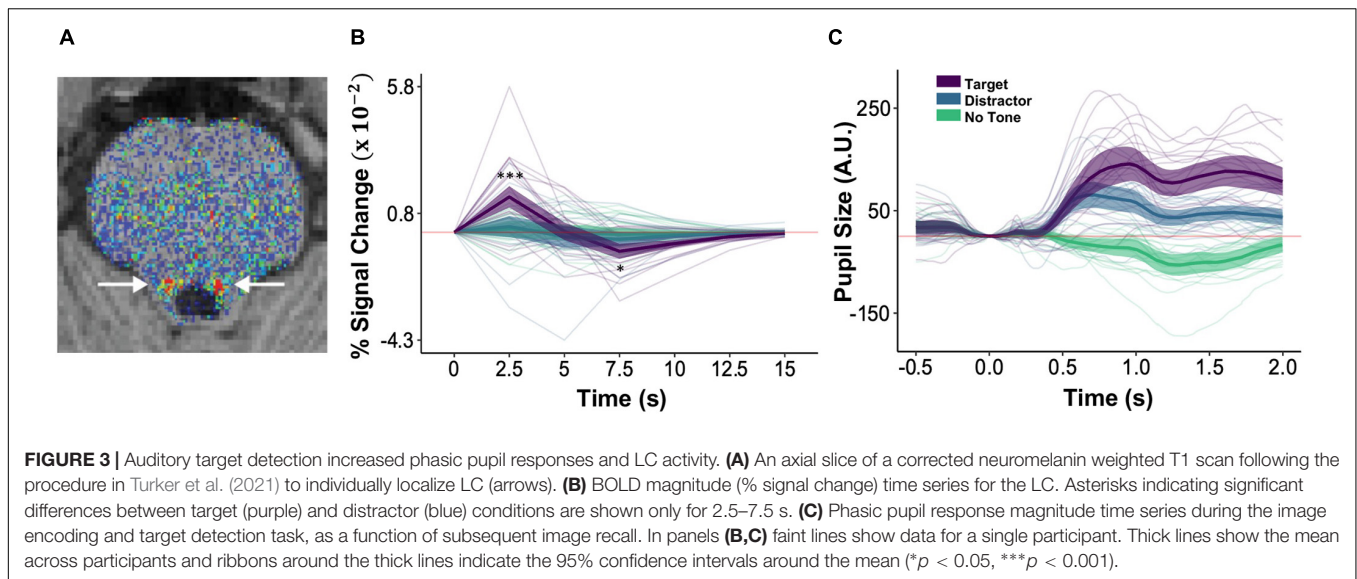
95% CI = [1.83, 9.32], $t(1899.08) = 3.57$, $p = 0.001$, $d = 0.57$, or presented without a tone ($M_{\text{Diff}} = 4.10$), 95% CI = [0.23, 7.97], $t(1573.68) = 2.54$, $p = 0.023$, $d = 0.44$, but confidence did not differ between correctly recognized images presented in the distractor and no tone conditions ($M_{\text{Diff}} = 1.48$), 95% CI = [-2.38, 5.34], $t(1578.25) = 0.92$, $p = 0.359$, $d = 0.10$. Target detection during image encoding thus increased the confidence with which those images were later correctly recognized, and distractor rejection did not significantly interfere with the encoding of a concurrently presented image (Figure 1B).

Whole brain analyses revealed that auditory target detection influenced BOLD activity in regions spanning medial occipital, medial parietal, anterior cingulate, superior temporal, middle frontal, and subcortical areas, including thalamus (time by tone type interaction, $F > 3.483$, $q < 0.001$; Figure 2A). In many of these regions, activity was initially higher on the target tone trials than in the other two types of trials, though this relationship reversed at subsequent timepoints (Figure 2B, top and middle row). Relative to no tone trials, the response to distractor trials was smaller in magnitude than the response to target trials in most regions (Figure 2B, bottom row).

Locus Coeruleus and Phasic Pupil Responses

To test our hypothesis that the LC is involved in the ABE, we examined whether target tone trials evoked greater phasic pupil responses and LC signal changes than did distractor tone and no tone trials. Consistent with this possibility, BOLD responses in the hand-traced LC ROIs (Figure 3A) exhibited an interaction of tone type and time, $F(10, 2225) = 8.28$, $p < 0.001$, reflecting greater increases in activity at 2.5 s on target tone trials than on





distractor tone trials, $t(2225) = 6.51$, $p < 0.001$, $d = 0.48$, and no tone trials, $t(2225) = 7.03$, $p < 0.001$, $d = 0.58$ (Figure 3B). Phasic pupil responses also varied across tone type, $F(2,2124.6) = 336.98$, $p < 0.001$: they were more positive on trials that included a target tone than on trials that included a distractor tone ($M_{Diff} = 0.47$), 95% CI = [0.37, 0.56], $t(2110) = 11.45$, $p < 0.001$, $d = 0.25$, or no tone ($M_{Diff} = 1.05$), 95% CI = [0.96, 1.15], $t(2102) = 25.86$, $p < 0.001$, $d = 0.39$. They were also greater on distractor tone trials than on no tone trials ($M_{Diff} = 0.59$), 95% CI = [0.49, 0.68], $t(2160) = 14.44$, $p < 0.001$, $d = 0.13$ (Figure 3C). These data demonstrate increased activity of the LC system on trials that require a response and provide no evidence for inhibitory effects of distractor rejection on this system.

BOLD Responses in Perceptual and Motor Regions

To examine the effects of target detection on the processing of episodic information, planned analyses tested whether tone type modulated BOLD magnitude within regions involved in stimulus processing, encoding, and response generation: bilateral MC, V1, V2, FG, PG, aHPC, and pHPC. These analyses evaluate whether previously reported effects of auditory target detection on BOLD responses in visual cortex (Swallow et al., 2012) (1) reflect an increase over a neutral baseline condition as well as over distractor conditions, and (2) are present in other regions important for episodic encoding.

The interaction of tone type and time was significant in V1, V2, FG, PG, aHPC, and pHPC, smallest $F(10,4492) = 12.48$, $p = 0.001$ for FG. Extending earlier reports (Swallow et al., 2012), V1 showed a larger initial increase in activity on target trials than on both distractor and no tone trials, smallest $z = 7.81$, $p < 0.001$, $d = 0.43$. Similar increases were also observed in V2, FG, and PG, smallest $z = 2.60$, $p = 0.019$, $d = 0.15$, as well, demonstrating that these effects can also be detected in higher-level visual regions as well as in early visual cortex. Additionally, in all cases BOLD activity showed a steeper drop-off in magnitude on target trials

relative to distractor and no tone trials (Figure 4 and see also Supplementary Figure 1).

The HPC generally showed larger decreases in activity on target trials than on distractor and no tone trials. This was true of both the aHPC and pHPC, which at 5 s were more strongly deactivated on target trials than on distractor trials, smallest $z = 4.50$, $p = 0.001$, $d = 0.28$, and no tone trials, smallest $z = 11.81$, $p < 0.001$, $d = 0.751$. However, activity in the aHPC decreased more rapidly than it did in the pHPC: at 2.5 s, activity in the aHPC was lower on target than on distractor, $z = 3.12$, $p = 0.002$, $d = 0.18$, and no tone, $z = 8.54$, $p < 0.001$, $d = 0.52$, whereas activity in pHPC was higher on target trials than on distractor trials, $z = 3.49$, $p = 0.001$, $d = 0.20$ (Figure 4).

Except for in the MC, there were no interactions between hemisphere and tone type, largest $F(2,4475) = 1.80$, $p = 0.165$, or between tone type, time, and hemisphere, largest $F(10,4475) = 1.77$, $p = 0.061$. In MC, at 2.5 s, BOLD activity was greater on target trials than on distractor and no tone trials in the left hemisphere, smallest $t(2225) = 13.55$, $p < 0.001$, $d = 0.98$.

These results demonstrate that target detection modulated the magnitude of activity in regions involved in representing visual and episodic information.

Decodable Stimulus Information in the Visual Cortex and Hippocampus

Increased BOLD activity on target trials does not necessarily entail that processing in these regions is enhanced. To test our hypothesis that target detection facilitates the processing of concurrently presented images, we conducted analyses of image category classification accuracy using voxel-wise patterns of activity in the visual and hippocampal ROIs. These revealed a main effect of tone type in V2, FG, PG, and pHPC, smallest $F(2,92) = 4.59$, $p = 0.013$ for pHPC, but not in V1 or aHPC, largest $F(2,92) = 1.36$, $p = 0.261$ for V1. Follow up analyses indicated that classification accuracy was higher on target trials than on no tone trials in V2, FG, PG, and pHPC, smallest

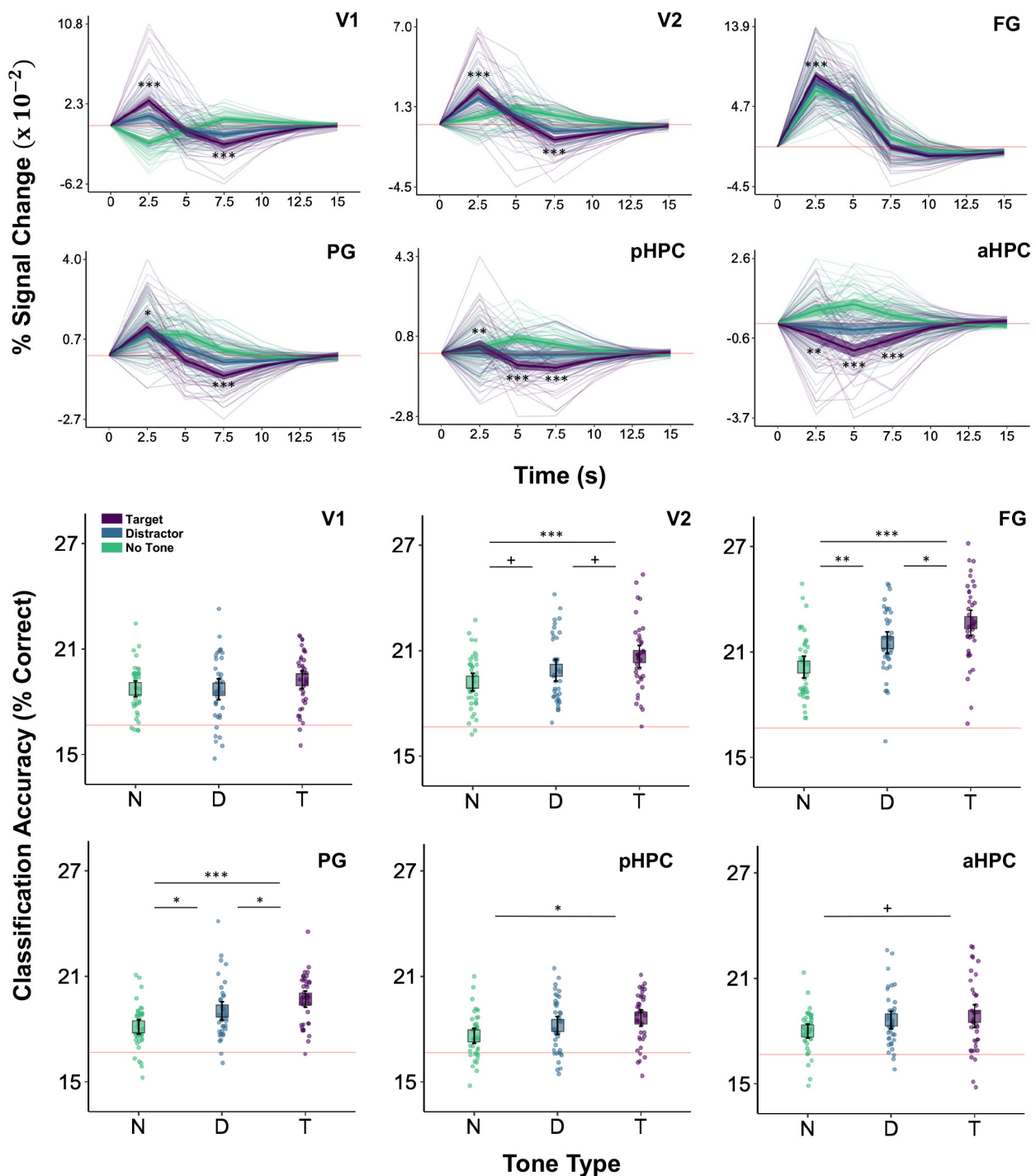
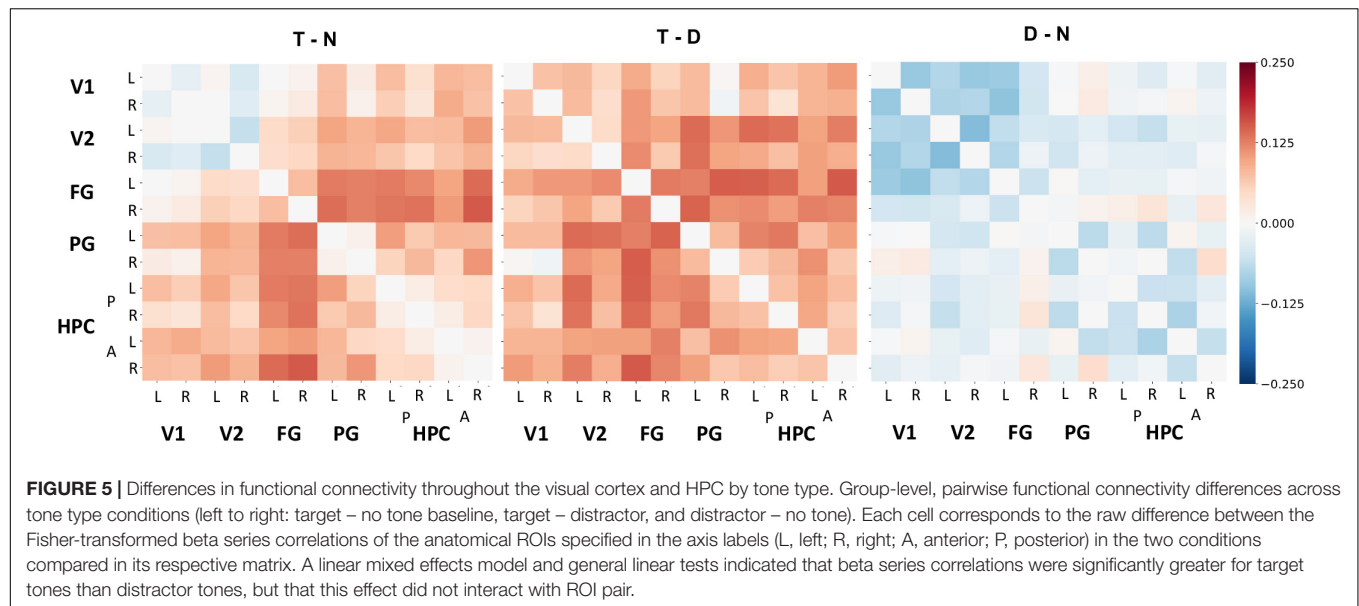


FIGURE 4 | BOLD magnitude and image category classification accuracy as a function of tone type. Top two rows: BOLD magnitude (% signal change) time series for the visual and HPC ROIs in the target (purple), distractor (blue), and no tone (green) conditions. Asterisks indicating significant differences between target and distractor conditions are shown only for 2.5–7.5 s (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Faint lines show data for a single participant. Thick lines show the mean across participants. Ribbons around the thick lines indicate the 95% confidence intervals around the mean. Bottom two rows: six-way image category classification accuracy in the same ROIs. Theoretical chance-level performance (16.67%) is marked by a red horizontal line. Each point represents classification accuracy for a single participant. Large squares are centered on the sample mean and error bars indicate 95% confidence intervals around the mean. Asterisks denote a significant difference (+ $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Region of interest abbreviations: primary visual cortex (V1), secondary visual cortex (V2), fusiform gyrus (FG), parahippocampal gyrus (PG), posterior hippocampus (pHPC), anterior hippocampus (aHPC), motor cortex (MC), auditory cortex (AC). See Section “Region of Interest Identification” in Materials and Methods for ROI definitions.



$t(92) = 3.01$, $p = 0.01$, $d = 0.96$ for pHPC. Classification accuracy was also higher on target compared to distractor tone trials in FG $t(92) = 2.60$, $p = 0.011$, $d = 0.62$, PG, $t(92) = 2.09$, $p = 0.039$, $d = 0.52$, and marginally in V2, $t(92) = 2.17$, $p = 0.065$, $d = 0.44$. Similarly, relative to no tone trials, distractor trials significantly enhanced classification accuracy in FG and PG, smallest $t(92) = 2.764$, $p = 0.014$, $d = 0.87$ for the latter, and showed a marginal effect in V2, $t(92) = 1.88$, $p = 0.065$, $d = 0.43$ (Figure 4). Thus, regions whose activity was enhanced by target detection also exhibited within-ROI patterns of activity that better correlated with image category on these trials than on distractor or no tone trials. This was particularly true in higher-level visual areas, FG and PG, which should be more tuned to image categories than V1 and V2.

Visuo-Hippocampal Functional Connectivity

To test our hypothesis that target detection enhances communication between regions involved in episodic processing, functional connectivity between all visual and hippocampal ROIs was quantified with beta series correlations (Figure 5). Our analysis examined the effect of tone type across each pairing of the following ROIs: l/r-V1, l/r-V2, l/r-FG, l/r-PG, l/r-aHPC, and l/r-pHPC. Tone type and ROI pair influenced functional connectivity, $F(2, \text{inf}) = 46.65$, $p < 0.001$ and $F(77, \text{inf}) = 122.24$, $p < 0.001$, respectively, but did not interact, $F(154, \text{inf}) = 0.33$, $p > 0.999$. Holm-corrected general linear tests indicated that functional connectivity was enhanced on target trials relative to both distractor trials, $z = 9.48$, $p < 0.001$, $d = 0.50$, and no tone trials, $z = 6.36$, $p < 0.001$, $d = 0.32$. Functional connectivity was also higher on no tone trials than on distractor tone trials, $z = 3.12$, $p = 0.002$, $d = 0.24$. Thus, relative to the no tone trials, target tones increased correlations between ROIs while distractor tones decreased them.

To more precisely identify the regions whose functional connectivity with the HPC changed with tone type, we calculated ROI-to-voxel functional connectivity maps and extracted candidate clusters by contrasting the tone type conditions. We refer to these clusters by the ROI seed that generated them and the anatomical area that they overlapped with most (e.g., l-pHPC < - > r-V2 refers to a cluster largely overlapping with r-V2 that was correlated with l-pHPC). No clusters were found when the distractor condition was contrasted with the no tone baseline, indicating that the distractor tones did not reliably alter functional connectivity between the HPC and visual cortex. However, three clusters (l-pHPC < - > l-FG, l-pHPC < - > r-FG, and r-aHPC < - > l-FG) were identified when target trials were contrasted with no tone trials and seven clusters were identified when target trials were contrasted with distractor trials (Table 1 and Figure 6). Both sets of clusters spanned voxels throughout visual cortex.

Confirmatory analyses on clusters identified in the target versus distractor contrast were performed by averaging functional connectivity across all voxels within a cluster and then testing the effect of tone type in a linear mixed effects model. This analysis indicated that all pairs showed an effect of tone type on functional connectivity, smallest $F(2,36) = 3.77$, $p = 0.033$ for l-aHPC < - > r-FG, except l-aHPC < - > l-FG, $F(2,36) = 3.02$, $p = 0.061$. In those pairs showing an effect of tone type, functional connectivity was higher on target trials than on distractor trials, smallest $t(36) = 2.61$, $p = 0.039$, $d = 0.54$ for l-aHPC < - > r-FG. Functional connectivity was also higher on target trials than on no tone trials in the pairs l-pHPC < - > r-V2, l-pHPC < - > l-V2, and r-aHPC < - > l-FG, smallest $t(36) = 2.39$, $p = 0.045$, $d = 0.46$ for l-pHPC < - > l-V2. No differences in functional connectivity were found between the distractor and no tone trials in any of the clusters, largest $t(36) = 1.12$, $p = 0.273$, $d = 0.29$ (Figure 6).

To test the hypothesis that increased visuo-hippocampal coordination during target tone trials is associated with better

TABLE 1 | Clusters showing higher functional connectivity with the HPC on target tone than on distractor tone trials in the seed-to-voxel beta series correlation analysis.

Seed	Cluster	Center of Mass	Size	% overlap with anatomical ROIs							
				l-V1	r-V1	l-V2	r-V2	l-FG	r-FG	l-PG	r-PG
l-pHPC	r-V2	−16.0, 72.5, −1.1	264	0.8%	23.6%	1%	50.2%	–	24.4%	–	–
l-pHPC	l-V2	20.3, 69.0, −10.8	253	8.3%	–	48.8%	–	42.9%	–	–	–
l-aHPC	l-FG	32.4, 52.6, −17.9	60	–	–	–	–	100%	–	–	–
l-aHPC	r-FG	−30.5, 61.9, −13.9	43	–	–	–	10.5%	–	89.5%	–	–
r-pHPC	l-V2	10.8, 74.1, −5.4	102	17.5%	–	79%	–	3.5%	–	–	–
r-pHPC	r-FG	−22.9, 64.3, −10.7	56	–	1.2%	–	48.9%	–	49.9%	–	–
r-aHPC	l-FG	25.1, 66.4, −14.5	148	1%	–	37.5%	–	61.5%	–	–	–

Center of mass is reported in Right Anterior Inferior coordinates (RAI, the AFNI default), volumes are in mm³, and the percentages of voxels in a cluster that overlapped with each anatomical ROI are the mean across subjects.

visual processing, we treated the ROI-to-voxel functional connectivity clusters as ROIs in an image category classification analysis. Tone type affected classification accuracy in all clusters except r-pHPC < - > l-V2, smallest $F(2,36) = 3.53$, $p = 0.04$. This effect reflected greater accuracy on target trials than on no tone trials, smallest $t(36) = 2.65$, $p = 0.035$, $d = 0.86$. Only the l-pHPC < - > r-V2 cluster showed higher classification accuracy on target trials than on distractor trials, $t(36) = 2.54$, $p = 0.031$, $d = 0.74$. Accuracy was higher on distractor trials than on no tone trials in r-pHPC < - > r-FG and r-aHPC < - > l-FG, smallest $t(36) = 2.48$, $p = 0.036$, $d = 0.77$ for the former (Figure 6).

Functional Connectivity of Regions Associated With the Locus Coeruleus

A functional connectivity analysis with the LC as a seed revealed small regions within l-FG, r-FG, and r-HPC that showed higher functional connectivity with the LC in the target tone condition than in the distractor tone condition (respectively, $ps > 0.007$, $ps > 0.012$, $ps > 0.045$; illustrated in **Supplementary Figure 4**). However, these regions were not large enough to survive corrections for multiple comparison using cluster size 32 ($\alpha < 0.05$). Voxels in l-MC also showed no evidence of differential connectivity with the LC on target relative to distractor trials, suggesting that this analysis may not have been powerful enough to detect differences in LC connectivity across conditions.

However, if the LC influences activity in regions involved in episodic encoding, then functional connectivity between HPC and regions whose activity is modulated by the LC during rest should be greater on target trials (when LC activity is strongest) than on distractor and no tone trials. To test this hypothesis, a set of 20 regions whose activity was associated with LC activity during a separate resting state scan—referred to as LC-iFC ROIs—were identified (see Section “Region of Interest Identification” in Materials and Methods and Turker et al., 2021; **Supplementary Table 1**) and their functional connectivity to the four hippocampal seeds was examined. A separate model was fit for each of l-pHPC, r-pHPC, l-aHPC, and r-aHPC.

Main effects were found for tone type, smallest $F(2,1062) = 10.11$, $p < 0.001$ for l-aHPC, and region, smallest $F(19,1062) = 13.05$, $p < 0.001$ for r-pHPC, but the two did not interact, largest $F(38,1062) = 0.49$, $p = 0.996$ for l-pHPC. General linear tests that collapsed across LC-iFC ROIs showed higher functional connectivity on target trials than on distractor

trials, smallest $t(1062) = 4.45$, $p < 0.001$, $d = 0.41$ for l-aHPC, and no tone trials, smallest $t(1062) = 2.45$, $p = 0.029$, $d = 0.24$ for l-pHPC. Functional connectivity to l-pHPC was lower on distractor trials than on no tone trials, $t(1062) = 2.06$, $p = 0.039$, $d = 0.32$. Tone type did not significantly influence functional connectivity between the LC and the LC-iFC ROIs, $F(2,1062) = 0.093$, $p = 0.911$, consistent with the possibility that functional connectivity analyses of LC during the encoding task were not sufficiently powerful.

DISCUSSION

In this fMRI study, we investigated the effects of target detection on how visual stimuli are processed and encoded by the brain. We examined how visual regions, the HPC, and the LC respond to images presented concurrently with an auditory target tone (requiring a motor response), a distractor tone (requiring no response), or no tone. The inclusion of a no tone baseline condition, which was absent in previous fMRI studies of similar effects, allowed us to test for both target-induced enhancement and distractor-induced disruption of encoding, perceptual processing, and functional connectivity. We found that, relative to both other conditions, target tones enhanced image recognition confidence (the ABE), the magnitude of phasic pupil responses, activity in LC and in visual regions, visuo-hippocampal functional connectivity, and image category classification accuracy from multivoxel patterns in FG and PG. Combined, these results suggest that auditory target detection enhances the processing of visual information by increasing inter-areal communication and enhancing the specificity of visual representations.

Consistent with existing evidence suggesting that target detection enhances episodic encoding in the attentional boost effect (Swallow and Jiang, 2013), recognition confidence ratings for correctly remembered images were greater when those were paired with a target tone as opposed to a distractor tone. Indeed, previous work has shown that target detection can enhance both recollection and familiarity of images presented during the encoding task even when they are presented one time (Broitman and Swallow, 2020). The absence of significant differences in recognition accuracy in the full sample is consistent with an earlier MRI study (Swallow et al., 2012) and may be a

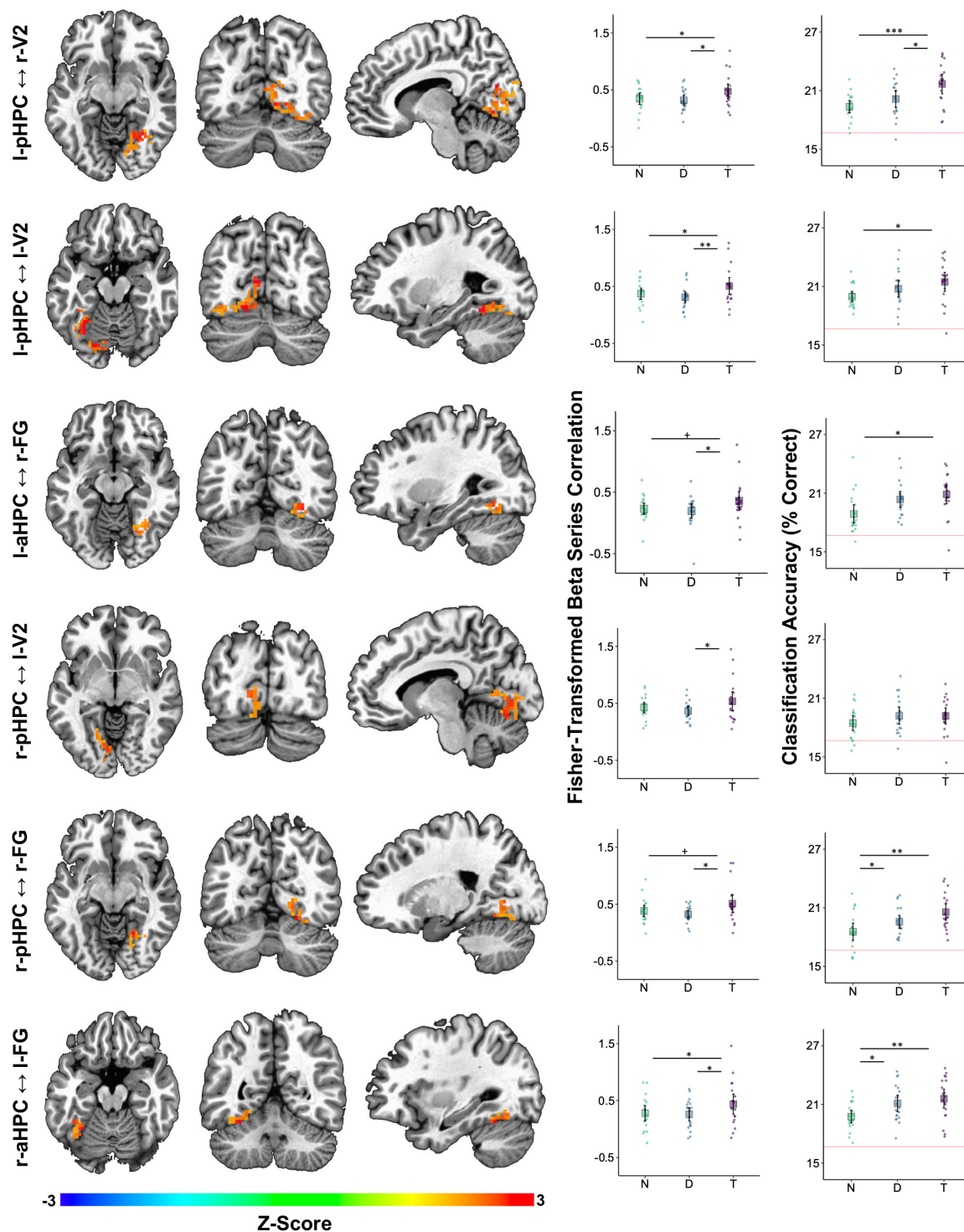


FIGURE 6 | Auditory target detection improved image classification accuracy in visual regions showing increased functional connectivity with the HPC. Each row corresponds to one cluster detected as being more strongly correlated with the HPC on target tone trials than on distractor tone trials. The seed-cluster pair label is denoted on the left. Left three columns: voxel colors correspond to z-scores obtained by contrasting the Fisher-transformed correlations between the mean beta series for the hippocampal seed region and that of each voxel in V1, V2, FG, PG, pHPC, and aHPC. Middle column: mean Fisher-transformed beta series correlations between each cluster and its respective hippocampal seed, obtained separately for each tone type condition—no tone (N), distractor tone (D), and target tone (T). Right column: six-way image category classification accuracy for each cluster. Theoretical chance-level performance (16.67%) is marked by a red horizontal line. Middle and Right columns: large squares are centered on the sample mean and error bars indicate 95% confidence intervals around the mean. Each point represents an observation from a single participant. Asterisks denote a significant difference ($^+p < 0.1$, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$).

consequence of the relatively long inter-trial intervals that had to be used in this study (cf. Mulligan and Spataro, 2015).

Throughout the visual areas examined, activity in the target tone condition was higher relative to the distractor and no-tone baseline conditions. This pattern was also present in other regions involved in orienting to relevant stimuli. Those included the thalamus, whose higher-order nuclei play a critical role in attention and in the maintenance of sensory representations in awareness and working memory (Saalmann and Kastner, 2011), and the LC, whose noradrenergic projections regulate gain throughout the cortex (Servan-Schreiber et al., 1990; Aston-Jones and Cohen, 2005) and which tends to exhibit larger responses following salient events (Bouret and Sara, 2005). Interestingly, the opposite pattern was observed in aHPC and pHPC: activity decreased on target tone trials relative to the two other conditions. Because the images were presented four times, these decreases may reflect greater repetition suppression of hippocampal activity for target-paired images than for other images (Henson and Rugg, 2003; Summerfield et al., 2008; Larsson and Smith, 2012; Kim et al., 2020). Measures of repetition suppression tend to positively correlate with subsequent recognition memory (e.g., Pihlajamäki et al., 2011) and with functional connectivity between the HPC, visual cortex, and prefrontal cortex (Zweynert et al., 2011). Though our results, as a whole, hint at a relationship between hippocampal repetition suppression and the effects of target detection on recollection, additional work is needed to confirm this possibility.

Changes in inter-areal coordination are thought to play a role in the maintenance and encoding of neural representations (Fries, 2005, 2015; Singer, 2013; Bonnefond et al., 2017; Moyal and Edelman, 2019; Moyal et al., 2020). Enhanced cortico-hippocampal functional connectivity, in particular, has been associated with working memory maintenance and long-term memory encoding (e.g., Gazzaley et al., 2004; for a review, see Poch and Campo, 2012). Target detection could influence perception and memory in a similar fashion, by enhancing communication between perceptual and medial temporal regions in critical moments (e.g., when responding to targets). Our findings are compatible with this idea: functional connectivity between aHPC and pHPC and the visual cortex was higher on target tone trials relative to both distractor and no tone trials. The effect of target tones on HPC to visual cortex functional connectivity was most pronounced for the left pHPC, which showed widespread, bilateral increases in functional connectivity with clusters in the ventral visual cortex—V1, V2, and FG. The aHPC exhibited a similar correlation with FG, but less so with V1 and V2. Differences in the effects of target detection on aHPC and pHPC connectivity are consistent with the differential functional connectivity of the anterior and posterior HPC previously reported in humans (Poppenk et al., 2013; Frank et al., 2019). They also suggest that future research should examine whether target detection has larger effects on the types of information processed by pHPC (perceptual features of stimuli) than on the types of information supported by aHPC (categories of stimuli).

The target-related enhancement of visuo-hippocampal connectivity was accompanied by a boost in image category classification accuracy throughout the ventral visual stream and in pHPC relative to the baseline condition. A similar

enhancement was found relative to the distractor tone condition in FG and PG. This suggests that the effect of target detection on subsequent recognition confidence could reflect improved perceptual encoding in higher level visual areas. Surprisingly, a smaller increase in classification accuracy was also observed on distractor tone trials relative to the no-tone baseline in FG and PG. Thus, although exposure to any auditory tone in this task may enhance the quality of visual information processing, target detection provides an additional boost. A similar pattern was also found in smaller ventral visual clusters that exhibited greater functional connectivity with HPC on target compared to distractor tone trials. This suggests a possible relationship between these two effects. Future studies may address the question of whether shifts in long-range coordination are directly related to the quality and extent of perceptual processing and memory encoding (Moyal and Edelman, 2019)—not only in terms of multivoxel classification accuracy and recognition confidence (as demonstrated in this study), but also in terms of subsequent memory test performance.

Phasic LC responses have been hypothesized to facilitate the updating of representations and contribute to the ABE (Swallow and Jiang, 2010; Swallow et al., 2012) by enhancing perceptual processing following target detection independent of modality or spatial location (Nieuwenhuis et al., 2005; Swallow and Jiang, 2013, 2014; see also Bouret and Sara, 2005). Our results are consistent with this view. They suggest a role for the LC in mediating the effects of target detection on perception and memory via the strengthening or reorganization of functional networks. In this study, both LC activity and phasic pupil responses (which may correlate; Joshi et al., 2016) increased on target tone trials relative to both distractor and no tone trials. These differences were observed despite the fact that each condition was equally likely. However, whereas LC activity did not increase on distractor trials relative to no tone trials, pupil diameter did. Indeed, other cognitive and neural factors contribute to pupil size in addition to LC activity (e.g., cognitive effort; van der Wel and van Steenbergen, 2018). Additionally, regions that were highly correlated with the LC during rest were also more strongly correlated with aHPC and pHPC on target trials than on distractor trials during the encoding task. Though a contrast of functional connectivity between LC and our cortical and hippocampal ROIs only yielded a marginal increase on target tone trials (reported in the **Supplementary Materials**), these findings hint at a possible link between target-related LC responses and the other effects we observed, which can be addressed directly in future studies.

In the encoding and detection task, target detection differs from distractor rejection in both cognitive and motor demands. However, the effects of target detection on activity in visual cortex, pupil responses, and memory can occur in the absence of an overt motor response and are absent when motor responses are self-generated (Jack et al., 2006; Swallow and Jiang, 2012; Swallow et al., 2012, 2019; Makovski et al., 2013; Mulligan et al., 2016; Toh and Lee, 2022). In this study, behavioral inhibition in the distractor tone condition also did not lower BOLD magnitude or classification accuracy relative to the baseline, arguing against the possibility of a disruptive effect of response inhibition on processing (as in inhibition-induced forgetting, which has been

tied to fluctuations in ventrolateral PFC activity, which were not found here; Chiu and Egner, 2015). While this confirms that our findings reflect a target-induced boost (Swallow and Jiang, 2014), target detection was confounded with motor responses in this study. Therefore, additional research is necessary to identify and confirm the source of the physiological effects we report here, whether it is from the motor system or otherwise (see **Supplementary Materials** for additional analyses).

Though the peak BOLD responses we observed were often earlier than is typical in human fMRI, they are consistent with expected BOLD response latencies (Miezin et al., 2000) and fall within the range of peak latencies reported in investigations of hemodynamic response variability (Handwerker et al., 2004) and BOLD responses to brief (<1 s) auditory tones (Hu et al., 2010). Rapid BOLD dynamics in our study may also reflect the relatively coarse temporal resolution of the EPI sequence (TR = 2.5 s), as well as the duration and periodicity of stimulus presentation in our task: BOLD responses are sharper and faster when stimuli are brief (Huettel et al., 2004; Tian et al., 2010; Hirano et al., 2011) and both effects may be exaggerated when brief stimuli are presented over a background of periodic stimulation (Lewis et al., 2016). Animal neuroimaging and physiological modeling further suggest that rapid increases and decreases in BOLD signal reflect changes in blood flow and volume within microvasculature supporting temporally and spatially localized neuronal activity (Tian et al., 2010; Hirano et al., 2011; Polimeni and Lewis, 2021). The rapid BOLD dynamics we observed therefore may reflect temporally and spatially precise neural responses to brief stimuli presented during periodic visual change.

Taken together, our data provide novel evidence that target detection facilitates the processing and encoding of information presented at the same time as stimuli that require a response. These events enhance perceptual processing and functional connectivity between the HPC and the ventral visual cortex. Both effects could be related to the stronger LC responses observed following auditory target detection. Our results and interpretation are compatible with the emerging view that, by increasing gain throughout the thalamocortical network at opportune moments, the phasic release of NE from the LC may facilitate functional network reorganization and promote more integrated, information-rich dynamics. Theoretical models and empirical findings have linked higher gain to increases in the topological complexity and variability of population activity (Shine et al., 2018; Moyal and Edelman, 2019) as well as to enhanced inter-regional information transfer (Li et al., 2019). Though LC-mediated changes in gain may be sufficient for mediating the facilitatory effects of target detection on memory, prefrontal influences are also likely to contribute—either by modulating LC output (Jodoj et al., 1998) or by directly regulating hippocampal activity and functional connectivity to support memory encoding (Ranganath et al., 2005; Schott et al., 2013). Future work may combine functional neuroimaging, electrophysiology, and computer simulations to explore these possibilities and provide a precise account of the mechanisms underlying the ABE. This work can further clarify the effects of attending to behaviorally relevant moments on neural dynamics, information representation, and incidental encoding.

DATA AVAILABILITY STATEMENT

The datasets presented in this article are not readily available because participants did not provide consent to make their data publicly available. Data are available from the corresponding author upon reasonable request and with proper approval from relevant research and ethics entities. Requests to access the datasets should be directed to KS, kms424@cornell.edu.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Cornell Institutional Review Board for Human Participant Research. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

RM: conceptualization, methodology, validation, formal analysis, investigation, data curation, writing – original draft, review and editing, and visualization. HT: conceptualization, methodology, validation, formal analysis, investigation, data curation, writing – review and editing, and visualization. W-ML: methodology, resources, and writing – review and editing. KS: conceptualization, methodology, formal analysis, investigation, resources, data curation, supervision, project administration, writing – review and editing, and funding acquisition. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fpsyg.2022.891682/full#supplementary-material>

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Grounding the Attentional Boost Effect in Events and the Efficient Brain

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Attention and memory for everyday experiences vary over time, wherein some moments are better attended and subsequently better remembered than others. These effects have been demonstrated in naturalistic viewing tasks with complex and relatively uncontrolled stimuli, as well as in more controlled laboratory tasks with simpler stimuli. For example, in the *attentional boost effect* (ABE), participants perform two tasks at once: memorizing a series of briefly presented stimuli (e.g., pictures of outdoor scenes) for a later memory test, and responding to other concurrently presented cues that meet pre-defined criteria (e.g., participants press a button for a blue target square and do nothing for a red distractor square). However, rather than increasing dual-task interference, attending to a target cue boosts, rather than impairs, subsequent memory for concurrently presented information. In this review we describe current data on the extent and limitations of the attentional boost effect and whether it may be related to activity in the locus coeruleus neuromodulatory system. We suggest that insight into the mechanisms that produce the attentional boost effect may be found in recent advances in the locus coeruleus literature and from understanding of how the neurocognitive system handles stability and change in everyday events. We consequently propose updates to an early account of the attentional boost effect, the dual-task interaction model, to better ground it in what is currently known about event cognition and the role that the LC plays in regulating brain states.

Keywords: predictive coding, locus coeruleus, episodic memory, temporal selection, event cognition, attentional boost effect

INTRODUCTION

Everyday experience tends to unfold predictably. Most of the time, the environment changes little from one moment to the next, and people and things behave according to learnable, predictable patterns (Saffran et al., 1996; Baldwin et al., 2008; Endress and Wood, 2011; Friend and Pace, 2011; Kidd et al., 2014; Kosie and Baldwin, 2019). However, situations can change rapidly: a task is completed, a fire alarm goes off, or a neighbor stops by with a request. In all of these cases the human cognitive system must shift from a relatively stable state that reflected the situation as it once was, to a new state that optimizes cognition and behavior in the changed environment. These aspects of everyday cognition are captured in research that examines how attention and memory dynamically respond to changes in situations and task demands. In this paper, we discuss

how the *attentional boost effect* (ABE), the phenomenon whereby increasing attention to one task boosts performance in another (Lin et al., 2010; Swallow and Jiang, 2010), could reflect neurocognitive mechanisms that help people adapt to behaviorally relevant changes in ongoing events.

The ABE is difficult to reconcile with fundamental characteristics of attention—that it is limited, and therefore selective for tasks, locations, objects, and features (Kinchla, 1992; Buschman and Kastner, 2015). The standard ABE paradigm requires participants to divide attention across two tasks, for which two unrelated streams of stimuli are briefly, but simultaneously presented in a long, uninterrupted series. For the *encoding task*, participants memorize all of the images that are presented on the screen. For the *detection task* they are instructed to press a button whenever a cue has a particular feature, such as when a blue square appears (a *target*, sometimes also called *go cue*) rather than a red square (a *distractor*, sometimes also called *no-go cue*; **Figure 1**). The limited and selective nature of attention suggests that there should be two sources of interference in this *continuous dual-task encoding paradigm*: constant interference resulting from having to maintain two sets of goals and divide attention across two stimulus streams (Trover and Craik, 2000; Wolfe et al., 2007) and transient redistributions of attention from the encoding task to detection

task stimuli when targets occur (Duncan, 1980; Kinchla, 1992). However, this paradigm and numerous variations upon it have shown that, while dual-task interference is clearly evident in this task, transient *boosts* rather than deficits to image encoding occur when a target is detected (Swallow and Jiang, 2013). In other words, memory for images is boosted by increasing attention to an unrelated stimulus that requires a response (Mulligan and Spataro, 2014; Swallow and Jiang, 2014b).

Though the surprising nature of the ABE is rightly highlighted in the literature, it was predicted by findings in event cognition (Swallow and Jiang, 2010). The human cognitive system divides continuous experience into discrete events in a process known as *event segmentation* (Zacks et al., 2007). For example, an individual watching someone else make dinner may identify a new event (creating an *event boundary*) when the cook switches from gathering ingredients, to chopping onions, and again when the cook pulls out a pan to start sautéing the onions. Event segmentation is known to be critically involved in dynamically regulating a variety of cognitive processes, but most notably attention and memory (e.g., Newtonson and Engquist, 1976; Swallow et al., 2009; Faber et al., 2018).

The ABE was proposed after it had been demonstrated that event boundaries have nearly immediate effects on the ability

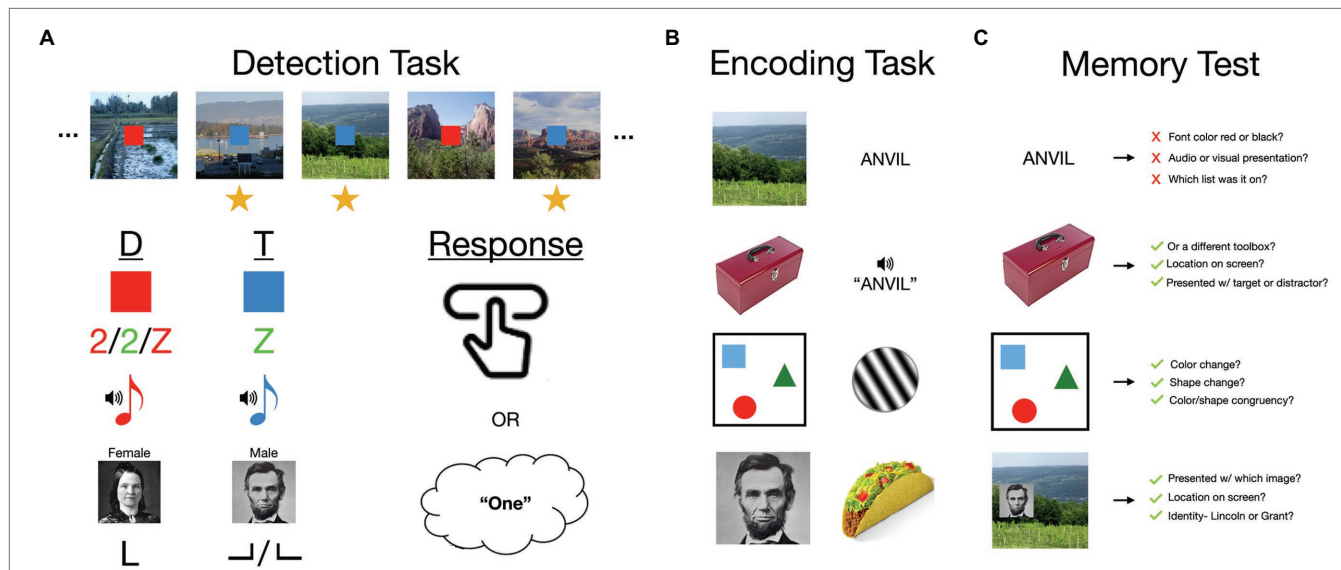


FIGURE 1 | An overview of the *attentional boost effect* (ABE). **(A)** The ABE is most frequently demonstrated in a continuous dual-task for which participants memorize individually presented items (e.g., scenes; 500 ms duration; 0 ms interval) and press a button or add to a mental count when a concurrently presented but otherwise unrelated target cue is presented (e.g., a blue square target rather than a red square distractor). Memory for items presented with a target is typically significantly better than that for items paired with distractors. This paradigm has been varied considerably across studies, demonstrating several key features of the ABE: that the ABE occurs for auditory and visual detection stimuli, when targets and distractors are visually similar, and when they are defined by the conjunction of two features. The ABE can also be observed when participants respond by pressing a button, silently counting, or identifying the targets. **(B)** The ABE or similar effects have also been observed for a variety of stimuli, including short- or long-term memory for scenes, faces, objects, valuable items like food, visually and auditorily presented words, and arrays of colored shapes. Related effects occur in visual habituation to Gabor patches. **(C)** The ABE sometimes includes information that individuates an item from others that are like it, or places it within a specific momentary context. This includes information distinguishing category exemplars from each other, identifying which item appeared with which cues, and where, as well as which features were part of the same object. However, while participants may be able to remember whether a word was paired with a target or distractor, verbal materials do not otherwise appear to result in the same effects. See main text for elaboration on these findings and references to specific studies. Image attributions: Scenes reproduced from the personal library of Khena Swallow with permission, objects from <https://bradylab.ucsd.edu/stimuli.html>, Abraham Lincoln image is in the public domain from https://en.wikipedia.org/wiki/List_of_photographs_of_Abraham_Lincoln#/media/File:Abraham_Lincoln_O-77_matte_colodion_print.jpg, Mary Todd Lincoln image is in the public domain from https://en.wikipedia.org/wiki/Mary_Todd_Lincoln#/media/File:Mary_Todd_Lincoln_1846-1847_restored.png, button click by Schmidt Sergey from <https://thenounproject.com/icon/button-click-691746/>.

to recognize objects in a movie (Swallow et al., 2009, 2011). In these studies, participants watched movies that were interrupted about once a minute for a recognition memory test on an object that had been presented 5 s earlier. Event boundaries had clear effects on object recognition: objects that were visible when an event boundary occurred were remembered better than objects that never overlapped with a boundary, particularly when they had to be retrieved from a prior event. Surprisingly, these effects were present regardless of whether participants had fixated the object when it was originally presented, suggesting that encoding was broadly enhanced at these times. This research demonstrated that the *boundary advantage* in long-term memory for events (Newton and Engquist, 1976; Lassiter and Slaw, 1991) emerged in the moment, as the event unfolded.

These and other data are explained (and were predicted) by models of naturalistic event perception that propose that the brain (and consequently the mind) is, at its core, predictive. In Event Segmentation Theory (EST; Zacks et al., 2007), event segmentation is described as a side effect of a system that minimizes computational demands by regulating memory and perceptual processing. According to EST, actively maintained representations of the current situation, called *event models*, generate predictions about perceptual input in the very near future (seconds or less; see also Zacks et al., 2011; Hasson et al., 2015; Baldassano et al., 2017; Eisenberg et al., 2018). Event models are maintained in a stable state for as long as they adequately predict perceptual information, which reduces energy demands on the system (Friston, 2009). When these predictions begin to fail, the increase in prediction error triggers a mechanism that resets the event model, causing the event to be segmented. The event model is then rebuilt using knowledge about events (e.g., knowledge about how events typically unfold) and incoming perceptual information about the current situation. As a result, representations of events should be most sensitive to perceptual information at event boundaries.

This perspective on event cognition describes how the temporal dynamics of attention and memory may reflect the transition from one stable cognitive and neural state to the next. Like increasingly prominent predictive coding views of cognition (Rao, 2005; Friston, 2009; Clark, 2013) it suggests that, to increase efficiency, the neurocognitive system forms and maintains stable states that guide ongoing perception and behavior (Richmond and Zacks, 2017). These stable states are updated only when the situation changes by temporarily increasing sensitivity to external information (Bouret and Sara, 2005). We propose that insight into the ABE, and the relationship between attention and memory more generally, may be had by directly considering whether it emerges from similar processes.

NEW PERSPECTIVES ON THE ABE

One of the earliest challenges for research on the ABE was accounting for how increasing attention to one task (i.e., a target in a detection task) can enhance performance of another task (i.e., encoding a background item). Though this suggested

that attentional capacity may briefly increase the ability to attend to external stimuli, most research on attention has been directed toward understanding how attending to one task, stimulus, feature, or modality interferes with performing other tasks or processing other information (Kinchla, 1992).

To account for the ABE, Swallow and Jiang (2013) proposed the *Dual-Task Interaction (DTI)* model. The model claims that the attentional systems that prioritize spatial locations and perceptual features operate independently of a mechanism that globally boosts attention at behaviorally relevant moments (*temporal selection*). The DTI model indicates that, in the continuous dual-task encoding paradigm, temporal selection is triggered by the decision that a detection task cue is a target and requires a response. Temporal selection was proposed to result from a phasic burst of activity in the LC, which then increased gain in the signal to noise ratio in perceptual processing. The LC is a brainstem nucleus that is the primary source of norepinephrine (NE) in the brain (Berridge and Waterhouse, 2003) and may be the major source of dopamine (DA) in the HPC (Kempadoo et al., 2016; Takeuchi et al., 2016). Phasic LC activity is most strongly associated with the decision to respond to a stimulus, preceding actions by roughly 100 ms in non-human primates (Rajkowski et al., 2004). Phasic bursts of LC activity occur in response to target detection in non-human primates and are thought to increase the contrast between signal and noise in targeted sensorimotor regions (Aston-Jones and Cohen, 2005). Because the LC projects diffusely throughout the brain (Loughlin et al., 1982; Aston-Jones and Waterhouse, 2016), the DTI model proposed that phasic bursts in LC activity could enhance the processing of all available stimuli in the environment, and these effects may be present even for information that is outside the current focus of attention.

In the nearly 10 years since the DTI model of the ABE was proposed, research has elaborated on the conditions in which the boost occurs, highlighting its generalizability and its specificity (**Figure 1**). At the same time, rapid advances in neuroscience and shifts in theoretical perspectives about the mind motivate new ways to think about the ABE and its relationship to event segmentation. Characterizations of LC structure and function increasingly suggest that it may have more localized effects on processing (Poe et al., 2020), implying that temporal selection could enhance memory in several, potentially independent, ways. These potential effects of the LC on memory are also increasingly grounded in perspectives that characterize the brain as active, predictive, and effort minimizing (Friston, 2009; Clark, 2013). For example, in predictive coding frameworks, the brain minimizes computational effort by generating predictions about the external state of the world that bias processing in a top-down manner. Predictions are compared to information coming in to the system, and actions re-align the system with the current state of the environment (Rao, 2005; Friston, 2009; Clark, 2013). In this framework, neuromodulatory systems like the LC may be involved in regulating the relative balance between top-down expectations and bottom-up sensory information (Clark, 2013).

These and similar developments in the literature on the ABE and the LC prompt several elaborations on the DTI

model. In the rest of this review, we therefore evaluate the DTI model in light of these new perspectives and both behavioral and neurophysiological evidence regarding the source of the ABE and its potential influences on memory. In many cases, the data motivate several updates to the original DTI model, which we present and illustrate in **Figure 2** as the *Dual-Task Interaction Model 2.0*. In addition to suggesting that the ABE reflects a boost to perceptual processing, new developments in the behavioral and LC literatures suggest the possibilities that the ABE includes some aspects of episodic memory, interacts with goal-based attention, and could modulate the stability of neurocognitive states over time. We discuss each of these in turn, and describe how particular aspects of the ABE may emerge from the interaction of the LC with other systems (**Figure 2B**). We then describe how these developments also clarify the relationship between the ABE and event segmentation, suggesting several new avenues for investigating how attending to behaviorally relevant moments, such as when targets appear or events change, influences the uptake and encoding of information from the world.

WHAT PRODUCES THE ABE?

The DTI model proposed that the ABE reflects phasic LC activity, and that this activity is elicited by the decision to respond to a target cue. Relative to distractor rejection, however, target detection involves multiple processes that could be the source of the ABE. Furthermore, the nature of a “response” and how it relates to the cognitive and neural states evoked in the continuous dual-task encoding paradigm needs further elaboration.

One important possibility is that the ABE is not a boost at all. Instead, it could reflect interference from distractors rather than a boost from a target. Memory for distractor-paired items is worse than memory for items encoded under single-task conditions (Swallow and Jiang, 2010), and related phenomena have been attributed to inhibition or forgetting associated with distractor rejection (Kiss et al., 2007; Chiu and Egner, 2014). However, when a no-cue baseline condition was introduced to the dual-task encoding paradigm, memory for target-paired images was better than memory for no-cue images, although there was some evidence that distractors may interfere with memory (Leclercq and Seitz, 2012c; Swallow and Jiang, 2014b; Rossi-Arnaud et al., 2018; Meng et al., 2019). An advantage for target-paired words relative to words presented in a single task has also been found when study time is sufficiently limited (400 ms/trial; Mulligan and Spataro, 2014) and in measures of perceptual priming (Spataro et al., 2013). Thus, target detection produces a true encoding enhancement, but its effects may be washed out by processes that require sufficient time or attention to take effect.

One of the first questions to arise about the ABE was the degree to which it is driven by the contextual distinctiveness of the target (e.g., as in the von Restorff effect; Hunt, 1995). However, the ABE is easily replicated when targets and distractors are equally frequent (Makovski et al., 2011; Swallow and Jiang, 2012), though one study found that it decreases as the frequency

of targets increases (Au and Cheung, 2020). The effects of target detection are also present for words that are distinct from other words presented during the encoding task (e.g., “building” in a list of animals), suggesting that they involve separable mechanisms (Smith and Mulligan, 2018). An exception is that a rare tone (occurring on 1 out of 8 trials) may boost immediate memory for coinciding scenes (Hoffing and Seitz, 2015). Thus, the evidence shows that the ABE is not simply a matter of targets “popping-out” out from distractors, though it may be modulated by the salience of the stimuli.

Because the ABE is connected to targets in these tasks, the effect could be triggered by detection task cues that partially, or completely, match the features that participants are told to search for. This is unlikely. Images paired with distractors that share features with a target are no better remembered than those paired with distractors that do not (Swallow and Jiang, 2014a). Moreover, in another study, the presence of a target was dissociated from the button press by telling participants to press a button only when there was no target on the screen. Under these conditions, memory for images that were paired with a target was impaired (Toh and Lee, 2022). This suggests that partial or full matching of items to a target stimulus is not sufficient for producing the ABE.

This research highlights, however, that another way that targets often differ from distractors is that responding to a target often involves an overt action (usually a button press). As a result, its effects have sometimes been attributed to the movement itself (Yebra et al., 2019). However, overt action is neither necessary nor sufficient for the ABE. Several studies have demonstrated that memory for items is enhanced when they coincide with a target that is covertly counted (Swallow and Jiang, 2012; Mulligan et al., 2016; Swallow et al., 2019; Toh and Lee, 2022), or whose identity is reported several seconds later (e.g., they name the white letter in a string of black letters; Lin et al., 2010). Furthermore, overt action in and of itself is not sufficient to enhance memory. One study reversed the relationship between an overt action and target detection by asking participants to press a button for all images (e.g., scenes and male faces) except when the image was in a pre-specified target category (e.g., female faces). Target faces, which required withholding a button press, were better remembered than distractor faces, which required producing one (Makovski et al., 2013). The ABE also has been found in studies that required participants to read aloud all words (Mulligan et al., 2014). In another study, increased visual cortical activity following auditory target detection was not observed following self-generated button presses (Swallow et al., 2012). Overt actions and target detection thus fail to produce the ABE and its neurophysiological correlates on their own.

The ABE thus appears to originate from the decision to respond to a cue or stimulus. We agree with Toh and Lee (2022) that the DTI model should be updated to better highlight the role of the response in the ABE rather than of a target. But, what exactly is a response? Answering this question requires addressing both when a response occurs, and what a response entails. Drawing on the event cognition and predictive coding literatures, we suggest that a response

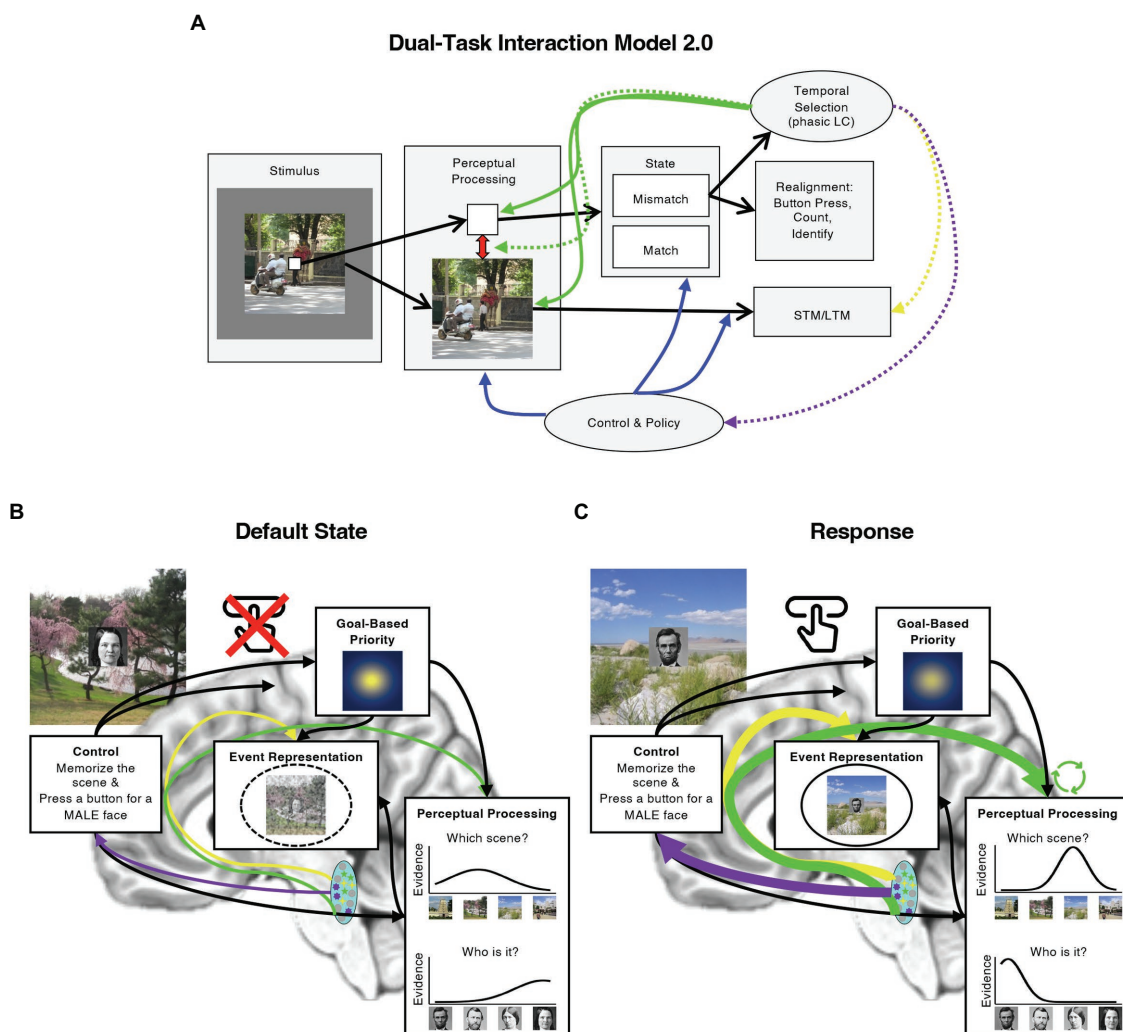


FIGURE 2 | Updating the Dual-Task Interaction Model. **(A)** Illustration of the original DTI model (Swallow and Jiang, 2013) with several proposed modifications (Dual-Task Interaction Model 2.0). Like the original DTI model, we assume that presenting multiple items at once results in competition among them (red arrow in “Perceptual Processing” box; e.g., Buschman and Kastner, 2015), that control mechanisms instantiate the task by guiding attention and processing in a top-down manner (“Control and Policy” box and arrows leading from it; e.g., Badre and Nee, 2018), that temporal selection facilitates perceptual processing by increasing gain and consequently sensory precision (green arrows to “Perceptual Processing” box), and that this effect is generated by phasic LC activity. We further specify that temporal selection occurs when mismatches between the state of the world and the state of the neurocognitive system (“State” second box from the right) require a response to bring them back into alignment (“Realignment,” far right box) and that these responses may enhance the formation of bound, multi-item representations of items in the MTL (yellow dashed arrow). Computational models further suggest that phasic LC increases competition between attended and unattended items (green dashed arrow; Mather et al., 2016) or promote shifts to new neurocognitive states by briefly weakening top-down influences (purple dashed arrow; Shine et al., 2016). We note that the former possibility is based on paradigms with different timings and that there is currently little evidence to support the latter possibility. We include it for completeness. **(B)** An example of the default state of the system when the task is to both memorize scenes and press a button for male, but not female faces. Once a continuous encoding dual-task has been started, the default state of the system is to prioritize the images and faces (illustrated by the “Goal-Based Priority” box), and to withhold a button press until there is enough perceptual evidence that a male face has been presented. Perceptual processing results in image specific evidence for both faces and scenes, and these are bound to each other and their context in the MTL. **(C)** An example of the state of the system when a response must be generated. Under these conditions, we propose that phasic LC activity (blue oval) increases sensory precision in perceptual areas (green arrow; indicated by the taller, narrower evidence curve). These effects could be greater for prioritized information (green circular arrows). The result is richer sources of information for episodic encoding (“Event Representation”) in conjunction with direct enhancements to the formation of bound event memories (solid circle; it is dashed in panel **B**). It may also be possible that phasic LC activity disrupts the influence of control representations, weakening top-down biases in stimulus processing (illustrated by the weaker spotlight in the “Goal-Based Priority” box). Each of these effects could arise from LC cellular ensembles that project to different regions of the brain, regardless of whether they are independently or globally activated (illustrated with differently colored cells in the LC; see “Modular circuitry and function in the LC”). Image attributions: As in **Figure 1**, additionally, Ulysses Grant image has no restrictions from <https://www.loc.gov/pictures/item/2017896375/>, and Julie Grant image CC0 from https://npg.si.edu/object/npg_NPG.81.M819.

occurs when external events create a discrepancy between the current state of an organism (for example, the system may be in a “count the red letters” state) and its relationship

to the world (a red letter has appeared, but it has not been counted, vs. a red letter has appeared but it does not need to be counted). This definition focuses on the relationship

between the organism and the world because responses do not (and should not) occur for all types of changes in the environment (Rao, 2005; Friston, 2009; Kok et al., 2012; Clark, 2013; Baker and Levin, 2015). A stranger walking to a snack table at a crowded party may not have been predicted, but the event may also not be attended, and may be irrelevant to one's current state. Therefore, no response would likely be generated. Rather, the mismatches that lead to response generation are those that are most relevant to understanding a situation as it relates to one's goals (explicit or implicit), motivation, or predispositions.

Responses entail the transient mobilization of the appropriate neurocognitive, sensory, and/or effector systems to align an organism with the changed state of the world (cf. Clark, 2013; Varazzani et al., 2015; Xiang et al., 2019). The end result could be a button press (Yebra et al., 2019), incrementing an internally maintained count (Swallow and Jiang, 2012), halting repeated button presses (Makovski et al., 2013), judging how common rather than how likeable an object is (e.g., DuBrow and Davachi, 2016), or even the updating of event models (which organize perception and action) when they fail to reflect the current situation (Zacks et al., 2007; Richmond and Zacks, 2017; Baldwin and Kosie, 2020). As these examples illustrate, some responses may entail a brief mobilization of effort but without a change in how an actor interacts with the world (e.g., the task is still to count red letters), whereas others may result in larger shifts that change response contingencies (e.g., the task itself changes to judging pleasantness). We return to the potential implications of this distinction in "*How the ABE relates to the effects of event boundaries on episodic memory*." Like earlier work, this proposal suggests that responses trigger temporal selection because they require participants to do something different than what they were doing before (Swallow and Jiang, 2012; Makovski et al., 2013; Toh and Lee, 2022). However, by emphasizing the discrepancy between an organism's internal state and the state of the world, this definition provides a more explicit basis for thinking about the ABE in a broader cognitive and evolutionary context.

Despite defining response to include both cognitive and behavioral outcomes, it is possible that covert responses are generated by systems that, in the phylogenetic past, evolved to generate overt actions. In many invertebrates, spatially distributed neuromodulatory systems disrupt functional neural states so new states can be created and new motor behaviors generated (Katz, 1991; Bouret and Sara, 2005). In vertebrates, neuromodulatory systems carry significant anatomical and neurochemical homology to neuromodulatory systems in older life forms (Katz, 1991). Evidence from mammals, including primates (Clayton et al., 2004; Joshi and Gold, 2022), shows that activation of the LC can promote shifts from one cognitive state to another, similar to neuromodulatory-driven shifts from one motor pattern to another in crustaceans (Bouret and Sara, 2005). Indeed, many systems involved in cognitive control and attention in primates may involve motor control and planning systems (Frank et al., 2001; Anderson, 2010; Krauzlis et al., 2013).

We note that some evidence may be inconsistent with this characterization of the ABE. One study suggests that

endogenously orienting attention to the moment when a target is expected to appear may enhance memory to a comparable degree as responding to a target (Sisk and Jiang, 2020). Hoffing and Seitz (2015) also found better memory for scenes paired with an oddball tone. Furthermore, though rewarding participants for their rapid responses to targets does not appear to increase the magnitude of the ABE (Yebra et al., 2019), other findings suggests that the effect of target detection on memory may be weaker for arousing, aversive, or unusual stimuli (Mulligan et al., 2014; Spataro et al., 2014; Rossi-Arnaud et al., 2018; Yebra et al., 2019), implying overlapping sources. We suggest that some of these events may be stronger indicators than others of a mismatch between the current state of the system and the state of the world, and that a response of some sort may be needed, even if that response is not defined by the task. Indeed, salient, unexpected stimuli have long been linked to the phasic activation of the LC system and increased flexibility in cognitive state (Bouret and Sara, 2005). Careful consideration of this and other possibilities in future research will help further characterize the relationship between variations in attention over time and the encoding of information from the environment.

Finally, the original DTI model also suggested that temporal selection may be more strongly enabled by the regular onset of trials in the continuous dual-task encoding paradigm (Swallow and Jiang, 2013). Attentional selection may be more efficient if it can capitalize on the rhythmic structure of experience (e.g., in eye movements; Schroeder et al., 2010; Besle et al., 2011; Zion Golumbic et al., 2013). Oscillatory activity in the brain also appears to play an important role in regulating the updating of information over time and space generally, and of phasic LC activity specifically (Buschman and Kastner, 2015; Sara, 2015; Totah et al., 2018). However, direct evidence that the ABE is stronger with rhythmic processing has yet to be published, and the findings that led to this proposal (Makovski et al., 2011; Swallow et al., 2012) may be explained by the longer duration of trials in these paradigms (Mulligan and Spataro, 2014). Additional research is therefore needed to characterize the relationship between temporal selection and oscillatory brain activity.

Evidence That the ABE Is Tied to Phasic LC Activity

The proposal that the ABE reflects phasic LC activity (Swallow and Jiang, 2010) stemmed from the contemporaneous view that afferent projections from the LC contacted nearly every part of the brain (with the exception of the striatum), including perceptual areas, and appeared to be relatively undifferentiated in their behavior (Aston-Jones and Cohen, 2005). This pattern, in conjunction with the clear relationship between phasic LC firing and decisions to respond to targets (Rajkowski et al., 2004; Aston-Jones and Cohen, 2005), suggested that the LC system could reasonably support the temporally precise, but spatially diffuse, effects that were hypothesized to produce the ABE. In this section we review evidence for whether the ABE is related to phasic LC activity.

Though there has been a burgeoning interest in characterizing the cognitive mechanisms of the ABE and its impact on memory,

only a handful of studies bear on its neurophysiological basis. Most of these have used an indirect measure of LC activity, pupil size, which increases with activity in the LC (Murphy et al., 2014; Joshi et al., 2016). Hoffer and Seitz (2015) found increased pupillary responses and better immediate recognition memory for images that were paired either with an alphanumeric target (e.g., a letter), or with an unexpected sound, than for other images. Swallow et al. (2019) came to a similar conclusion with covert counting of auditory targets and an extended encoding period before a final recognition memory test. Larger pupillary responses to targets than distractors only occurred when the scene was subsequently remembered rather than forgotten. Similar results were reported by Yebra et al. (2019) who found that encoding related pupil dilation was greatest when a subsequently remembered object was paired with a cue to press a button.

Linking the ABE to phasic increases in pupil diameter supports its association with phasic LC activity, but is not sufficient. Though LC activity drives changes in pupil size, pupil size ultimately reflects the combined effects of several neuromodulatory systems and subcortical structures (Larsen and Waters, 2018), is correlated with activity throughout the brainstem (de Gee et al., 2017), and can produce correlation maps that differ from those produced by LC activity (Turker et al., 2021). Furthermore, studies examining the relationship between the ABE and cardiovascular activity, which suppresses LC activity during the systole phase of the cardiac cycle, have provided mixed results (Li et al., 2018, 2020).

More direct measures of activity in the LC are needed to evaluate the hypothesis that the LC is involved in generating the ABE. This can be found to some extent in fMRI studies examining the effects of target detection on BOLD activity. In one study, auditory target tones, but not distractor tones or no tones, increased BOLD activity in LC regions defined using neuromelanin imaging (Moyal et al., in press). These conditions also increased BOLD activity in early visual processing regions (Swallow et al., 2012; Moyal et al., in press). Ventromedial prefrontal cortex may also be preferentially activated by target-paired images (Schonberg et al., 2014). Yebra et al. (2019) further demonstrated an interaction between cue (target vs. distractor) and subsequent memory in activation of brainstem voxels consistent with the LC. These effects are consistent with known LC projections and support the idea that LC activity, when engaged, makes the difference between a stimulus being remembered and a stimulus being forgotten. This conclusion is broadly consistent with findings that schizophrenia, bipolar disorder, and aging, which can sometimes negatively impact LC function, are associated with a reduction in the magnitude of the ABE (Rossi-Arnaud et al., 2014; Bechi Gabrielli et al., 2018, 2021; Prull, 2019).

Notably, there are characteristics of LC activity that have not yet been investigated in the ABE, or for which there is little evidence that they play a role in the effect. One major point of disconnect is that phasic LC responses are larger when targets are less frequent (Berridge and Waterhouse, 2003). Few studies have directly compared the impact of rare versus frequent targets on the magnitude of the ABE. However, two

studies found comparable ABEs in both short-term and long-term memory tasks for rare and frequent targets (Makovski et al., 2011; Swallow and Jiang, 2012), while a third study suggested that frequent targets produce a smaller boost in long-term memory (Au and Cheung, 2020). Computational modeling suggests that phasic LC responses to Go cues should occur even when they are slightly less frequent than No-Go cues (Sales et al., 2019), so it is possible that stronger manipulations are needed to consistently observe these effects in the ABE. Another, related characteristic of phasic LC activity is that it habituates over time (Berridge and Waterhouse, 2003). There is relatively little research on habituation in the ABE paradigm. However, one study did not find a reduction in the encoding boost when a target was preceded by several target cues rather than distractor cues (Yebra et al., 2019). Finally, the timing of the effects of phasic LC activity on how information is processed and encoded into memory is far from clear. Non-human animal research suggests that phasic LC activity could influence processing as much as 300 ms after the onset of a stimulus (Devilbiss and Waterhouse, 2011). However, images that appear 100 ms after a target are not better remembered than those that appear immediately after a distractor (Swallow and Jiang, 2011), unless the cue remains on the screen when the image is presented (Yebra et al., 2019). These are important characteristics of phasic LC activity that should be examined in future research.

Though we have focused on the LC, many characteristics of LC function overlap with those of the DA, serotonergic, and cholinergic systems, and all of these may interact with each other (Briand et al., 2007). For instance, detection of Go cues in Go/No-Go paradigms produces brain-wide DA neuromodulation (e.g., Guitart-Masip et al., 2012), which impacts attention (Niv et al., 2015). Serotonin may also play an enabling role in visuo-spatial processing (Park et al., 1994). Like NE, acetylcholine enhances attentional precision and transiently biases HPC dynamics to boost encoding (Hasselmo and Sarter, 2011; Decker and Duncan, 2020). Nevertheless, there are also important differences between neuromodulators. For example, acetylcholine may aid in the maintenance of a given brain state whereas NE may not (Munn et al., 2021). Thus, although we currently consider phasic LC activity to be the most promising candidate for generating the ABE, other systems may also play a role. Future research is needed to tease apart the influence of each system.

How Might Responses Boost Memory in the ABE?

Though research on the ABE suggests that responses are necessary to produce it, it is unclear how responses boost memory. The DTI model suggests that the cognitive mechanism responsible for the ABE is *temporal selection*, which prioritizes the perceptual processing of information that is encountered at a specific time. It also proposes that temporal selection reflects the phasic release of NE from the LC. Because the ABE is most frequently examined with memory measures, however, it could reflect effects on a variety of perceptual and

cognitive processes that intervene between the presentation of an item and performance on the memory test. These possibilities are explored in the next sections.

As will become evident, the proposal that the ABE results mainly from a boost to perceptual processing does not clearly address several new findings from the literature. However, current research describes several ways that phasic LC activity could influence memory encoding. These include the potential role of the LC in (1) modulation of perceptual regions, boosting bottom-up signal from the external environment, (2) modulation of HPC sensitivity to new environmental information, promoting the formation of new mental models of the external environment or events in memory, and (3) further enhancing the effects of goal-directed attention and salience on competitive interactions in perceptual processing. The effects of LC activity on the ability to shift to new cognitive states may also provide additional insight into the relationship between the ABE and event segmentation. We discuss each of these possibilities and their relationship to extant data in the following sections. We emphasize, however, that these mechanisms are not necessarily mutually exclusive and their effects may be independent of or in conjunction with others.

PERCEPTUAL PROCESSING MAY BE BOOSTED IN THE ABE

Research on the ABE provides broad consensus on two aspects of what it captures: that its effects generalize to information presented across modalities and materials, and that its effects on encoding occur, at the least, early on. The ABE has been generalized to a broad spectrum of encoding materials, including arrays of colored shapes, objects, faces, and visually and auditorily presented words (e.g., Mulligan et al., 2014; Li et al., 2018; Sisk and Lee, 2021; Spataro et al., 2021; **Figure 1B**). However, it does not appear for all types of stimuli equally. For example, in a series of studies examining the ABE for words, Mulligan and colleagues showed that the ABE is stronger for high frequency words than low frequency words (Mulligan et al., 2014; Smith and Mulligan, 2018) and is reduced for orthographically distinctive words (Spataro et al., 2014), which are thought to attract attention early in encoding. The ABE therefore appears to influence memory for a wide range of stimuli, but may have larger effects on items that would otherwise be more poorly remembered.

Still other evidence suggests that the ABE enhances early encoding mechanisms. The ABE is present only for displays that overlap with a target in time: it is not observed when the target appears immediately before an image, immediately after an image, during the retention interval, or during retrieval (Makovski et al., 2011; Swallow and Jiang, 2011). The ABE also appears to be stronger when trials are shorter and elaborative processing is limited. In a particularly informative study with verbal materials, Mulligan et al. (2014) found that the magnitude of the ABE decreased as trial duration (and consequently encoding time) increased. Increasing encoding time resulted in greater gains for distractor-paired words than for

target-paired words, suggesting that whatever generates the ABE, its benefit can be offset by later processes. This finding is consistent with an effect of temporal selection on early encoding processes. However, limiting the opportunity to encode an item too much may reduce or eliminate the ABE with visual materials: the ABE is weak when encoding time is limited to 250 ms (Hutmacher and Kuhbandner, 2020).

Evidence for early effects on encoding also can be found in tasks that are sensitive to perceptual processing. The ABE has been observed in implicit measures of perceptual priming but not in measures of conceptual priming (Spataro et al., 2013, 2017). The ABE also incorporates enough perceptual information to allow people to better distinguish scenes from their mirror-reversed counterparts (Swallow and Jiang, 2010) and exemplars within the same category of objects (Sisk and Lee, 2021) or faces (Turker and Swallow, 2019). However, these effects may not generalize to the color, font, or modality of verbal materials (Mulligan et al., 2016). Target detection also enhances visual short-term memory for faces, arrays of 3 or 5 colored squares, and combinations of shape and color (Makovski et al., 2011; Li et al., 2018; Spataro et al., 2020). Psychophysical studies are also consistent with an effect on perceptual processing. Perceptual learning of sub-threshold visual features is enhanced following their repeated pairing with targets in an unrelated detection task (*task-irrelevant perceptual learning*; Seitz and Watanabe, 2009). Target detection has also been shown to increase habituation to tilted gratings (Pascucci and Turatto, 2013). Finally, detecting a target (e.g., an auditory tone) increases BOLD activity in perceptual regions of the brain that would not normally be involved in processing it (e.g., primary visual cortex; Swallow et al., 2012; Moyal et al., in press).

In summary, consistent with the DTI model, a wide range of data and measures suggest that the condition that generates the ABE—responding to a cue—influences perceptual processing. As a result, its effects extend to a wide variety of materials, across modalities, and emerges in multiple measures. This is true as long as later processing is sufficiently limited by dual-task interference or brief trial durations and the items are not inherently likely to attract attention early in encoding (e.g., Smith and Mulligan, 2018).

Increasing Sensory Precision by Boosting Gain in Perceptual Areas

Like the original DTI model we suggest that the early effects of responses on perceptual processing reflect the phasic release of NE in perceptual processing regions of the brain (Swallow and Jiang, 2013; green lines in **Figure 2**). In this way, the phasic release of NE may increase the influence of sensory information on higher level processing, allowing it to more strongly influence representations that capture the state of the world (e.g., event models).

This proposal is consistent with a large number of findings on the impact of LC on sensory processing (Waterhouse and Navarra, 2019). When background LC activity is moderate, NE increases the excitability of sensory neurons and suppresses spontaneous discharge, resulting in an increase in the signal

to noise ratio, or sensory gain, in these regions (Berridge and Waterhouse, 2003; Aston-Jones and Cohen, 2005; Devilbiss, 2019). LC activity has also been shown to sharpen the receptive fields of sensory neurons and increase functional connectivity between thalamic and cortical sensory neurons (Hurley et al., 2004; Devilbiss, 2019). In one study using optogenetics, phasic activation of the LC resulted in sensory neurons exhibiting enhanced responses to sensory input, comparable to the effects of increasing stimulus intensity (Vazey et al., 2018). Human neuroimaging data also suggest that NE modulates sensory gain and enhances sensory precision, or the amount of information that can be decoded from neural activity (Eldar et al., 2013; Warren et al., 2016). However, it should be noted that both studies were more focused on the impact NE availability over extended, rather than brief, periods of time. This literature suggests that the phasic activation of the LC following the decision to respond to a cue during an encoding task could increase sensory precision. Consistent with this possibility, responding to auditory targets boosts LC activity and the amount of decodable information in patterns of activity in ventral visual cortex (Moyal et al., in press). As a consequence, systems involved in encoding these moments into memory may have a richer, more detailed perceptual representation with which to work.

However, relatively few studies have directly examined the effects of temporal selection on perceptual processing, or its relationship to phasic LC activity. Future research should further investigate the impact of responses on the momentary availability of perceptual information for encoding using more proximate and sensitive measures of visual and auditory processing. Characterizing how responses and context changes modulate the quality and quantity of information processing in psychophysical studies, or how they impact decision thresholds and evidence accumulation rates in perceptual decision making would also be informative.

TEMPORAL SELECTION MAY ALSO DIRECTLY ENHANCE EPISODIC MEMORY

If the ABE is related to the effects of boundaries on event memory, then it may capture information about the event in which an item was encountered, not just the item itself (Rubin and Umanath, 2015; Moscovitch et al., 2016). There are several aspects of encoding that contribute to episodic memory, including those that bind features of objects (Erez et al., 2016), that bind items to their spatial or temporal context in episodic memory (Eichenbaum, 2004; Hannula et al., 2007), or that prioritize valuable items for subsequent memory (Shohamy and Adcock, 2010). The available data suggest that some, but not all, of these mechanisms could be at play in the ABE.

Responding to targets may facilitate the binding of object features, like color and shape, into object representations. Participants are better able to report a task-irrelevant feature of a target than a distractor (e.g., the shape of the cue when

color defines whether the cue is a target or distractor; Turker and Swallow, 2019). A short-term memory study (Spataro et al., 2020) found responses during encoding may improve participants' ability to report when two items on the screen swapped colors, a condition that may reflect feature binding (cf. Wheeler and Treisman, 2002). These effects seem unlikely to be limited to short-term memory, as responding to targets also enhances the ability to distinguish within category exemplars (Sisk and Lee, 2021). This suggests that responses can facilitate the binding of features of visual stimuli into a unified representation that individuates them from others, an ability that contributes to episodic memory (Erez et al., 2016).

One study suggests that responses do not enhance memory for the perceptual features of words (Mulligan et al., 2016). However, visual materials may produce different results (cf. Intraub and Nicklos, 1985; Weldon et al., 1995; Onyper et al., 2010; Baddeley and Hitch, 2017) perhaps because participants may prioritize different types of information when memorizing visual rather than verbal materials. This explanation implies that the ABE interacts with goal-directed attention, a possibility that we discuss in "*Goal-directed attention modulates the effects of temporal selection on encoding*." Additional research is needed to understand the discrepancy between the effects reported with words and with visual stimuli, and to ensure that findings demonstrated with one type of stimulus generalize to the other.

Episodic memory includes the ability to bind items to their locations or to other items on the screen (Konkel and Cohen, 2009; Ranganath, 2010). There is mixed evidence that this type of binding is enhanced in the ABE. Several studies have demonstrated that participants are more likely to report that an item was paired with a target during encoding when it actually was presented with a target rather than a distractor (Swallow and Atir, 2018; Turker and Swallow, 2019; Mulligan et al., 2021). However, this specific effect could reflect a strength-based inference that better remembered items were more likely to have been paired with a target rather than a distractor cue (Mulligan et al., 2021). Other evidence cannot be attributed to such an inference. In these studies, a target-related advantage was found when participants were asked to distinguish between two options that were unrelated to whether the image was presented with a target or distractor: on which side of the screen a scene appeared (Leclercq et al., 2014), where the detection task cue appeared relative to the scene, and the identity of the cue itself (Turker and Swallow, 2019). These findings align with work showing that participants' subjective ratings of memory quality are enhanced for target paired items (Leclercq et al., 2014; Meng et al., 2019; Yebra et al., 2019; Broitman and Swallow, 2020). Together, these results imply that the ABE can sometimes incorporate the momentary context in which an item appeared.

In contrast, it appears unlikely that temporal selection enhances episodic memory through other means. Current evidence argues against responses enhancing the formation of inter-item associations (Mulligan et al., 2016; Spataro et al., 2021) or access to semantic associations (Spataro et al., 2017), at least with verbal materials. Thus, any effect of responses on binding items to their context may be limited to information presented in that moment. We note,

however, that whether target detection boosts temporal context memory for visual materials has not been adequately tested and there is some evidence that it could. Several studies demonstrating an ABE did so with a task that required participants to know not just that a scene had been presented, but whether it was presented on the previous trial (Lin et al., 2010; Leclercq and Seitz, 2012b; Hoffing and Seitz, 2015). The ABE in these tasks could thus reflect better memory for when an image was presented.

Another possibility explored in the literature is whether the ABE enhances memory by modifying the perceived value of items that appear with targets relative to distractors. Pairing an image with a target cue rather than a distractor cue increases its perceived value (*cued approach*; Schonberg et al., 2014), leading to a willingness to pay more for it, greater liking and trust ratings for faces, and greater wanting ratings for objects (Swallow and Atir, 2018; Li et al., 2020; Botvinik-Nezer et al., 2021). This raises the possibility that the ABE is due to changes in the perceived value of target-paired items (cf. Shohamy and Adcock, 2010). However, the evidence indicates that value does not improve image memory in the standard ABE paradigm (Swallow and Atir, 2018) and that the effect of responses on perceived value reflects better memory for these items, rather than the reverse (Botvinik-Nezer et al., 2021).

The behavioral data thus suggest two possibilities: (1) consistent with the DTI model, temporal selection boosts perceptual processing only, resulting in a richer source of information for subsequent binding and episodic memory formation mechanisms to act on; and (2) temporal selection additionally facilitates the formation of bound, multi-item representations in memory. Neural data provide some support for the latter possibility: to the extent that the HPC and broader MTL support the formation of bound episodic representations, findings that responding to a target increases connectivity between the parahippocampal gyrus and putative LC (Yebra et al., 2019), and between the HPC and visual cortex (Moyal et al., in press) provide evidence that its impact is not limited to early visual or auditory cortical activity. If this is the case, then the original DTI model may be incomplete.

Direct Modulation of Episodic Encoding in Medial Temporal Lobe

The original DTI model suggests that temporal selection enhances memory encoding by improving or speeding perceptual processing. However, observations that temporal selection enhances key characteristics of episodic memory points to the involvement of processes that individuate remembered items and events, tying together what was present and where. Because this ability is critically dependent on the HPC and MTL (Moscovitch et al., 2016) we propose that, in addition to boosting perceptual processing, temporal selection may directly enhance encoding in the MTL (yellow line in **Figure 2**). Like event models, the resulting representations may then contribute to internal characterizations of the current state of the world and how one may act within it.

The involvement of phasic LC activity in episodic memory formation has received growing support in the non-human

animal and neuroimaging literatures. The LC projects directly to the HPC, and may be the primary source of DA and NE in the dorsal hippocampus in rodents (Kempadoo et al., 2016; Takeuchi et al., 2016; Seo et al., 2021). LC activity enables the recognition of novel environments (Grella et al., 2019) and learning new contexts and spatial layouts (Kempadoo et al., 2016; Takeuchi et al., 2016; Wagatsuma et al., 2018). Phasic LC activity has also been tied to shifts in HPC representations, allowing animals to associate learning periods with separate episodes in memory (Grella et al., 2019). Activation of LC neurons appears to enhance stimulus related activity in the HPC tens of milliseconds later (Quinlan et al., 2019) and impact theta and gamma oscillatory activity in CA1 subfield (Sara, 2015). These results have been interpreted as implying an attentional role of phasic LC activity in HPC mediated associative memory (Kempadoo et al., 2016; Quinlan et al., 2019).

There is also growing evidence that the LC modulates hippocampal processing in humans. In addition to findings that responses to cues may increase connectivity between the MTL, the LC and visual cortex (Yebra et al., 2019; Moyal et al., in press), LC activity is correlated with activity in the HPC during rest (Jacobs et al., 2015; Turker et al., 2021). Degradation in the LC has been further linked to cognitive impairments in dementia (Jacobs et al., 2015; Giorgi et al., 2017) and individual variability in a range of memory performance measures in older adults (Mather et al., 2016; Lee et al., 2018; Dahl et al., 2019). These findings may provide some insight into the reduced ABE in older adults (Bechi Gabrielli et al., 2018; Prull, 2019). LC-NE release may also increase the likelihood that an old object will be perceived as new and increases the ability of the HPC to distinguish similar stimuli and contexts from each other (i.e., pattern separation; Yassa and Stark, 2011; Segal et al., 2012; Jefferies and Di Lollo, 2018).

These data point to a critical role of the LC in memory encoding and consolidation in the MTL. However, there are many differences between the paradigms in which LC contributions to HPC dependent memory have been shown in non-human animals, and those involved in the ABE. One important question is whether LC modulates episodic memory for smaller shifts in task demands, like the presentation of a cue requiring a response, or only occurs for more salient changes, like entering a novel environment or encountering an aversive stimulus. Another concern is whether temporal selection during encoding results in better consolidation of items presented with, before, or after the cue to respond. Many (but not all, cf. Mather et al., 2016; Grella et al., 2019; Quinlan et al., 2019) of the studies examining LC's contributions to episodic memory focus on its role in memory consolidation, which is enhanced for information presented prior to emotionally arousing events (Anderson et al., 2006; Mather et al., 2016). Investigations directly examining the effects of temporal selection on representations in the MTL, as well as its influence on pattern separation and pattern completion are needed. Furthermore, examinations of how the ABE changes with more salient cues and delay intervals of 24h

or more could better characterize its relationship to arousal and memory consolidation.

GOAL-DIRECTED ATTENTION MODULATES THE EFFECTS OF TEMPORAL SELECTION ON ENCODING

The original DTI model proposes that temporal selection operates independently of, or along-side, mechanisms that prioritize locations and features in a scene. This proposal stemmed from the observation that attending to a target in a detection task resulted in better memory for other unrelated information presented at that time. However, it also implies that, like the boundary advantage (Swallow et al., 2009, 2011), the ABE could incorporate information that is outside the current focus of attention. The results of studies investigating this issue have been mixed: some studies report a boost to ignored or task-irrelevant information (Dewald et al., 2013; Swallow and Jiang, 2014a; Walker et al., 2017; Turker and Swallow, 2019; Yebra et al., 2019; Broitman and Swallow, 2020), others report no effect of target detection on memory for ignored images (Swallow and Jiang, 2011; Leclercq and Seitz, 2012a; Huttmacher and Kuhbandner, 2020), and one study found poorer memory for ignored background words paired with targets (Dewald et al., 2011).

One factor that may account for the variety of effects of target detection on incidental memory is whether the images could be attended despite instructions to ignore them. As argued by Huttmacher and Kuhbandner (2020), the presence of an ABE for incidentally presented images may depend on how long, and how many times, they are presented. When participants were instructed to memorize the objects presented in 250 ms long trials, they showed a small memory advantage (~2%) for objects that appeared with a target. No effect was observed when the objects were ignored. The authors suggested that participants may attend to irrelevant items that are presented multiple times or for longer durations. Consistent with this argument, those studies that have shown an ABE for incidentally encoded images have typically presented them more times or with longer trials than those that have not.

However, the small magnitude of the ABE with 250 ms long trial durations raises another possibility: that the ABE depends on having sufficient opportunity to encode the images, even when they are intentionally memorized. If the mechanisms that generate the ABE are engaged by the response (Toh and Lee, 2022), then presenting a new image every 250 ms could disrupt the effect. Indeed, the ABE may be modulated by the opportunity to encode the images even when participants are instructed to memorize them. In a series of experiments, Broitman and Swallow (2020) found that a response-related boost to recollection, but not familiarity, was comparable for intentional and incidental encoding instructions. However, for intentionally encoded faces the recollection effect was present only when participants had sufficient time (2000 ms total) to study the face, whether within a single study trial, or spread

out across two. Others also have reported greater recollection, but not familiarity, rates in surprise memory tests of target-paired objects presented for 1 s (Yebra et al., 2019). These findings are consistent with research suggesting that visual memory for complex scenes can require longer than 250 ms to be established even when tested immediately (Liu and Jiang, 2005), and that context memory may require sufficient encoding opportunity to manifest (Malmberg and Nelson, 2003; Litman and Davachi, 2008).

Whether the ABE can incorporate information that is outside the current focus of attention is therefore unresolved. We believe, however, that the bulk of the evidence supports two conclusions for now. First, target detection does not reliably increase dual-task interference for ignored background images. This was true even when ignored images were presented very briefly and/or only one time (e.g., Yebra et al., 2019; Broitman and Swallow, 2020; Huttmacher and Kuhbandner, 2020). Second, at the least, goal-directed attention to the background item increases the magnitude of the ABE (Swallow and Jiang, 2014a; Broitman and Swallow, 2020). The effect of target detection on memory for background items may be difficult to detect when participants are given a surprise memory test on the items. But it is highly replicable when participants are told of the memory test in advance. It is unclear how these effects can be explained by the DTI model in its original formulation. In the next section we describe a mechanism that could produce such an effect.

Interactions Between Stimulus Priority and NE in Perceptual Processing

The observation that the magnitude of the ABE is itself boosted for attended or intentionally encoded information suggests that the effects of phasic LC activity on sensory precision or episodic encoding may interact with those of goal-directed attention (green dashed line in **Figure 2**). One prominent model of LC function describes a process by which such effects could emerge. In the Glutamate Amplifies Noradrenergic Effects (GANE; Mather et al., 2016) model, phasic arousal further boosts the processing advantage of items that have been prioritized and inhibits those that have not *via* local, positive feedback loops. According to this account, cortical areas representing prioritized information are expected to be high in glutamate, which promotes the local release of NE. NE then amplifies competitive interactions between more active and less active representations through local inhibition, and promotes more release of glutamate in the prioritized areas, which further increases NE release. These dynamics could help explain why the ABE is easier to detect for background scenes when they are intentionally memorized. Under these circumstances, control and frontoparietal systems may prioritize the scenes relative to other sources of information during task performance (e.g., the room in which the task occurs) throughout the task, only to have these effects magnified by positive feedback loops between glutamate and NE when the LC is physically activated by the decision to respond to a target.

The GANE model may provide a basis for thinking about how temporal selection could interact with the prioritization of

different sources of information by attention. However, there are reasons to be cautious about its ability to account for the effects of goal-directed attention in the ABE. It is unclear why responding to a target does not more consistently interfere with incidental memory for background items, especially under conditions that limit their processing. To our knowledge only one study has found that unattended background items are more poorly remembered when they are paired with a cue that required a response (Dewald and Sinnet, 2012). Furthermore, the GANE model focused on interactions between arousal induced by aversive events (the presentation of a conditioned stimulus associated with an electrical shock) and visual salience or attentional priority of subsequently presented stimuli (e.g., Lee et al., 2018). It also describes effects that may evolve over longer time intervals than those in the ABE (e.g., Sakaki et al., 2014). Additional research further clarifying the time course of the ABE and its relationship to arousal induced by aversive events should provide additional insight into whether the GANE model helps to explain how the ABE is modulated by goal-directed attention.

HOW THE ABE RELATES TO THE EFFECTS OF EVENT BOUNDARIES ON EPISODIC MEMORY

If our account of the ABE is correct, then it may reflect how behaviorally relevant events (those that require a response) dynamically modulate attention and memory over time in naturalistic situations. However, research on how naturalistic events influence attention and memory has been conducted more or less in parallel to examinations of the ABE, with few attempts to integrate these literatures. In the next section, we address this gap in the literature. We start by describing research on event segmentation that converges on two broad effects on episodic memory: (1) the enhancement of information presented with an event boundary, and (2) the separation of representations of what happened before an event boundary from what happened next (Figure 3).

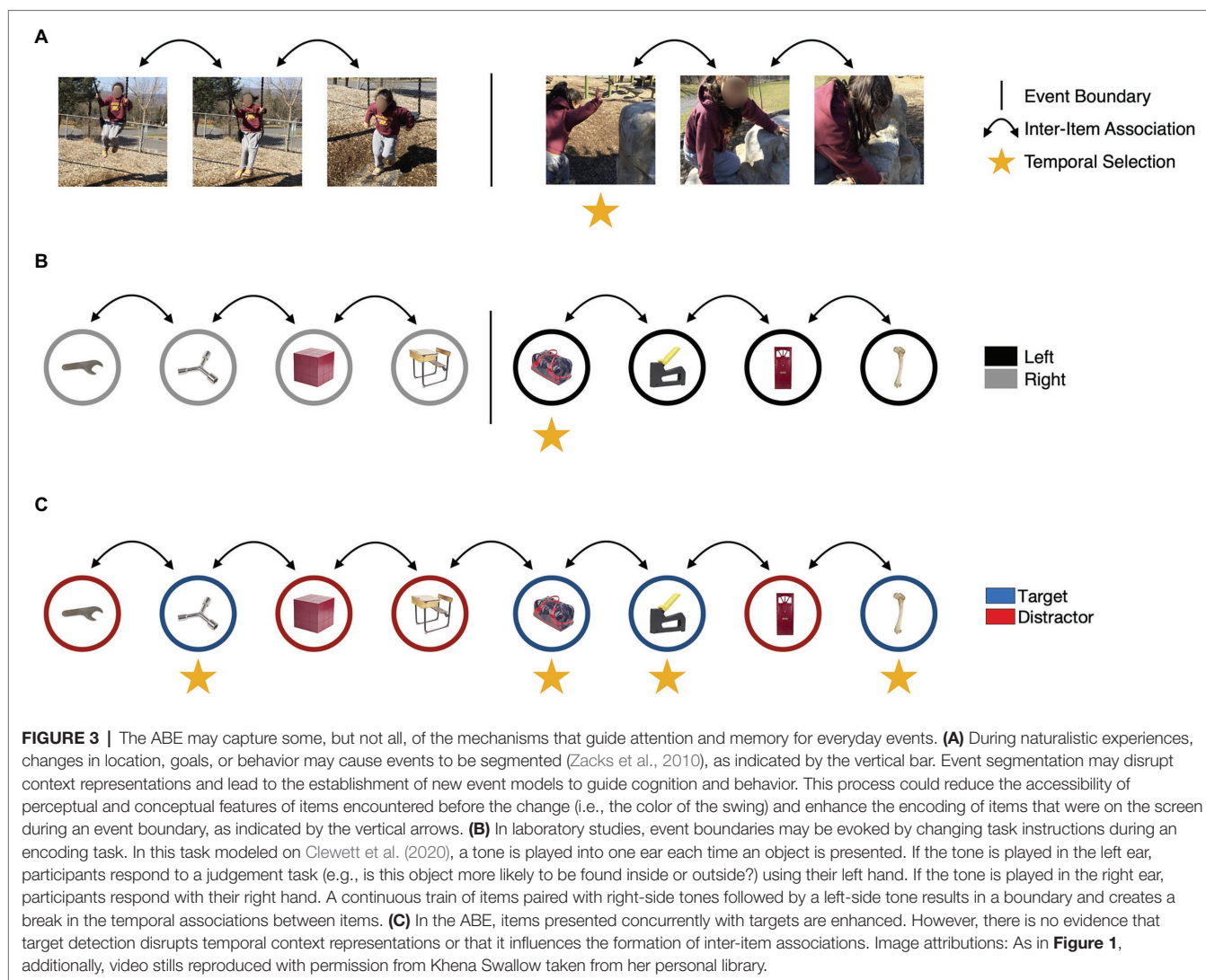
In naturalistic viewing, event segmentation is measured by asking participants to press a button to mark the boundaries between naturalistic units of activity as they watch a movie (e.g., of someone doing the dishes; Newton, 1973). People tend to identify event boundaries when the situation changes in meaningful ways (i.e., when spatial configurations change; Schwan and Garsoffky, 2004; Zacks et al., 2010; Baker and Levin, 2015; Figure 3A) and the boundaries people identify track significant changes in brain activity and cognition during task-free viewing (e.g., Baldassano et al., 2017). More recently, laboratory tasks have examined event segmentation by creating context shifts (Figure 3B) that signal, for example, which task to perform on an item (DuBrow and Davachi, 2013, 2014, 2016), which hand to use to respond on that task (Clewett et al., 2020), or that increase reward prediction error (Rouhani et al., 2020). Despite using very different methods, research using naturalistic events and laboratory tasks both support the view that event representations are updated at event boundaries.

Both types of studies provide strong evidence that attention and memory are boosted at event boundaries, just as in the ABE. Attention to naturalistic movies increases (Faber et al., 2018; Kosie and Baldwin, 2019), encoding is enhanced (Ben-Yakov and Henson, 2018), and perceptual and conceptual information encountered at these times is better remembered than information encountered during nonboundary periods (Newton and Engquist, 1976; Lassiter and Slaw, 1991; Swallow et al., 2009, 2011). Controlled laboratory tasks similarly find enhanced hippocampal activity at context changes (DuBrow and Davachi, 2016; Bulkin et al., 2020) and a memory advantage for items presented at, or soon after context changes during an encoding task (Heusser et al., 2018; Clewett et al., 2020; Rouhani et al., 2020).

Event segmentation plays a critical role in organizing episodic memory as well (Sargent et al., 2013). In naturalistic perception, segmentation influences the accessibility of information within versus across events (Radvansky and Copeland, 2006; Swallow et al., 2009, 2011; Kurby and Zacks, 2021), the quality of later memory (Kurby and Zacks, 2011), and estimates about their duration (Faber et al., 2018). Controlled laboratory tasks provide additional evidence that event segmentation organizes episodic memory: relative to objects presented in two different events, judgments about the temporal order of objects presented in the same event are enhanced (DuBrow and Davachi, 2013, 2014, 2016) and estimates of their temporal proximity to each other are decreased (Ezzyat and Davachi, 2014). Context changes during encoding also influence duration judgments (Brunec et al., 2017) and the order in which objects are later recalled (Heusser et al., 2018). These results thus demonstrate that boundaries influence how episodic memories are organized and subsequently remembered.

From this quick review, it is clear that the ABE is comparable to some effects of event boundaries on episodic memory, but it may not be comparable to others. The ABE is consistent with the boundary advantage because it shows that behaviorally relevant changes in task demands trigger a transient increase in attention and memory encoding (Figure 3C). It also parallels other aspects of the boundary advantage: the potential for incorporating information that is outside the current focus of goal-directed attention (Swallow et al., 2009, 2011; Yebra et al., 2019; Broitman and Swallow, 2020), better memory for which task was performed on which image (Heusser et al., 2018; Swallow and Atir, 2018; Turker and Swallow, 2019; Clewett et al., 2020; Mulligan et al., 2021), and the inclusion of features that distinguish category exemplars (Swallow et al., 2009; Sisk and Lee, 2021). While there is some evidence that the ABE also includes relational memory and spatial configurations (Swallow and Jiang, 2010; Leclercq et al., 2014; Turker and Swallow, 2019), we are not aware of similar effects having been examined in the segmentation literature.

Event segmentation also appears to impact memory in ways that have not yet been observed in the ABE. In contrast to segmentation, there is no evidence that responding to targets in the continuous dual-task encoding paradigm influences temporal context memory. The available data are not encouraging. In two studies, Mulligan et al. (2016, 2021) reported that measures that are sensitive to inter-item associative memory or when a word appeared are not influenced by target detection. Variability



in attention over time also may have little effect on temporal context memory (Jayakumar et al., 2022). It is possible that the transient nature of responses in the continuous dual-task paradigm boosts episodic memory while having little effect on the formation of inter-item associations (cf. Heusser et al., 2018), especially in designs that present targets and distractors at equal rates (e.g., Swallow and Jiang, 2012; cf. McDaniel and Bugg, 2008). In contrast, event segmentation tasks maintain low-level perceptual cues or tasks over extended periods of time, creating new stable, temporally extended contexts in which items or actions can be associated (Grella et al., 2019; Rouhani et al., 2020).

These effects are consistent with the perspective highlighted in this review: that internal, stable states that generate efficient cognition are updated in response to mismatches between those states and the environment (Zacks et al., 2007; Friston, 2009; Brunec et al., 2018). However, they highlight important differences between paradigms that produce the ABE and those used to examine event segmentation. We propose that responding to targets in a continuous detection task boosts attention and encoding, just like event boundaries (**Figure 3**). However, responses

in this task are also importantly different than responses in segmentation paradigms. In naturalistic perception, event boundaries require a response that results in an extended shift in the state of the system, promoting the formation of within event inter-item associations. In contrast, in the continuous dual-task paradigm, aligning the state of the system to the state of the environment requires a transient response (pressing a button, counting, temporarily withholding a button press). We suggest that this is the primary source of the difference between the ABE and the effects of event segmentation on episodic memory. However, it will be necessary for future research to test this possibility, as research on the ABE and event segmentation have tended to focus on different aspects of episodic memory.

Boosting State Changes by Disrupting Top-Down Control

To better account for the effects of event boundaries on memory, we propose that phasic LC activity could contribute to memory by temporarily increasing cognitive flexibility under the right

circumstances (dashed purple line in **Figure 2**). This is a speculative proposal, but it provides a more complete description of the impact of phasic LC activity on brain function. It also provides a straightforward basis for characterizing why responses to targets and event boundaries have common and uncommon effects on memory: whereas a transient response is needed to align the system after a target is detected, adapting to situational changes at event boundaries requires a larger and/or longer lasting shift in an animal's internal state. As a result, context representations should shift more in response to event boundaries than to targets, and disruptions to the formation of inter-item associations in memory should be larger.

Several perspectives of phasic LC activity link it to this type of cognitive shift. Theoretical accounts of LC function suggest that it signals contextual volatility (Yu and Dayan, 2005; Parr and Friston, 2017) and facilitates the emergence of new functional states (Bouret and Sara, 2005). Consistent with these proposals, recent neuroimaging work finds evidence that LC activity could promote cognitive shifts by reducing the threshold for transitioning to a new state (Munn et al., 2021) and integrating processing across the brain (Shine et al., 2016). Similarly, the contributions of phasic LC activity to Go/No-Go task performance was captured in a computational model by a parameter that sped the decay of old control states, increasing the influence of more recent experiences (Sales et al., 2019). LC activity may even promote cognitive flexibility in the presence of cues that once predicted aversive events (Uematsu et al., 2017). Together, these findings suggest that phasic LC activation (probably in concert with other neuromodulatory systems) could promote cognitive flexibility.

In controlled laboratory tasks examining segmentation, increased cognitive flexibility might allow an animal to rapidly integrate new sources of information to adapt to changed contingencies between the environment (e.g., the stimuli that appear in an encoding task) and internal task sets (e.g., whether one should judge their size or whether they are likely to be found inside or outside). In naturalistic situations, increasing cognitive flexibility at event boundaries may facilitate the adoption of new event models and goals that better match the new situation. The contributions of phasic LC to shifts in HPC representations could also contribute to these shifts, segmenting episodic representations as they unfold (DuBrow and Davachi, 2016; Ben-Yakov and Henson, 2018; Grella et al., 2019; Clewett et al., 2020). LC mediated pattern separation could be one basis for this effect (Segal et al., 2012; Rouhani et al., 2020).

One implication of this idea is that, by increasing cognitive flexibility, phasic LC activation may transiently weaken (but not eliminate) goal-oriented attention during encoding. Though speculative, this possibility may account for observations that the ABE can incorporate information that is irrelevant to the ongoing task (see "*Goal-directed attention modulates the effects of temporal selection on encoding*"), while still allowing for interactive effects of temporal selection with the intention to memorize background items. If phasic LC activity weakens control states then top-down inhibition of task-irrelevant background items may decrease at the same time sensory gain

increases. This account has similarities to explanations for the role of attention in task-irrelevant perceptual learning. Task-irrelevant perceptual learning occurs for stimuli paired with a target, but these effects are most reliable for stimuli that are presented below threshold, or outside focused attention, making them less likely to be inhibited by control mechanisms (Tsushima et al., 2008; Choi et al., 2009). It also overlaps with proposals suggesting that the attentional blink (the impaired ability to detect a target that occurs 200–500 ms after an earlier target), could reflect disruptions to control or selection mechanisms (Kawahara et al., 2006; Zivony and Lamy, 2021). In a similar way, disrupting control could also result in the inclusion of task-irrelevant information by the ABE. Finally, increased cognitive flexibility could explain why selecting stimuli for one task sometimes increases the likelihood that a prepared button press will be erroneously produced (Jiang and Swallow, 2014).

We emphasize, however, that weakening control states when a response is required does not mean that their influence is erased (cf. Sales et al., 2019). In the continuous dual-task that produces the ABE, instructions to memorize the background items should be maintained, even if a transient weakening increases the likelihood that irrelevant information will be caught up by temporal selection. Interactive effects of temporal selection with goal-directed attention (e.g., as in Mather et al., 2016) should therefore occur even if phasic LC activity briefly disrupts control. Indeed, higher rates of LC activity may be more likely to cause state transitions than a single phasic response on its own (Chandler, 2016). These considerations call for a careful evaluation of whether larger effects on memory would result from stronger or more arousing responses, as well as computational or cognitive modeling to capture the dynamics of the various effects of phasic LC on brain wide processing and how it is modulated by longer-lasting changes in arousal.

Modular Circuitry and Function of the LC

Rapid advances in understanding the structure and function of the LC of the last 5–10 years (some of which was reviewed above) have led to the broad recognition that the LC may have a modular organization and the ability to shift between global and localized activity patterns (Poe et al., 2020). Rather than being a uniform nucleus that globally modulates neural activity, the LC may consist of multiple functional units that differ in their projection targets. These include separable projections to brain areas that could play an important role in generating responses to targets or changes in events: sensory and perceptual processing areas, hippocampal and limbic systems, and frontal control systems (Chandler, 2016; Poe et al., 2020).

The release of NE globally or at specific sites could lead to diverse effects on cognition. For example, in rats, separate cellular ensembles within the LC were found to have distinct and opposing effects on avoidance learning and extinction, *via* projections targeting prefrontal cortex and the amygdala, respectively (Uematsu et al., 2017). Single-unit recordings in both rats (Totah et al., 2018; Chandler et al., 2019) and monkeys (Usher et al., 1999; Joshi and Gold, 2022) demonstrate that levels of synchronous firing in the LC vary with cognitive

state. Recent evidence further suggests that distinct LC ensembles produce distinct cognitive states in rats (Noei et al., 2022). Taken together, advances in characterizations of LC function and projection patterns describe a neuromodulatory system that is more sophisticated and precise than previously believed, and yet has an overarching purpose of facilitating changes of cognitive state as needed.

A natural question arising from this new perspective is whether the ABE reflects activity of specific ensembles projecting to specific brain regions, or whether it may result from more global signaling. The circumstances under which LC ensembles function jointly or independently (and are therefore more modular) are not yet well understood (Poe et al., 2020). Numerous differences between the conditions that cause segmentation or generate the ABE versus those under which modular versus global firing patterns in the LC have been examined make predictions difficult. However, because independence may be more likely with milder inputs into the LC, whereas global firing may occur with stronger input (Schwarz and Luo, 2015) it is possible that the ABE reflects more modular LC signaling, whereas context shifts in segmentation studies may be more likely to produce global LC signaling. The relatively new nature of these ideas demand caution, but also provide exciting new ways to think about the mechanisms by which attention and memory reflect neuromodulation by this and other systems.

CONCLUSION

Attention and memory are coupled to changes in the external world. In this paper we suggest that this is because they are modulated by systems that stabilize internal representations of the world and update them when they no longer adequately reflect what is currently happening. A knock at the door, a partner's call for help bringing the groceries in, or the sound of a cat knocking a plant off of a stand while one is reading all signal that the world has changed and so too must one's model of it. In the perspective we have outlined here, for example, the sound of the pot crashing to the floor causes a mismatch between one's internal representation of the situation (that the surroundings are amenable to reading) and the actual state of the world (a sudden noise suggests that something has broken). Because this mismatch could change how one should act in this situation, LC activity briefly increases, boosting sensory gain to facilitate the uptake of external information,

individuating that moment from others, and causing a shift in event representations. At the same time, phasic LC activity could increase cognitive flexibility by promoting the decay of old states. Such flexibility would allow one to more rapidly adopt new, context appropriate states to then chase after the cat. Alternatively, if the crash one heard was just the cat jumping off the table, one could return to the book and the old state would persist.

In our view, the ABE is one manifestation of the mechanisms that tie attention and memory to changes in ongoing events. Just as in the cat example, we suggest that the ABE reflects the transient mobilization of effort to compensate for differences between internal states and the external world, and that this is mediated by the LC neuromodulatory system. Importantly, the effects of responses on memory are not limited to the paradigms that produce the ABE. Evidence from research on event segmentation using both naturalistic and controlled laboratory tasks shows that moments when events change are also moments that are more likely to be remembered. However, unlike in the ABE, changes in everyday events also create new contexts, leading to longer lasting, rather than transient, shifts in representations that guide cognition and behavior. In both cases, however, the critical factor regulating attention and memory is the need to respond to change.

AUTHOR CONTRIBUTIONS

KS, AB, ER, and HT contributed to the development of ideas presented in this paper. KS and AB outlined the paper. KS drafted the majority of the manuscript. All authors contributed to the article and approved the submitted version.

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Motor engagement enhances incidental memory for task-irrelevant items

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Actions shape what we see and memorize. A previous study suggested the interaction between motor and memory systems by showing that memory encoding for task-irrelevant items was enhanced when presented with motor-response cues. However, in the studies on the attentional boost effect, it has been revealed that detection of the target stimulus can lead to memory enhancement without requiring overt action. Thus, the direct link between the action and memory remains unclear. To exclude the effect of the target detection process as a potential confounder, this study assessed the benefit of action for memory by separating items from the response cue in time. In our pre-registered online experiment ($N = 142$), participants responded to visual Go cues by pressing a key (i.e., motor task) or counting (i.e., motor-neutral cognitive task) while ignoring No-go cues. In each trial, two task-irrelevant images were sequentially presented after the cue disappearance. After encoding the Go/No-go tasks, participants performed a surprise recognition memory test for those images. Importantly, we quantified the impact of overt execution of the action by comparing memories with and without motor response and the impact of covert motor processes (e.g., preparation and planning of action) by comparing memory between the motor and cognitive tasks. The results showed no memory differences between Go and No-go trials in the motor task. This means that the execution itself was not critical for memory enhancement. However, the memory performance in the motor No-go trials was higher than that in the cognitive No-go trials, only for the items presented away from the cues in time. Therefore, engaging the motor task itself could increase incidental memory for the task-irrelevant items compared to a passive viewing situation. We added empirical evidence on the online interaction between action and memory encoding. These memory advantages could be especially brought in action preparation and planning. We believe this fact may expand our present understanding of everyday memory, such as active learning.

KEYWORDS

episodic memory, action execution, action preparation, action-induced memory enhancement, attentional boost effect

Introduction

Episodic memory is a core function of cognition and has been one of the most classic and popular topics in empirical psychology and neuroscience. In these fields, researchers have typically measured one's memory in passive situations (Heuer et al., 2020), wherein participants were asked to see stimuli without intentional body movements to minimize noises in the data. In reality, however, humans constantly explore the external world *via* their movements. The actions strongly influence what we experience and what information is encoded. Literature has demonstrated how concurrent actions shape our perception (Nicolelis et al., 1996; Zwickel et al., 2007; Liu et al., 2008; Kirsch, 2015; Kumar et al., 2015; van Ede et al., 2015; Arikan et al., 2017; Heuer and Schubö, 2017; Schneider et al., 2017; Yon et al., 2018; Gallivan et al., 2019), attention (Hannus et al., 2005; Baldauf et al., 2006; Baldauf and Deubel, 2008), and working memory (Boon et al., 2014; Hanning and Deubel, 2018; van Ede et al., 2019). Moreover, in the framework of active learning, educators have augured the benefit of active involvement in memory (Michael, 2006). Nevertheless, there has been insufficient empirical evidence on the online interaction between action and memory.

A recent work by Yebra et al. (2019) shed light on this issue and reported the memory advantage of actions. In their experiments, participants first performed a motor Go/No-go task for incidental encoding. In the task, a rectangle frame and a grayscale image of a daily object in the frame were simultaneously presented at random intervals. The frame was colored in one of the two colors. Depending on the frame color, participants either executed or withheld a keypress (Go and No-go trials, respectively). The images were task-irrelevant; participants were instructed to just look at them. In the surprise recognition memory test, participants remembered images presented in the Go trials better than images presented in the No-go trials. Yebra et al. (2019) referred to this advantage in memory performance by active involvement as the “action-induced memory enhancement” (AIME).

The relationship between action and memory processes was further explored by Kinder and Buss (2020). In their experiment, participants pressed a key when the images of a face of specific sex were presented while ignoring the face of the other sex. Kinder and Buss (2020) employed a cognitive Go/No-go task as a motor-neutral baseline, in which participants counted every presentation of the target sex. Here, the face images were response cues, as well as study items and, thus, were task-relevant. The memory performance for the face images was compared among the motor Go, motor No-go, and motor-neutral conditions. The authors considered the difference between motor Go and motor No-go items to represent the impact of action execution, whereas that between motor No-go and motor-neutral baseline to represent the covert motor processes that include action preparation and inhibition. These

contrasts suggested that both action execution and covert motor processes could contribute to memory enhancement. Kinder and Buss (2020) collectively referred to these overt and covert processes as motor engagement.

In contrast, another body of work provides an alternative explanation for the interaction of action and memory. Attention research reported a similar memory enhancement, that is, a memory advantage for items presented concurrently with to-be-responded targets compared to those presented with distractors. Named the “attentional boost effect” (ABE; Swallow and Jiang, 2010), this effect is thought to occur because attention to targets *spills over into* peripheral stimuli and facilitates encoding (Swallow and Jiang, 2013). This means that target detection, not motor engagement, is critical for ABE. Indeed, ABE can be elicited not only by the motor response but also the cognitive response, like counting the targets (Swallow and Jiang, 2012; Makovski et al., 2013; Toh and Lee, 2022). This fact casts a doubt on the direct link between action execution and memory encoding. Given that the items were presented simultaneously with the behavioral targets, better memory for the Go items in Yebra et al. (2019) may be attributed to attention to the targets, not the motor response¹. A similar interpretation is also plausible for Kinder and Buss (2020), where the motor Go items were response cues themselves. On the contrary, better memory for motor No-go vs. motor-neutral items cannot be explained by ABE. Although this could support the motor-specific enhancement, such a role of the covert process has not yet been explored with incidental memory for the task-irrelevant items.

As such, the pure impact of concurrent motor engagement on task-irrelevant memory is still unclear. To solve this problem, this study attempted to separate the AIME from ABE. Swallow and Jiang (2011) manipulated the temporal asymmetry between a response cue and a study item and observed the ABE only for the item presented simultaneously with the cue, leaving the item presented before or after it. This allowed us to reason that, if enhancement occurred for items presented after the disappearance of cues, the memory enhancement should not be attributed to the known ABE. Therefore, we investigated whether motor engagement would cause memory enhancement, even when the items were temporally separated from the behavioral targets (i.e., Go cue). Naturally, such separation from target detection is possible only when study items are task-irrelevant. Excluding the potential confounding with ABE enabled us to assess the influence of motor engagement on memory. Specifically, we explored the impact of the overt process on memory by comparing Go and No-go in the motor

1 Yebra et al. (2019) did not favor the attentional account of AIME and suggested that the Go cues were as frequent as the No-go cues and thus not highly salient. However, in previous studies, the attentional boost effect occurred when targets were as common as distractors (Swallow and Jiang, 2012; Makovski et al., 2013).

task, and the impact of the covert process on memory by comparing the motor task with the cognitive task as the motor-neutral baseline.

Accordingly, we conducted a pre-registered online experiment ($N = 142$) and employed motor and cognitive Go/No-go tasks for encoding. In these tasks, we sequentially presented the Go/No-go cues and grayscale images of daily objects without temporal overlap. Moreover, following the presentation of the Go/No-go cues, we presented the images at two different periods, separated by the action execution. Yebra et al. (2019), as well as our previous work (Shimane et al., 2021), indicated the presence of a temporal window of memory enhancement; the effect of the action was relatively unreliable for items presented before action execution. Considering such a confounding influence, we separately evaluated the memories before and after the action execution. In the motor Go trial, the pre-action image was presented after the Go cue disappeared. Then, the participants' keypress caused the disappearance of the pre-action image and the presentation of the post-action image. In the motor No-go trial, the pre-action image automatically replaced the post-action image without a keypress. The sequence of events was the same for the cognitive task except the participants counted the number of Go cues instead of pressing a key. Finally, we compared the incidental memory for those images between conditions.

Materials and methods

Participants

We used a web-based power application PANGAEA (v0.2) (<https://jakewestfall.shinyapps.io/pangea/>) to conduct an *a priori* power analysis. Assuming the effect size of the action on memory observed in our previous work ($d = 0.27$; Shimane et al., 2021), we calculated the sample size to achieve 0.95 power at the standard 0.05 alpha error probability. This analysis revealed that 129 participants and 12 observations per condition were needed. As this experiment would be performed online, we predicted that several participants' data may need to be excluded. We thus recruited 162 participants to achieve 0.99, 0.95, or 0.80 power when 100%, 80%, or at least 50% of samples would be available, respectively. As mentioned below, we finally analyzed the data from 142 participants (80 women, mean age \pm standard deviation (SD) = 40.27 ± 9.55). The participants were recruited via an online crowdsourcing service (CrowdWorks; <https://crowdworks.jp/>).

Material

We used grayscale images of icons that depict everyday objects (e.g., books, cars, clocks, etc.). The 288 images were

collected from an open online database (<https://icooon-mono.com>). The images were divided into two pre-determined datasets, which were assigned to study (old) and non-study (new) items in a counterbalanced way across participants (i.e., 144 items each).

Procedure

Encoding phase

Two types of tasks were provided in the encoding phase: motor and cognitive Go/No-go tasks (Figure 1). These tasks were conducted in separate blocks of eight trials, and participants were instructed on which task would be carried out at the beginning of each block.

In both tasks, rectangular frames as response cues were presented for 100 ms at the center of a black screen, with random intervals between 2.3 and 3.3 seconds. The cue was randomly colored either blue or yellow at equal frequencies. In the motor task, participants responded to the Go cues with a particular color (e.g., the blue cues) with a keypress while ignoring the No-go cues (e.g., the yellow ones). In the cognitive task, they counted the Go cues instead of keypress and reported the total number at the end of the block. Every frame was followed by the presentation of two task-irrelevant images. The first image (i.e., pre-item) appeared simultaneously with the cue disappearance. In motor Go trials of the motor task (i.e., motor Go trials), the participants' keypress terminated the presentation of the pre-item and initiated the presentation of the second image (i.e., post-item) at the same location. The post-item was presented for the same duration as the pre-item; that is, the response time (RT) of keypress in that trial. In the other three conditions (i.e., motor No-go, cognitive Go, and cognitive No-go trials), a pre-item appeared for average RT of keypresses in past motor Go trials, and then the post-item was presented for the same amount of time. The average RT was updated in every motor Go trial. The study items were randomly assigned into pre/post condition and motor/cognitive tasks. The assignment of images to the colors of the frame was counterbalanced across the participants.

Participants first practiced the motor and cognitive Go/No-go tasks for 16 (eight each) trials, each without presentation of the images. Then, participants performed six blocks of the motor Go/No-go task and three blocks of the cognitive one with item presented in a random order². Each block comprised one

² Based on previous work, we expected no difference between cognitive Go and No-go conditions after the target disappeared. We thus planned to aggregate these conditions into the motor-neutral one as done by Kinder and Buss (2020). This was why the number of trials were equaled between motor Go, motor No-go, and cognitive Go/No-go conditions (24 items per condition) but not between motor and cognitive tasks. Note that, however, our sample size was sufficient even

condition (cf., Kinder and Buss, 2020). The independent variables were item presentation onset (pre or post) and motor engagement (motor Go, motor No-go, or motor-neutral), whereas the dependent variable was memory performance. However, combining two heterogeneous conditions into one would lead to the wrong conclusion. Thus, when there was a significant memory difference between Go and No-go trials in the cognitive task, we orthogonally assessed the effect of cue type and task type instead of aggregating them. In such a case, we conducted a three-way within-participants ANOVA, including the task type, as an additional independent variable. The independent variables were item presentation onset (pre or post), cue type (Go, No-go), and task type (motor or cognitive). The statistical analysis and data visualization were conducted using R [Version 4.1.2; R Core Team (2021)] and the R-packages *dabestr* [Version 0.3.0; Ho et al. (2019a)], *ggplot2* [Version 3.3.5; Wickham (2016)], and *reticulate* [Version 1.24; Ushey et al. (2022)]. The $p < 0.05$ (two-tailed) were deemed significant.

Ethical considerations

This study was approved by the institutional review board of the University of Tokyo (no. 202119) and conducted in accordance with the ethical standards of the 1964 Declaration of Helsinki. All participants provided informed consent before the commencement of experiments.

Results

Five participants were excluded from the analysis because of low performance in the motor ($n = 2$), cognitive ($n = 2$), or both Go/No-go tasks ($n = 1$). After rejecting these participants' data, the mean ratio \pm SD of correct motor Go/No-go responses was $99.80 \pm 0.73\%$, and the mean RT \pm SD in the motor Go trials was 293.35 ± 69.95 ms. Moreover, data from 15 participants were excluded due to extremely low memory performance in the test. Thus, the data from 142 participants were analyzed.

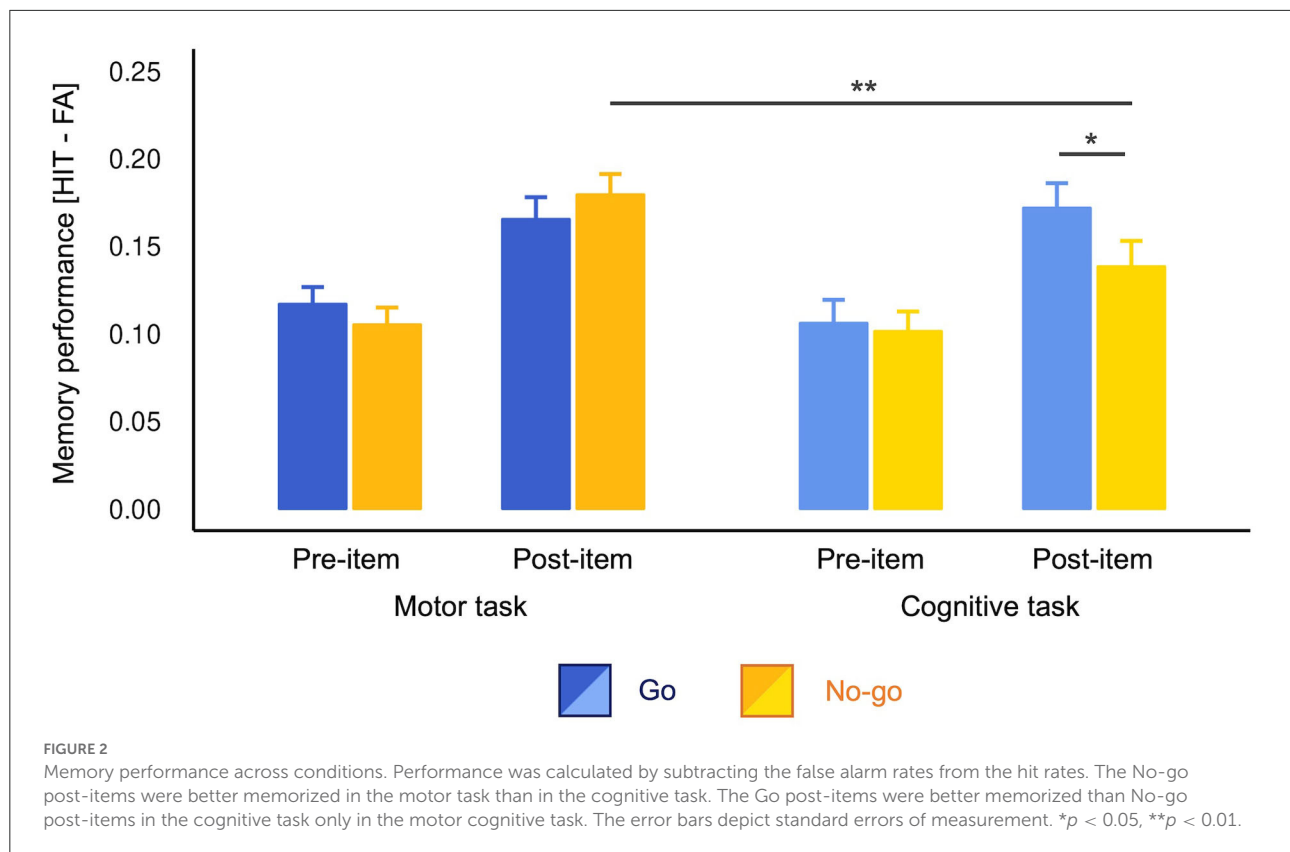
As planned, we first assessed the difference in memory performance between Go and No-go conditions. The t -tests detected a significant difference only for the post-items in the cognitive task [$t_{(141)} = 2.08$, $p = 0.039$, $d = 0.19$, 95% confidence interval (CI) = $(-0.04, 0.42)$]. In the cognitive task, the post-items presented in the Go trials were better remembered than No-go trials. There was no significant difference in pre-items in the cognitive task [$t_{(141)} = 0.32$, $p = 0.746$, $d = 0.03$, 95% CI = $(-0.19, 0.28)$] and pre- [$t_{(141)} = 1.15$, $p = 0.254$, $d = 0.10$, 95% CI = $(-0.13, 0.34)$] and post-items [$t_{(141)} = 1.20$, $p = 0.232$, $d = -0.10$, 95% CI = $(-0.33, 0.14)$] in the motor task.

As we observed the difference between Go and No-go conditions in the cognitive task, we conducted a three-way

ANOVA without lumping them together. The results revealed a significant three-way interaction [$F_{(1, 141)} = 4.05$, $p = 0.046$, $\eta_G^2 = 0.002$]. Consistent with the t -tests above, the *post hoc* analyses revealed simple-simple main effects of cue type only for post-items in the cognitive task [$F_{(1, 141)} = 4.35$, $p = 0.039$, $\eta_G^2 = 0.009$; Figure 2]. Again, there was no significant Go vs. No-go difference in other three conditions [cognitive pre-item: $F_{(1, 141)} = 0.11$, $p = 0.746$, $\eta_G^2 = 0.000$, motor pre-item: $F_{(1, 141)} = 1.31$, $MSE = 0.01$, $p = 0.254$, $\eta_G^2 = 0.003$, motor post-item: $F_{(1, 141)} = 1.44$, $p = 0.232$, $\eta_G^2 = 0.002$]. Furthermore, in the Go trials, simple-simple main effects of task type were non-significant for both pre- [$F_{(1, 141)} = 0.68$, $p = 0.409$, $\eta_G^2 = 0.002$] and post-items [$F_{(1, 141)} = 0.21$, $p = 0.644$, $\eta_G^2 = 0.000$]. These results indicate that action execution itself modulated neither pre- nor post-item memory. However, we found a simple-simple main effect of task type for No-go post-items [$F_{(1, 141)} = 9.39$, $p = 0.003$, $\eta_G^2 = 0.017$]. That is, No-go post-items were better memorized in the motor task than in the cognitive task, indicating that motor engagement promoted memory encoding compared to the motor-neutral baseline. Simple-simple main effects of onset for all conditions were also significant (post-items > pre-items; $F_s > 7.169$, $p_s < 0.008$). There were no other significant simple-simple main effects ($p_s > 0.05$). For more detailed results concerning this ANOVA, see Supplementary Table S2.

Discussion

We investigated whether motor engagement would enhance incidental memory for task-irrelevant items. Specifically, we examined whether overt action execution and/or covert motor processes would enhance memory for the task-irrelevant items presented separately from the behavioral cues. Consequently, we observed no memory differences between Go and No-go trials in the motor task nor between the motor and cognitive Go trials. The AIME reported in Yebra et al. (2019) was not replicated, at least, in its original form. Our results suggested that action execution itself was not critical for memory enhancement. Given that the items were presented simultaneously with behavioral cues in Yebra et al. (2019), the influence of action execution might be confounded with that of target detection. However, only for the items presented away from the cues in time, did we find higher memory performance in the motor No-go trials than that in the cognitive No-go trials. This suggested that motor engagement, especially the covert motor processes, such as action preparation and planning, enhanced the memory encoding. These results are consistent with previous studies on task-relevant memory (Chiu and Egner, 2015a,b; Kinder and Buss, 2020). While denying the advantage of action execution, this study first specified the memory difference between the motor and cognitive No-go



trials, thereby clarifying the contribution of the covert motor process to task-irrelevant memory.

Following Swallow and Jiang (2011), we assumed that ABE would not occur by temporally separating the study items from the response cues. However, in the cognitive task, the memory for the post-item was higher in the Go than in the No-go trials. This effect might be attributed to the target detection process as in ABE that there is a possibility that the target presentation enhances memory even after its disappearance in some situations. For example, if a cue and an item are presented with a short time lag, attention may be transiently suppressed after target detection (e.g., attentional blink; Raymond et al., 1992), impeding memory encoding³. Indeed, the memory for pre-items was generally inferior to that for post-items, in our experiment, implying the possibility that target detection interfered with the encoding of the pre-items but not the post-items. If this account is the case, target presentation may facilitate memory for an item presented after the suppression period. Otherwise, the ABE-like effect for the post-item might be specific to incidental memory. While we employed the surprise memory task, prior studies

³ Raymond et al. (1992) showed that the detection of the second target was suppressed for ~500 ms after that of the first target in the rapid serial visual presentation task.

on ABE, including Swallow and Jiang (2011), typically used an intentional memory task. Under incidental encoding situations, previous studies yielded mixed evidence about the occurrence of ABE (Swallow and Jiang, 2011; Spataro et al., 2013; Turker and Swallow, 2019; Broitman and Swallow, 2020; Huttmacher and Kuhbandner, 2020). Although it is debatable whether the enhancement that we observed in the cognitive task has the same basis as the known ABE, our results may cast doubt on the limited temporal window and requirement of intentionality in ABE.

Importantly, the potential effects of target detection cannot explain the memory difference between the No-go items in the motor vs. cognitive task. Some previous studies provided a possibility of memory enhancement for the No-go cues in specific situations. For instance, relatively rare No-go cues could induce greater memory than frequent Go cues (Makovski et al., 2013). Researchers explained such observation by speculating that a cue that requires switching of response plans triggers the ABE (Swallow and Jiang, 2013). Yet, this idea predicts the trade-off between Go and No-go memory and cannot explain why in this study, both Go and No-go memory increased compared with the cognitive No-go condition. This prediction was not consistent with the comparable memory for the motor Go and No-go items observed here. Rather, the engagement in the motor No-go

trials itself, especially the covert process of motor engagement, seemed to improve memory encoding. Notably, it remains unclear which covert process in motor engagement was critical for the enhancement. With task-relevant memory, [Kinder and Buss \(2020\)](#) attributed a similar contrast between motor and cognitive task memory to the requirement of action preparation. However, besides action preparation, the motor No-go condition should be accompanied by the planning and selection of action. For instance, the inhibition of action might drive cognitive resources and boost concurrent memory compared with a motor-neutral baseline. Although we provided a concept-of-proof of AIME for task-irrelevant incidental memory, further investigation is needed to identify its underlying mechanism.

Our findings are subject to at least two limitations. First, a confounding factor in this experiment is the cognitive load required by different tasks; counting and retaining the number of Go cues could have impaired memory encoding during the cognitive task (cf., [Kinder and Buss, 2020](#)). To minimize the influence of the cognitive load, we made the number of trials in each block small (eight trials per block). Moreover, given that the difference between motor and cognitive task memories was limited to the specific (i.e., post No-go) condition, it is difficult to assume that the cognitive load impaired the memory performance throughout the cognitive task. Thus, although the influence of cognitive load should be further investigated, we believe that it was not critical for our main findings. Second, the sequential presentation of pre- and post-items might induce interference in the memory. This presentation manner was originally designed to consider the unreliable effect of the action on memory before execution. As expected, we observed memory enhancement only for the post-items and not for the pre-items. However, the presentation of post-items might mask the sensory representation of the pre-item and impede its encoding. This may have concealed the effects of motor engagement in the pre-item in the current and previous studies ([Shimane et al., 2021](#)). Future research can examine this possibility by presenting only one item, which is either before or after the action execution (i.e., keypress) in a trial.

As a final note, this study has several practical limitations. First, as our experiment was conducted in an online environment; it was less controlled compared to a laboratory experiment. It is possible that some participants were distracted during the task and there were some artifacts due to the devices or internet connection. Furthermore, the age of our participants was on average higher and more varied than in previous studies with young adults (e.g., [Yebra et al., 2019](#); [Kinder and Buss, 2020](#)). However, our participants showed a memory performance comparable to the previous study ([Yebra et al., 2019](#)), indicating that they performed the task appropriately. Although we believe that the variability in the samples and experimental settings of this study

contributes to the generalizability of our findings, the possibility that these factors may have led to differences from previous studies, such as the absence of AIME, is worth considering.

In conclusion, this study demonstrated motor-specific memory enhancement, which is not explained by the classic ABE. Nevertheless, action execution does not appear to play a critical role. Engaging in the motor task itself is sufficient to increase incidental memory for the task-irrelative items compared to a passive viewing situation. To date, most studies have examined memory in physically restricted situations. In contrast, our evidence indicated that the action automatically modulates the memory through online interaction, emphasizing the importance of further examination of motor-mnemonic interaction. This may expand on our existing understanding of everyday memory, such as active learning, for example, the advantage of active interaction between teachers and students over passive learning.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://osf.io/9gbxq/?view_only=a3d21d84c3a24199b487d5569e271cdc.

Ethics statement

The studies involving human participants were reviewed and approved by the Institutional Review Board of the University of Tokyo. The patients/participants provided their written informed consent to participate in this study.

Author contributions

DS and TT: conceptualization, data curation, formal analysis, and investigation. DS, TT, KT, and KW: funding acquisition. KT and KW: supervision. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fpsyg.2022.914877/full#supplementary-material>

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Effect of familiarity and recollection during constrained retrieval on incidental encoding for new “foil” information

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Behavioral studies have demonstrated differences in the effect of constrained retrieval of semantic vs. non-semantic information on the encoding of foils. However, the impact of recognition on foils between semantic and non-semantic trials remains unclear. This study thus examines the roles of recognition—familiarity and recollection—in constrained retrieval for foils. We applied the event-related brain potentials (ERPs) data of new/old effects to elucidate the neural mechanisms underlying the “foil effect.” Participants encoded semantic and non-semantic tasks (Phase 1), were tested in a blocked memory task with new words presented as foils (Phase 2), and performed a surprise recognition task involving foils and completely new words (Phase 3). Behavioral results showed better recognition performance regarding reaction times and accuracy by hit and correct reject for semantic vs. non-semantic trials in Phase 2. Conversely, inferior recognition performance in reaction times and accuracy by hit and correct reject was noted for semantic vs. non-semantic foils in Phase 3. ERP results showed more positive Frontal N400 (FN400) for hit in non-semantic trials, more positive late positive component (LPC) for correct rejects in semantic trials in Phase 2, and more positive LPC for hits in both semantic and non-semantic trials only in Phase 3. Through dual-processing theory, we prove that different task types in constrained retrieval depend on different retrieval processes. Particularly, familiarity may be applied more often in non-semantic trials, and recollection in semantic trials. The difference in processes between semantic and non-semantic trials during constrained retrieval affects incidental encoding of foils.

KEYWORDS

familiarity, recollection, constrained retrieval, foils, ERPs

Introduction

The levels-of-processing (LoP) theory maintains that semantic processing tasks result in better memory storage compared to perceptual tasks (Craik and Tulving, 1975). According to the transfer-appropriate processing framework, higher retrieval success in semantic trials depends on deeper involvement of the cognitive operations engaged during

encoding in the retrieval (Roediger et al., 2002; Hayama et al., 2008). This model suggests that memory retrieval entails re-implementing the neurocognitive processes involved during encoding; therefore, retrieval attempts also involve some degree of encoding (Buckner et al., 2001; Vogelsang et al., 2016).

In some studies, participants studied words in a semantic task block (pleasant/unpleasant judgment) and a non-semantic task block (letter judgment) (Phase 1). Next, a recognition memory test was administered (Phase 2) in which the studied and new words (“foils”) were intermixed. To participants’ surprise, there was a recognition test for semantic foils, non-semantic foils, and completely new words (Phase 3). Behaviorally, the recognition performance for “foil” words was significantly better for the semantic compared to the non-semantic condition (Jacoby et al., 2005; Danckert et al., 2011; Halamish et al., 2012; Messmer et al., 2020; Salhi and Bergstrom, 2020). Based on brain imaging, Vogelsang et al. (2016) revealed significant overlap in activities between Phases 1 and 2 for the semantic block in the left inferior frontal gyrus. Vogelsang et al. (2018) also observed that constrained retrieval of semantic information involved re-implementing semantic encoding operations mediated by alpha oscillations. It has thus been proposed that retrieval is strategically oriented toward the relevant processing mode to facilitate memory search (Jacoby et al., 2005; Halamish et al., 2012; Vogelsang et al., 2016, 2018).

Jacoby et al., 2005 state that recognition often involves source-constrained retrieval. The explanation for better incidental encoding of semantic foils compared to non-semantic foils is that the participants strategically constrain their retrieval to match a semantic processing mode while attempting to recognize semantic probe words, and a non-semantic processing mode while recognizing non-semantic information (Marsh et al., 2009; Alban and Kelley, 2012; Halamish et al., 2012). This viewpoint is similar to the concept of “retrieval orientation” in Rugg and Wilding (2000), which refers to the type of processing that participants engage in when they are prompted with a retrieval cue to increase the likelihood of retrieval success. Rugg and Birch, 2000 also indicate that the depth of the study processing evokes a different old/new effect. The “old/new effect” has been interpreted as evidence that memory retrieval engages a range of naturally and functionally distinct processes. It refers to the phenomenon in which event-related brain potentials (ERPs) elicited by a hit (correctly identifying old items as “old”) have more positive-going amplitudes compared to a correct rejection (correctly identifying new items as “new”) (Rugg and Curran, 2007; Hayama et al., 2008; Halamish et al., 2012).

Rugg and Birch, 2000 analyzed the ERP differences between semantic and non-semantic conditions in the recognition phase. The ERPs elicited by new words in the block following the non-semantic study task exhibited more positive-going waveforms. The late old/new effects were only

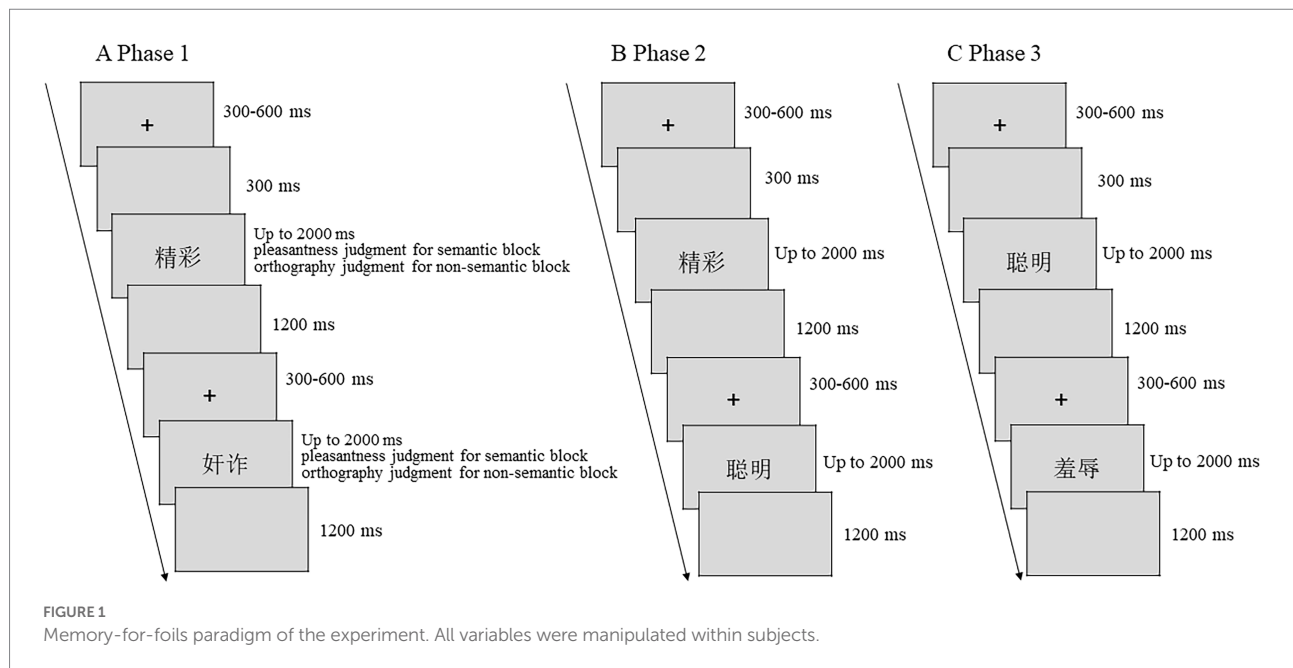
evoked in the semantic condition, whereas the early old/new effects were evoked for both the semantic and non-semantic studied words. Together, these findings indicate that the depth of the study processing influences the different neural activities associated with memory search operations as well as the processing of retrieved information.

Furthermore, the dual-process theory of recognition memory states that recognition decisions can be based on either recollection or familiarity (Rugg and Curran, 2007). However, familiarity-based recognition does not provide qualitative information about the study episode. Meanwhile, recollection is a more effort-intensive process that gives rise to consciously accessible information on prior and later occurrences of the test item (Yonelinas, 2001). Frontal N400 (FN400, also called the early old/new effect) has been associated with the familiarity process, and the late positive component (LPC, also called late old/new effect) with recollection (Allan et al., 1998; Friedman and Johnson, 2000; Rugg and Curran, 2007). According to this view, the late old/new effect in the semantic condition in Rugg and Birch (2000) reflects recollection-based recognition, while the early old/new effect in both the semantic and non-semantic conditions reflects familiarity-based recognition (Rugg and Curran, 2007). This suggests that both familiarity and recollection are required in a semantic recognition task, while only familiarity is required in a non-semantic task.

Buckner et al. (2001) found that encoding occurs even during retrieval tasks, and the foil effect provides evidence for the difference in foil recognition performances between the semantic and non-semantic conditions (Jacoby et al., 2005; Marsh et al., 2009; Danckert et al., 2011; Zawadzka et al., 2017; Vogelsang et al., 2018; Salhi and Bergstrom, 2020). It implies that participants will encode all words during the recognition test, irrespective of whether they are old or foils. Furthermore, the difference in memory performance between semantic and non-semantic foils arises from the strategic retrieval orientation (Jacoby et al., 2005; Danckert et al., 2011; Salhi and Bergstrom, 2020). Thus, the roles of familiarity and recollection during incidental foil encoding differ in semantic vs. non-semantic conditions (Rugg and Birch, 2000; Rugg and Curran, 2007). Unfortunately, the ERP results of this LoP effect have not been incorporated into the foil effect explanation. Instead, the literature has tended to focus on behavioral (Alban and Kelley, 2012; Zawadzka et al., 2017; Salhi and Bergstrom, 2020) and brain imaging studies (Vogelsang et al., 2016, 2018; Messmer et al., 2020).

Therefore, in the current study, we compared both the foil effect and the old/new effect in the memory-for-foils paradigm directly, to investigate the effect of the retrieval strategy on the encoding of new words that were added as foils in Phase 2. We assumed that familiarity and recollection played different roles during the incidental encoding for “foils” in semantic and non-semantic trials when constrained retrieval is accrued. In particular, we predicted that, in line with prior findings (Jacoby et al., 2005; Marsh et al., 2009), final recognition would be enhanced for foils previously shown in the semantic condition compared to non-semantic foils in behavioral terms. We also

Abbreviations: ERP, event-related brain potential; EEG, electroencephalogram; FN400, frontal N400; LPC, late positive component; LoP, levels-of-processing; RT, response time.



expected that the semantic condition would evoke both FN400 and LPC, while the non-semantic condition would only evoke FN400 in Phase 2 and produce the larger amplitude, in line with prior evidence that the depth of study processing modulates retrieval orientation (Rugg and Birch, 2000; Rugg and Curran, 2007). Based on dual-process theory, we predicted a smaller difference between semantic and non-semantic foils in Phase 3. Specifically, both semantic and non-semantic foils are incidentally encoded by the participants in Phase 2. Hence, the available information is limited in the final recognition test, and the participants will evoke LPC when they try to recollection. Furthermore, the semantic condition produces the more positive amplitude.

Materials and methods

Participants

The participants were 21 students (9 men) aged 18–26 years ($M = 20.24$ years, $SD = 1.85$). All had normal or corrected-to-normal visual acuity and did not have any history of neurological or mental disease. The number of participants per group was similar to that in Vogelsang et al.'s (2016) experiment ($N = 22$), which used a similar paradigm. A sensitivity analysis using G* Power 3.1 (Faul et al., 2009) revealed that, assuming a power of 0.80 with our sample size ($N = 21$), the experiment was sufficiently sensitive to detect an effect size of 0.64 for paired samples t -tests. The Research Ethics Committee of the Northeast Normal University of China approved this study. Participants provided written informed consent, per the Declaration of Helsinki.

Materials

The stimuli consisted of 432 Chinese words from the *Modern Chinese Frequency Dictionary*. These words were split into six lists according to familiarity ($M = 5.25$, $SD = 0.72$) and frequency ($M = 1.86$, $SD = 2.50$). The assignment of the lists was balanced according to the experimental conditions of the participants.

Procedure

Participants were fitted with an electroencephalogram (EEG) cap and seated in a sound-and light-attenuated room. During Phase 1, participants made semantic judgments ("Is this word pleasant?") for 72 words and non-semantic judgments ("Does this word have left-right construction?") for 72 words in two different study blocks. An instruction was presented at the beginning of each block to remind participants about the presence of a semantic or non-semantic block. Trials started with a randomly jittered 300–600 ms fixation cross, followed by a blank screen for 300 ms; finally, the stimulus was presented at the center of the screen for 2,000 ms. During this time, participants were asked to complete their semantic judgments (semantic block) or non-semantic judgments (non-semantic block) by pressing the "F" or "J" key on the keyboard. If participants did not respond within the duration of stimulus presentation, the stimulus was removed from the screen. The next trial started after a 1,200 ms blank screen (Figure 1, A Phase 1).

In Phase 2, the participants were given an old/new recognition test. In the semantic block, 72 old words from the semantic study phase were intermixed with 72 new words (semantic foils). In the non-semantic block, 72 old words from the non-semantic study

phase were intermixed with 72 new words (non-semantic foils). Each test trial started with a randomly jittered 300–600 ms fixation cross, followed by a blank screen of 300 ms, and then a stimulus presented at the center of the screen for 2,000 ms. During this time, participants were asked to determine whether the word was “Old” (studied word) or “New” (unstudied word) by pressing the “F” or “J” keys, respectively, on the keyboard. If participants did not respond within the duration of stimulus presentation, the stimulus was removed from the screen. The next test trial started after a 1,200 ms blank screen. Participants were told in advance that the old items were from the Phase 1 semantic or non-semantic blocks (Figure 1, B Phase 2).

In Phase 3, we administered a surprise source memory test. Participants were asked to distinguish between the 72 semantic foils, 72 non-semantic foils, and 144 entirely new words. Each trial in the final foil recognition test started with a randomly jittered 300–600 ms fixation cross, followed by a blank screen of 300 ms, and then a stimulus presented at the center of the screen for 2,000 ms. During this time, participants were asked to determine whether a word was old or new by pressing the “F” and “J” keys on the keyboard, respectively. If participants did not respond within the duration of stimulus presentation, the stimulus was removed from the screen. The next foil test trial started after a 1,200 ms blank screen (Figure 1, C Phase 3).

Data recording and analyses

Behavioral data

For the data of Phase 2, the mean proportions of hits of semantic/non-semantic words and correct rejections of semantic/non-semantic foils were calculated. For the data of Phase 3, the mean proportions of hits of semantic/non-semantic foils were calculated. Finally, we analyzed the response accuracy and response time (RT) for both phrases using paired samples *t*-tests with task types (semantic, non-semantic) as the within-subject factor.

Event-related potentials

We recorded brain electrophysiological activity using the Neuroscan system according to the extended international 10–20 system using 62 Ag/AgCl electrodes positioned in an elastic nylon cap, with the reference on the left mastoid. We positioned the electrodes above and below the left eye, and on the left and right canthi of the eyes to record the vertical and horizontal electrooculograms, respectively. The impedance of all electrodes was maintained at below 10 K Ω . The EEG and electrooculogram were amplified using a 0.05–100 Hz band-pass and continuously sampled at 1,000 Hz.

Off-line analyses were performed in MATLAB using the EEGLAB (Delorme and Makeig, 2004) and ERPLAB toolbox (Lopez-Calderon and Luck, 2014). The EEGs were filtered using IIR-Butterworth filters with 30 Hz low-pass and 0.1 Hz high-pass filters (Luck, 2014). After independent component

analysis for ocular correction, we supplemented the artifact correction process with artifact rejection to eliminate trials with clear artifactual voltage deflections or when peak-to-peak voltage within the EEG epoch exceeded 300 μ V in any 200 ms window in any channel (Lopez-Calderon and Luck, 2014; Bacigalupo and Luck, 2018). We segmented the ERPs for all trials into 1,000 ms epochs surrounding the stimulus onset and corrected the baseline to account for the 200 ms pre-stimulus epoch.

Based on the grand-averaged ERPs of different waveforms, our ERP analysis strategy was similar to that of previous studies that analyzed the FN400 and LPC components (Duzel et al., 1997; Vilberg et al., 2006; Rugg and Curran, 2007). We analyzed the ERP data from F3, F4, P3, and P4. We conducted separate analyses for the 350–450 and 700–800 ms time windows, corresponding to the FN400 and LPC epochs, respectively. In Phase 2, a three-factor repeated-measures analysis of variance (ANOVA) with 2 (task type: semantic, non-semantic) \times 2 (response: hit, correct reject) \times 4 (electrode: F3, F4, P3, and P4) as within-subject factors was performed on mean amplitudes for the FN400 and LPC epochs. In Phase 3, a three-factor repeated-measures ANOVA with 2 (task type: semantic, non-semantic) \times 3 (response: semantic hit, non-semantic hit, correct reject) \times 4 (electrode: F3, F4, P3, and P4) as within-subject factors was performed. Greenhouse–Geisser correction was performed when the assumption of sphericity was violated for a particular sample. Holm corrections were used to adjust for multiple comparisons.

Results

Reaction time and accuracy

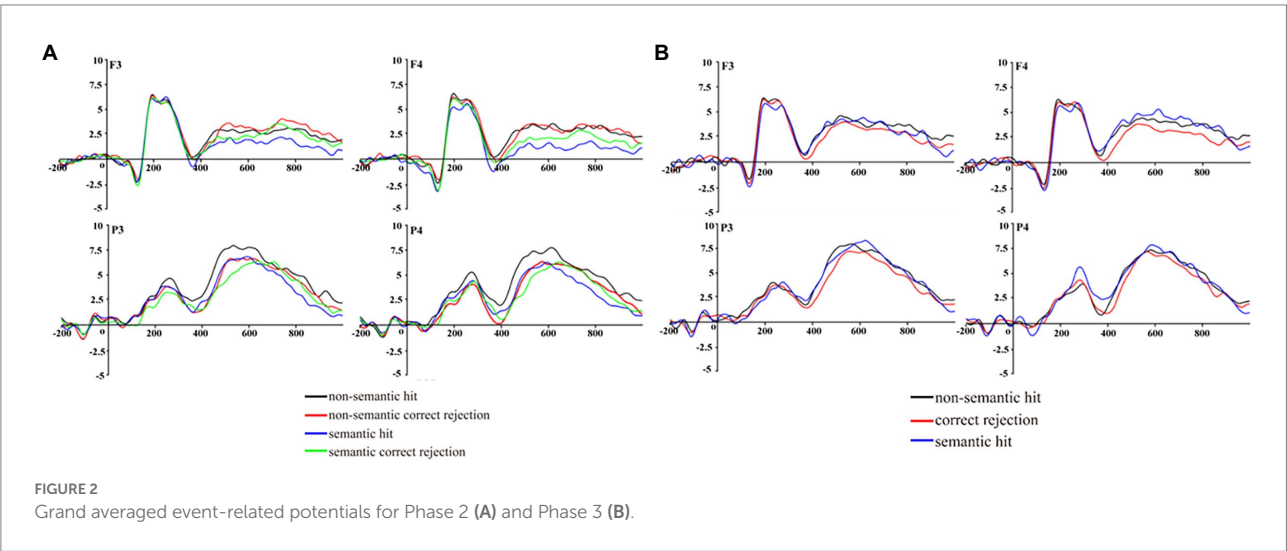
In Phase 2, hits were higher for semantic trials than for non-semantic trials [$M = 0.77 \pm 0.03$ vs. $M = 0.70 \pm 0.02$, respectively; $t(20) = 2.713$, $p = 0.013$, 95% CI (0.02, 0.12), Cohen's $d = 0.60$]. Correct rejection of foils was higher for semantic trials than for non-semantic trials [$M = 0.68 \pm 0.02$ vs. $M = 0.55 \pm 0.03$, respectively; $t(20) = 5.71$, $p < 0.001$, 95% CI (0.08, 0.17), Cohen's $d = 1.25$]. The RTs of hits were shorter for semantic trials than for non-semantic trials [$M = 850.86 \pm 20.45$ vs. $M = 891.20 \pm 31.21$, respectively; $t(20) = 2.18$, $p = 0.042$, 95% CI (1.70, 78.98), Cohen's $d = 0.48$]. There was no significant difference in the RTs of correct rejections between semantic and non-semantic trials [$t(20) = 1.50$, $p > 0.15$] (Table 1).

In Phase 3, hits were lower for semantic foils than for non-semantic foils ($M = 0.32 \pm 0.03$ vs. $M = 0.44 \pm 0.02$). The RTs of hits were marginally longer for semantic foils than for non-semantic foils [$M = 1078.54 \pm 40.96$ vs. $M = 1041.60 \pm 37.22$, respectively; $t(20) = 1.89$, $p = 0.074$, 95% CI (−3.94, 77.82), Cohen's $d = 0.48$] (Table 1).

TABLE 1 Performance during Phase 2 and Phase 3 in the semantic and non-semantic conditions.

	Recognition accuracy				Reaction time (ms)			
	Old words		New words		Old words		New words	
	Semantic	Non-semantic	Semantic	Non-semantic	Semantic	Non-semantic	Semantic	Non-semantic
Phase 2	0.77 (0.03)	0.70 (0.02)	0.68 (0.02)	0.55 (0.03)	850.86 (20.45)	891.20 (31.21)	919.49 (26.91)	942.19 (27.44)
Phase 3	0.32 (0.03)	0.44 (0.02)	0.51 (0.03)		1078.54 (40.96)	1041.60 (37.22)	987.30 (27.83)	

Note: Values are Mean (SD).



Event-related potentials

In Phase 2, during the FN400 (350–450 ms) epoch, we found a main effect of response [$F(1,20)=6.29, p=0.02, \eta_p^2=0.24$], with post-hoc multiple comparisons revealing that hits were significantly more positive than correct rejects ($p=0.02$). A marginally significant main effect of task type was also observed [$F(1,20)=3.74, p=0.06, \eta_p^2=0.16$], with post-hoc multiple comparisons revealing that the non-semantic condition was marginally significantly more negative than the semantic condition ($p=0.06$). A significant interaction effect between the task type and response was observed [$F(2,20)=5.98, p=0.02, \eta_p^2=0.23$]. A simple effects analysis showed that FN400 was more negative for correct rejects of foils than for hits of old words in non-semantic trials ($p=0.002$) and that there was no FN400 effect in semantic trials; non-semantic trials were significantly more negative than semantic trials in terms of hits for old words ($p=0.01$). This result indicates that the recognition process in non-semantic trials is more dependent on familiarity than in semantic trials. No other significant main or interaction effects were observed.

During the LPC (700–800 ms) epoch, we found a main effect of task type [$F(1,20)=6.57, p=0.02, \eta_p^2=0.25$] and a significant interaction effect between the task type and response [$F(2,20)=7.59, p=0.01, \eta_p^2=0.28$]. A simple effects analysis

showed that LPC was more positive for correct rejects of foils than for hits of old words in semantic trials ($p=0.006$), but not so for the non-semantic trials ($p=0.35$); non-semantic trials were significantly more positive than semantic trials in terms of hits for old words ($p=0.001$). This result indicates that the recognition process in semantic trials is more dependent on recollection than in non-semantic trials. No other significant main or interaction effects were observed ($ps>0.1$) (Figure 2A).

In Phase 3, during the FN400 epoch, no significant main or interaction effects were observed ($ps>0.1$). During the LPC epoch, we found a main effect of task type [$F(2,40)=3.03, p=0.04, \eta_p^2=0.14$]. Post-hoc multiple comparisons revealed that non-semantic hits for foils were significantly more positive than were correct rejects for new words ($p=0.03$); semantic hits for foils were significantly more positive than were correct rejects for new words ($p=0.04$). No significant main effect for electrode [$F(3,60)=0.93, p>0.1$] or interaction effects between task type and electrode [$F(6,120)=0.78, p>0.1$] were observed (Figure 2B).

Discussion

The aim of this study was to investigate the effect of the retrieval strategy involved in the successful encoding of new “foil” information

presented during a recognition test when participants engaged in a semantic vs. non-semantic task. In doing so, we demonstrate the influence of the retrieval strategy in different tasks on foils encoding in recognition tests, and further discuss differences in the foil effect between Chinese and English character materials.

Our behavioral results showed that the recognition performance in the semantic condition was better than in the non-semantic condition in Phase 2, thus supporting the results from earlier studies by demonstrating the typical LoP effect (Rugg and Wilding, 2000; Roediger et al., 2002). Notably, the foil effect refers to semantic foils, which were remembered significantly more accurately than non-semantic foils in Phase 3 (Jacoby et al., 2005; Marsh et al., 2009; Salhi and Bergstrom, 2020). However, interestingly, we found higher accuracy and shorter RTs for non-semantic foils. To investigate the influence of the recognition process on foils encoding, we focused on the analysis of old/new effects in the recognition test, thereby providing a new perspective for clarifying the mechanism underlying the foil effect. In Phase 2, there was significant FN400 in the non-semantic condition and LPC in the semantic condition. To some extent, this finding is similar to previous results (Rugg and Wilding, 2000; Rugg and Curran, 2007). There was an LPC effect in both the semantic and non-semantic foils in Phase 3.

Clearly, the behavioral results in Phase 3 are significantly different from the foil effect. By comparing previous studies and our research, it is evident that both semantic and non-semantic tasks are used to control processing depth. However, whereas English was used as the experimental material in previous studies (Jacoby et al., 2005; Halamish et al., 2012; Vogelsang et al., 2016, 2018), this study used Chinese; the orthographic characteristics of words in Chinese and English affect memory performance (Phase 3) for foils.

English is different from Chinese in terms of the representations and mappings between orthography, phonology, and semantics (Booth et al., 2006). English is an alphabetic language whereas Chinese is a logographic language, with less systematic information on phonology (Zhu et al., 2014). In English, the structure of a word is fixed by the order of the letters from left to right, with most of the letters having one pronunciation. The composition of Chinese characters, which uses radicals, does not follow one-to-one pronunciation rules (Booth et al., 2006; Zhu et al., 2014; Tian et al., 2020). Thus, compared to English, Chinese has a different orthographic system that has more clues to semantics (Booth et al., 2006; Tian et al., 2020; Wu et al., 2020). Chinese characters encode meaning by including a semantic radical (Booth et al., 2006; Zhu et al., 2014; Liu et al., 2020). Therefore, participants judged the orthographic characteristic of the words in the non-semantic study task, and there was a by-product of semantic information in Phase 1. Therefore, the recognition test in non-semantic conditions mainly relies on the familiarity of glyph features. This causes the participants to pay attention to the glyph features of all the test words, thereby enhancing their memory of new words. In the semantic task, the participants generated rich details during pleasure judgment, making the judgments based on one or more

specific pieces of detailed information during recollection. However, this causes the participants to ignore the processing of other information related to the test words and weakens their memory of new words. Therefore, in Phase 2, the semantic and non-semantic conditions were driven by recollection and familiarity, respectively. This difference led to differences in the encoding level of new words under the two conditions. The difference in orthography between Chinese and English resulted in better memory performance in relation to non-semantic foils in the final recognition test.

In Phase 2, the ERP effect differed in semantic vs. non-semantic trials. Specifically, we observed the FN400 component on non-semantic trials, which is associated with familiarity, and the LPC component on semantic trials, which is associated with recollection, in line with previous opinion. This result indicates that the non-semantic test block mainly depends on familiarity, whereas the semantic test block mainly depends on recollection in constrained retrieval (Friedman and Johnson, 2000; Rugg and Birch, 2000; Rugg and Wilding, 2000). However, there was an LPC effect in both the semantic and non-semantic foils in Phase 3, in line with our hypothesis. This suggests that the participants engage in recollection during the final recognition test, which can be inferred from previous literature. In the memory-for-foils paradigm, participants did not know the existence of Phase 3 in advance (Jacoby et al., 2005; Vogelsang et al., 2016; Salhi and Bergstrom, 2020), so they did not consciously memorize test words, especially foils, in Phase 2. Therefore, when the final surprise recognition test was administered, participants tried to recollect relevant details to improve their memory performance.

Of note, the LPC was more positive for correct rejects than for hits during semantic trials in Phase 2. Previous recognition memory research has suggested that the old/new effect is associated with decision accuracy and participants' confidence about familiarity and recollection (Finnigan et al., 2002; Gao et al., 2019). According to this view, the reversed LPC suggests that participants were less confident about old words than about new words in the semantic test block.

In the non-semantic task, the participants formed perceptual memories of word shapes and radicals, and the familiarity thus generated helped word recognition. The participants compared the memorized information with the test words in this process. Consequently, they incidentally embedded similar perceptual information in non-semantic foils. In the semantic task, the participants generated accurate semantic information for test words, which helped quickly distinguish between words. Therefore, semantic foils had less embedded information. The difference in the information embedded in foils led to better incidental memory for non-semantic foils.

Conclusion

The present study used FN400 and LPC to delineate the influences of familiarity from those of recollection on incidental

encoding for new foils during constrained retrieval. Behavioral results indicated that semantic trials that performed better in Phase 2 performed worse in Phase 3, while non-semantic trials that performed worse in Phase 2 performed better in Phase 3. The ERP results indicated that non-semantic and semantic trials evoked FN400 and LPC, respectively, in Phase 2, but both evoked LPC in Phase 3. This study thereby demonstrated that constrained retrieval is associated with familiarity and recollection during non-semantic and semantic trials, respectively. Different retrieval strategies affect incidental encoding for new words as foils during semantic and non-semantic trials, and the difference may be influenced by the perceptual information involved in the study materials.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The studies involving human participants were reviewed and approved by the Research Ethics Committee of the Northeast Normal University of China. The patients/participants provided their written informed consent to participate in this study.

Author contributions

MY and YJ contributed to the conception and design of the study. MY organized the database and wrote the first draft of the manuscript. MY and CC performed the statistical analysis. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Attentional attenuation (rather than attentional boost) through task switching leads to a selective long-term memory decline

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Allocating attention determines what we remember later. Attentional demands vary in a task-switching paradigm, with greater demands for switch than for repeat trials. This also results in lower subsequent memory performance for switch compared to repeat trials. The main goal of the present study was to investigate the consequences of task switching after a long study-test interval and to examine the contributions of the two memory components, recollection and familiarity. In the study phase, the participants performed a task-switching procedure in which they had to switch between two classifications tasks with pictures. After a short vs. a long study-test interval of a week, the participants performed a surprise memory test for the pictures and gave remember/know judgements. The results showed that recognition memory declined after 1 week and this was mainly due to a decrease in “remember” responses. The results also showed that the task-switching effect on memory was enduring. Whereas the results of the immediate test were mixed, the results of the delayed tests showed that the task-switching effect was based on recollection, expressed in more “remember” responses for repeat than for switch trials. As recollection is more sensitive to attention manipulations than familiarity, the results align with the notion that attentional requirements at study determine what we remember, in particular after a long study-test interval.

KEYWORDS

task switching, recollection, remember/know paradigm, attention attenuation, delayed memory

Introduction

Attention and memory are fundamentally connected (Chun and Johnson, 2011). While our memories influence what we attend to, attention determines what we remember later (Becker and Rasmussen, 2008). Attending to or focusing on an event enhances the likelihood of encoding this event for later memory retrieval (Chun and Turk-Browne, 2007). For example, transient increases in attention to one task can enhance memory

performance in a second task, an effect known as the *attentional boost effect* (Swallow and Jiang, 2010, 2013). In contrast, when cognitive control demands increase, the ability to attend to an item is reduced and as a consequence memory performance is impaired (Gardiner and Parkin, 1990; Lavie, 2010; Richter and Yeung, 2012, 2015; Craik et al., 2018; Muhmenthaler and Meier, 2019; Greene and Naveh-Benjamin, 2022). For example, when people perform multiple tasks simultaneously (Craik et al., 1996; Naveh-Benjamin et al., 1998), when they are distracted by irrelevant stimuli (Jenkins et al., 2005; Wais et al., 2010) or when they have to switch between two competing tasks, target memory is impaired (Richter and Yeung, 2012; Muhmenthaler and Meier, 2019; Dubravac and Meier, 2020; Muhmenthaler and Meier, 2021a). In the present study, we used a task-switching procedure with pictures to manipulate the attentional demands, then we assessed recognition memory either immediately or after a week. The main goal of our study was to extend the research on task switching by investigating recognition performance after a long retention interval. Moreover, we examined the contributions of recollection and familiarity on memory performance. As recollection relies on attention during encoding (Jacoby et al., 1989; Gardiner and Parkin, 1990), we assumed that the effect may be based mainly on recollection.

The task-switching paradigm has been developed as an experimental approach to explore the mechanisms of cognitive control by comparing task switch and task repetition trials (Rogers and Monsell, 1995; Wylie and Allport, 2000). Task switching usually results in slower performance for switch compared to repeat trials (i.e., switch costs) due to the enhanced attentional requirements. Recently, several studies have investigated the impact of task switching on subsequent memory. For example in a study by Richter and Yeung (2012), compound stimuli which consisted of picture–word pairs were used at study and participants had to switch between classifying pictures versus words, after a brief delay recognition memory was tested. The results showed that task switching compared to task repetition resulted in lower recognition memory of the targets. Switching requires more attention than repeating and thus reduces the working memory resources available for encoding these stimuli. The consequence is reduced memory performance (Lavie, 2005; Chun and Turk-Browne, 2007; Uncapher and Wagner, 2009; Chun and Johnson, 2011; Meier and Muhmenthaler, 2021). Several studies have replicated that task switching results in a memory cost for switch stimuli (Richter and Yeung, 2015; Muhmenthaler and Meier, 2019; Dubravac and Meier, 2020). The goal of the present study is to expand this research by investigating the impact of task switching on memory after a longer delay (i.e., 1 week) and to investigate the contributions of recollection and familiarity to the task-switching effect.

Recollection and familiarity reflect two distinct processes of declarative memory (Yonelinas, 2002). Recollection reflects controlled processing and strategic elaboration and is accompanied by vivid and rich contextual details of previously experienced events. Familiarity reflects automatic processing and is accompanied by the feeling that an event has been

experienced before, in the absence of contextual information about that event (Jacoby and Witherspoon, 1982; Jacoby et al., 1989; Yonelinas, 2002). The subjective qualitative estimates of memories can be derived using the “remember/know” paradigm which was developed by Tulving (1985). A “remember” response indicates that seeing the stimulus brings back to mind some specific recollection with contextual details of what was experienced. A “know” response indicates that seeing the stimulus brings to mind a feeling of familiarity, without any contextual details (Gardiner and Java, 1991; Hockley and Consoli, 1999).

Dual-process theories posit that both forms of recognition memory decrease with time, but at different rates with a faster decline for recollection than for familiarity (Gardiner and Java, 1991; Hockley and Consoli, 1999; Joordens and Hockley, 2000; Meier et al., 2013). The different trajectories of the memory components provide evidence that they reflect different processes and not just correspond to strong and weak memory traces (Gardiner, 1988; Gardiner and Java, 1991). Specifically, the processes underlying recollection are more attention demanding than familiarity-based processes. This is reflected in the evidence that full-attention conditions at study lead to more “remember” responses than divided-attention conditions, whereas “know” responses are quite unaffected (Jacoby and Witherspoon, 1982; Gardiner and Parkin, 1990; Mangels et al., 2001; Yonelinas, 2002). As the task-switching effect also relies on attentional processes, it is straightforward to assume that it is associated with recollection. Indeed in a recent study, the task-switching effect was driven by significantly more “remember” responses in repeat than in switch trials, whereas “know” responses did not vary with task switching (Muhmenthaler and Meier, 2019). However, it is unclear whether this effect is enduring.

The present study

In two task-switching experiments, we used pictures as stimuli and the participants had to classify them as “smaller” or “bigger than a soccer ball” or as “living” or “non-living” (cf., Muhmenthaler and Meier, 2019). All the stimuli could be used for both tasks, the stimuli were therefore bivalent (Woodward et al., 2003). After the study phase, a surprise recognition memory test was conducted. The participants had to decide whether a stimulus was “old” or “new,” then we applied the “remember/know” procedure to assess the estimates of recollection and familiarity (Tulving, 1985; Yonelinas, 2002). In Experiment 1, the participants performed the recognition test either immediately or after 1 week. In Experiment 2, in order to increase the statistical power for the delayed task switching on memory effect, all the participants performed the memory test after 1 week.

We expected overall lower recognition memory performance after 1 week. As recollection-based memory declines more rapidly than familiarity-based memory, we hypothesized that the decline would be due to a decrease in “remember” responses

(Gardiner, 1988; Gardiner and Java, 1991; Sadeh et al., 2014). Based on previous research, we expected a task-switching effect on immediate memory. We further hypothesized that this effect may be enduring and thus be intact in the delayed tests. Due to more available attentional resources in repeat than in switch trials, more elaborated processing is possible, and this boosts sustainable learning, that is, a benefit after a longer delay (Gardiner, 1988; Gardiner and Java, 1991; Meier and Muhmenthaler, 2021). As recollection is more sensitive to attention manipulations than familiarity, we expected that the task-switching effect would be based on recollection. We wanted to explore whether this effect would be enduring.

Experiment 1

Method

Participants

The participants were 80 undergraduate students (18 male and 62 female) from the University of Bern. The age ranged from 18 to 31 years ($M = 22.10$, $SD = 2.47$) and they received course credits for participation. Due to the pandemic, the experiment was conducted as an online-study. The study was approved by the local ethical committee.

Material

For the experimental trials, a total of 128 colored photographs were used (cf. Muhmenthaler and Meier, 2019). The stimuli derived from four categories: Objects which were larger than a soccer ball and living (e.g., an elephant), larger than a soccer ball and not living (e.g., a car), smaller than a soccer ball and living (e.g., a fly), smaller than a soccer ball and not living (e.g., a lipstick). All the stimuli could unambiguously be classified both as smaller-or-bigger than a soccer ball and as living or non-living, thus the stimuli could be used for both tasks, that is, they were bivalent. Each stimulus category involved 32 stimuli. Stimuli were arranged in separate lists of 64 pictures, counterbalanced across trial type, classification task and assigned response key. One of the lists was used in the study phase, and both lists were presented in the test phase. Lists were counterbalanced across participants. Four additional stimuli were used for a short practice block, one per category.

The experimental task was programmed with the Open Sesame interface (Mathôt et al., 2012). The study was hosted on a JATOS open-source server (Lange et al., 2015).

Procedure

After signing up for the experiment, the participants received web links *via* email. Half of the participants were assigned to the immediate test condition. They received three web links with the instruction to open them in a given order. The first link contained the study phase, the second link contained a questionnaire about digital habits (to create a filled retention interval of about 10 min)

and the third web link contained the test phase. The other half of participants were assigned to the delayed test condition. They received the study phase link only. They were told that they would receive a second link 6 days later with the instruction to perform the second part of the experiment exactly at the same day and time 1 week after they conducted the first part. They were not informed that their memory would be tested a week later.

Study phase

In the study phase, the participants were instructed to categorize stimuli as fast and as accurately as possible and to switch between the two tasks in a predictable AABB order. Participants had to perform the size task (smaller or bigger than a soccer ball) when the stimulus appeared in the upper part of the screen, and to perform the animacy task when it appeared in the lower part. The stimuli were presented clockwise, beginning in the upper half, see Figure 1. Half of the participants had to press the *a*-key when an object was bigger than a soccer ball or living, and the *l*-key when the object was smaller than a soccer ball or non-living. For the other participants, the response key assignment was *vice-versa*. The stimuli were presented until a response key was pressed, then the next stimulus was presented after a response–stimulus interval of 200 ms. The stimuli were presented randomized, each task twice in succession. After a brief practice phase with eight trials, participants performed the study phase with 64 trials.

Test phase

The test phase involved a surprise recognition memory test. Half of the participants conducted the test phase after a short retention interval, the other half conducted the test phase after 1 week. They were informed that they would see more pictures and that they had to indicate whether they had seen each picture already during the first phase of the experiment by pressing the *j*-key for an old-response or by pressing the *n*-key for a new response. In case of an old-response, they were asked to give an additional “remember/know” judgement by pressing the *1*-key for “remember” or the *2*-key for “know” on the number pad. They were instructed to give a “remember” response when they were sure that they had seen the picture and to give a “know” response when they perceived a feeling of familiarity. For each trial, the stimulus was presented until a response key was pressed. The stimuli appeared in randomized order with a response stimulus interval of 200 ms. One half of the stimuli were old (presented in the study phase) and the other half were new (not presented in the study phase).

Statistical analyses

In an *a priori* power analyses we computed the sample size as a function of the required power level, the significance level and the population effect size we expected, using G*Power for dependent-samples t-tests (Faul et al., 2007). We used an expected effect size for task switching of $f = 0.25$, based on previous results (cf. Muhmenthaler and Meier, 2019), a significance level of 0.05 and 0.90 as power level. The analysis computed 36 participants as

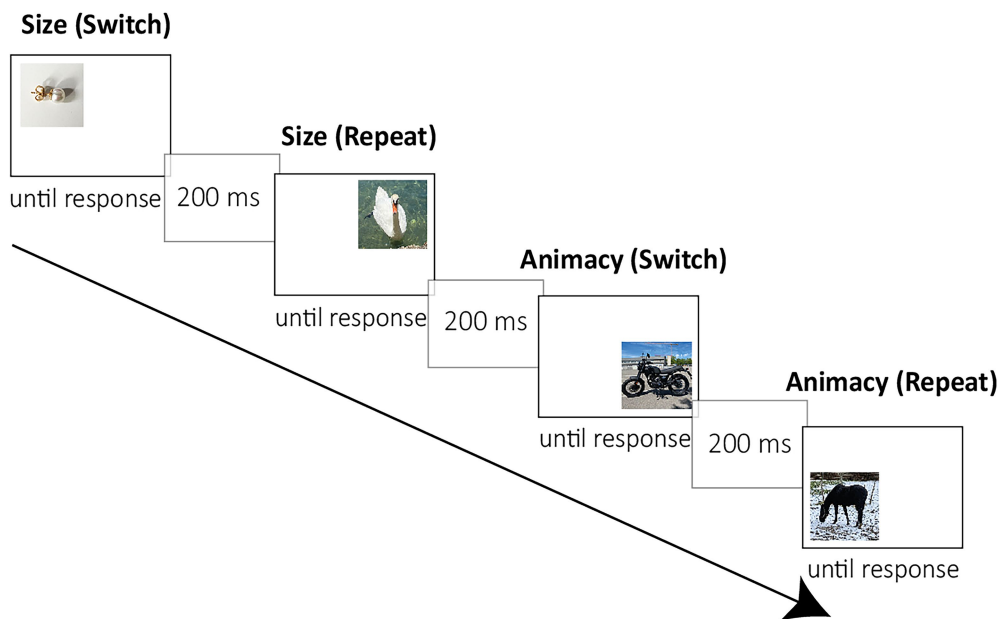


FIGURE 1

Example of a study trial sequence. The participants had to switch between two tasks in a predictable AABBA order. All the stimuli were bivalent (that is, they could be used for both tasks). All the images in the figure are photographs taken by MM.

an optimal sample size. As we conducted two independent recognition memory tests and due to counterbalancing considerations, we decided to test 80 participants (40 per test).

For the study phase, task-switching performance was analyzed using two-tailed paired sample *t*-tests for reaction times (RTs) and accuracy. For the test phase, we conducted a 2×2 ANOVA on study-test interval and on task switching, followed by planned paired sample *t*-tests on the task-switching on memory effect, separately for the immediate and the delayed test. As it is not possible to assign the false alarm rates to repeat or switch trials, we used hit rates only as recognition scores (Ortiz-Tudela et al., 2017; Muhmenthaler and Meier, 2019). To assess the contribution of recollection and familiarity on memory performance, “remember” and “know” responses were analyzed accordingly. An alpha level of 0.05 was used. Effect sizes are expressed as Cohen’s *d*. Non-significant results were followed up by Bayesian analyses.

Results

Study phase

Task switching performance was analyzed using two-tailed paired sample *t*-tests for accuracy and RTs. We considered responses slower than 200 ms and longer than 2,500 ms as outliers (11.9% of all responses). The analysis of the accuracy revealed that participants were more accurate on repeat ($M=0.94$, $SE<0.01$) than on switch trials ($M=0.92$, $SE<0.01$), $t(79)=3.48$, $p<0.001$, $d=0.389$. For the RTs, we moreover excluded error trials (7.7% of all responses). The analysis of the trimmed reaction times revealed

faster RT on repeat ($M=1165$ ms, $SE=24$) than on switch trials ($M=1777$ ms, $SE=48$), $t(79)=16.7$, $p<0.001$, $d=1.86$. The results showed the expected switch costs.

Test phase

Hits

The 2×2 repeated measures ANOVA with the between-subject factor study-test interval and the within-subject factor task switching on the hits (correctly recognized old pictures) revealed better memory performance in the immediate ($M=0.80$, $SE=0.03$) than in the delayed memory test ($M=0.45$, $SE=0.03$), $F(1, 78)=93.50$, $p<0.001$, $\eta_p^2=0.55$. Overall, more repeat stimuli ($M=0.64$, $SE=0.02$) were correctly recognized than switch stimuli ($M=0.61$, $SE=0.02$), $F(1, 78)=8.73$, $p=0.004$, $\eta_p^2=0.10$. The interaction between study-test interval and task switching was not significant, $F(1, 78)<1$, $p=0.844$, $\eta_p^2<0.01$. We further conducted planned contrasts for each study-test interval separately. These two-sided paired sample *t*-tests revealed that the task-switching effect on memory remained intact in both tests (immediate: $t(39)=2.63$, $p=0.009$, $d=0.428$; delayed: $t(39)=2.07$, $p=0.045$, $d=0.319$).

“Remember” responses

The same 2×2 ANOVA on “remember” responses revealed that the study-test interval was significant with more “remember” responses in the immediate ($M=0.67$, $SE=0.02$) than in the delayed test ($M=0.21$, $SE=0.02$), $F(1, 78)=180.74$, $p<0.001$, $\eta_p^2=0.70$. More “remember” responses were associated with repeat ($M=0.47$, $SE=0.02$) than with switch trials ($M=0.41$, $SE=0.02$),

$F(1, 78) = 25.12, p < 0.01, \eta_p^2 = 24$. The interaction between interval and task switching was not significant, $F(1, 78) < 1, p = 0.403, \eta_p^2 = 0.01$. We further conducted planned contrasts for both study-test intervals separately. These two-sided paired sample t -tests revealed that the effect on “remember” responses on task switching was significant in both tests (immediate: $t(39) = 3.93, p < 0.001, d = 0.614$; delayed: $t(40) = 3.04, p = 0.004, d = 0.469$).

“Know” responses

The 2×2 ANOVA on “know” responses revealed that the study-test interval was significant with more “know” responses in the delayed ($M = 0.24, SE = 0.01$) than in the immediate test ($M = 0.13, SE = 0.01$), $F(1, 78) = 29.91, p < 0.001, \eta_p^2 = 0.28$. More “know” responses were associated with switch ($M = 0.20, SE = 0.01$) than with repeat trials ($M = 0.17, SE = 0.01$), $F(1, 78) = 8.19, p = 0.005, \eta_p^2 = 0.10$. The interaction between interval and task switching was not significant, $F(1, 78) = 1.56, p = 0.215, \eta_p^2 = 0.02$. We further conducted planned contrasts for both study-test intervals separately. These two-sided paired sample t -tests revealed a significant result in the immediate test ($t(39) = 2.65, p = 0.012, d = 0.413$) and a non-significant result in the delayed test ($t(39) < 1, p = 0.416, d = 0.128$). In order to test the robustness of the null effect, a Bayesian analysis was conducted (Dienes et al., 2018). Using JAMOV, we calculated a Bayesian two-sided paired sample t -test on the “know” responses. The resulting BF of 0.313 indicates evidence for the null hypothesis (i.e., is 3 times more likely than the alternative hypothesis; Jarosz and Wiley, 2014). Accordingly, the contribution of “know” responses did not differ for repeat and switch trials in the delayed test.

False alarms

In the immediate test false alarm rate was 7% in the immediate test and 27% in the delayed test, $t(78) = 10.50, p < 0.001, d = 2.34$.

Achieved power

The achieved power in the immediate test was 0.84, when calculating power with the empirical effect size of $d = 0.428$, an alpha level of 0.05 and the sample size of 40. The achieved power in the delayed test was 0.63, when calculating power with the empirical effect size of $d = 0.319$, an alpha level of 0.05 and the sample size of 40.

Discussion

The results replicated that task switching hurts memory for switch stimuli. Moreover, they showed that this effect was enduring. The results also showed more “remember” responses in repeat than in switch trials for both study-test intervals. Thus, the task-switching effect on memory was mainly based on recollection. The results for the “know” responses were somewhat less clear. Overall, familiarity also seemed to contribute to the task switching effect on memory, but planned comparisons revealed a

contribution only in the immediate, but not in the delayed test. This may indicate that this contribution washed out over time.

In Experiment 2, we wanted to replicate the delayed memory effects with higher statistical power. Toward this goal, we designed a similar experiment, but all the participants were tested after 1 week only. Moreover, this study was conducted in the lab, thus providing the opportunity to replicate the results of the online study under controlled laboratory conditions.

Experiment 2

Method

Participants

The participants were 82 undergraduate students (20 male and 62 female) from the University of Bern. The age ranged from 18 to 42 years ($M = 23.20, SD = 3.50$) and they participated in the study for course credits. The study was approved by the local ethical committee and all the participants gave their written consent.

Materials and procedure

The materials and the procedure were identical to Experiment 1, with the following exceptions: The participants were tested individually in a lab at the University of Bern. The experiment was programmed with Eprime 2.0. Recognition memory was tested only after 1 week, in order to enhance statistical power and as we were mainly interested in delayed memory performance.

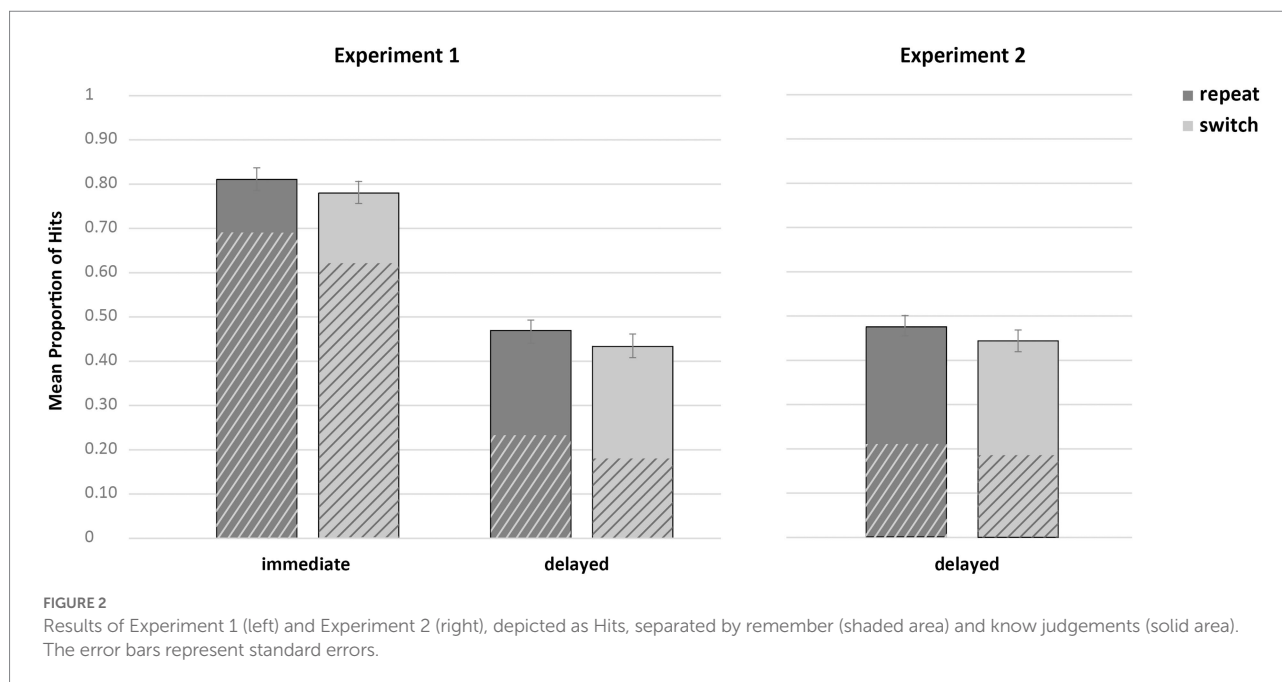
Analyses

In an *a priori* power analyses we computed the sample size as a function of the required power level, the significance level and the population effect size which we expected, using G*Power for dependent-samples t -tests (Faul et al., 2007). We used an expected effect size for task switching of $d = 0.319$, based on the result of the delayed test of Experiment 1, a significance level of 0.05 and 0.90 as power level. The analysis computed 86 participants as an optimal sample size. The statistical analyses were similar to Experiment 1.

Results

Study phase

We excluded 15.8% of all trials (error trials and outliers). The analysis of the trimmed reaction times revealed that the participants were significantly faster on repeat ($M = 1,203$ ms, $SE = 31$) than on switch trials ($M = 1,663$ ms, $SE = 39$), $t(81) = 18.17, p < 0.001, d = 2.01$. The analysis of the accuracy revealed that participants were more accurate on repeat ($M = 0.94, SE < 0.01$) than on switch trials ($M = 0.91, SE < 0.01$), $t(81) = 3.58, p < 0.001, d = 0.395$. The results showed the expected switch costs.



Test phase

The overall recognition memory performance was 46% ($SD=0.15$) with a false alarm rate of 18% ($SD=11$). The critical results are depicted in Figure 2. The two-tailed paired sample t -test on the hits revealed that more repeat stimuli ($M=0.48$, $SE=0.02$) were recognized than switch stimuli ($M=0.44$, $SE=0.02$), $t(81)=3.04$, $p=0.003$, $d=0.335$. To assess the contribution of recollection and familiarity on memory performance, additional t -tests on “remember” and “know” responses were conducted. The results showed that significantly more “remember” responses were given for repeat ($M=0.21$, $SE=0.01$) than for switch trials ($M=0.19$, $SE=0.01$), $t(81)=2.54$, $p=0.013$, $d=0.280$. The “know” responses did not vary with trial type (both: $M=0.26$, $SE=0.01$), $t(81)<1$, $p=0.714$, $d=0.041$. A Bayesian two-sided paired sample t -test on the “know” responses gave a BF of 0.130, indicating that the evidence for the null hypothesis is 8 times more likely than the alternative hypothesis (Jarosz and Wiley, 2014). Accordingly, the contribution of “know” responses for repeat and switch trials did not differ.

Achieved power

The achieved power in this experiment was 0.91, when calculating power with the empirical effect size of $d=0.335$ in the delayed memory test, an alpha level of 0.05 and the sample size of 82.

Discussion

Replicating Experiment 1, the results of Experiment 2 showed the task-switching effect after 1 week. Moreover, recollection was critical for this effect, as more “remember” responses were given for repeat than for switch stimuli. In contrast, familiarity did not differ, as “know” responses did not vary with trial type.

General discussion

The *attentional boost effect* denotes that transient increases in attention to one task can enhance memory performance in a second task (Swallow and Jiang, 2010, 2013). Here, we rather provided evidence for an *attentional attenuation effect*: When the cognitive control demands are high, the ability to attend to an item is reduced which results in lower memory performance (Reynolds et al., 2004; Craik et al., 2018; Muhmenthaler and Meier, 2019). In two experiments, we showed this effect by using a task-switching procedure at study. The results revealed a consistent memory cost for switch compared to repeat stimuli, regardless whether memory was tested immediately or after 1 week.

Interestingly, enhanced cognitive control demands do not necessarily reduce encoding capacity in all circumstances. Studies of Stroop or Flanker conflict on subsequent memory performance found improved memory performance for incongruent compared to congruent stimuli (Krebs et al., 2015; Rosner et al., 2015; Muhmenthaler and Meier, 2021a,b). In contrast, in dual-task and divided-attention situations typically a memory deficit occurs for target stimuli, similarly to the effect of task switching (Dell'Acqua and Jolicoeur, 2000; Vachon and Jolicoeur, 2011; Greene and Naveh-Benjamin, 2022). Thus, there are conditions, which divert cognitive resources away from stimulus encoding, leading to lower memory and there are conditions which increase encoding of conflict stimuli (Botvinick et al., 2004). So far, these memory effects have been mainly investigated after a short study-test interval. Here we demonstrate similar consequences after a longer retention interval.

To our knowledge, there is only one task-switching study that has also investigated a longer study-test interval (Dubravac and Meier, 2022). In this study, the participants had to switch between a word and a picture classification task on compound

stimuli (i.e., targets and distractors) similar to Richter and Yeung (2012). Across five experiments, memory selectivity, that is, the relative advantage of targets over distractors was tested either immediately, after one day or after 1 week. With longer retention intervals, memory selectivity washed out, but the recognition memory advantage of switch vs. repeat targets persisted. In line, our results showed a robust task-switching effect after 1 week. Compared to task switching, task repeating requires fewer working memory resources and thus provides the opportunity for more elaborated processing (Barrouillet et al., 2007; Liefooghe et al., 2008; Lavie, 2010). As elaborated processing leads to deeper memory traces, sustainable effects on learning occur, resulting in better long-term memory (Gardiner, 1988; Gardiner and Java, 1991; Bjork and Bjork, 2011; Meier and Muhmenthaler, 2021).

Our study focused on the contributions of recollection and familiarity to recognition memory performance. The results of both experiments revealed that the task-switching effect was driven by recollection. More “remember” responses were given for repeat than for switch trials. This result is in line with a recent study, in which we found the task-switching effect with a free recall test (Muhmenthaler and Meier, 2021a,b). Free recall is based on self-initiated retrieval processes which is more similar to recollection than to familiarity (Jacoby et al., 1989; Yonelinas, 2002). Thus, the present study demonstrates that recollection is at the core of the task-switching on memory effect for both free recall and recognition.

The present study also revealed that the effect of recollection was enduring. Similar results were obtained by Gardiner (1988). He investigated the long-term effects of a generation-versus-read manipulation and the contributions of recollection and familiarity. The generation effect occurs when people remember words presented as fragments better than words that are complete from the start. The effect relies on more elaborated processing in the word-generating compared to the word-reading condition (Graf, 1978; Begg et al., 1991). The results showed an enduring generation effect, and this effect was driven by recollection. Thus, as with task switching, the results showed that elaborated and effortful processing can foster long-term learning (Bjork and Bjork, 2011).

Evidence for enduring memory effects may be inferred from a neuroimaging study (Carr et al., 2010). In this study, the authors assessed memory performance for studied items both after ten minutes and after a one-week interval with the remember/know paradigm. The results showed that the encoding activity in the prefrontal cortex was significantly greater for items that later were consistently recollected (i.e., recollective in both tests) than for items which became familiar within a week or were consistently familiar. This highlights that items which are recollected later are differently processed at encoding. As enhanced prefrontal activity indicates elaborated and effortful processes, the neuropsychological data are in line with our results. An avenue for future research may be to use imaging methods to test the

hypothesis that repeat items which lead to an experience of recollection at test engage more frontal activity at study.

In our study, the estimates of recollection and familiarity were assessed on a subjective level, which can be seen as a limitation. The participants were asked whether they were sure about their decisions or whether they perceived a feeling of familiarity (Tulving, 1985). In order to assess recollection on a more objective level, besides using imaging, one could also assess the retrieval of contextual detail by asking the participants in which task or on which position they had encountered a specific stimulus (cf., Yonelinas and Levy, 2002). When participants can accurately respond this indicates that they have recollected some qualitative information about the encoding episode. Assessing the familiarity of the stimulus should not provide the contextual information. Assessing recollection and familiarity in this fashion might be an avenue for further research.

Finally, we want to note that the online study and the lab study resulted in very similar results, thereby giving us confidence in the validity of the results of our online experiment.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

Ethics statement

The studies involving human participants were reviewed and approved by Ethical committee of the Human faculty of the University of Bern. The participants provided their written informed consent to participate in this study.

Author contributions

MM and BM designed the experiments and wrote the manuscript. MM analyzed the data. Both authors contributed to the article and approved the final version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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The attentional boost effect and perceptual degradation: Assessing the influence of attention on recognition memory

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Researchers have suggested that the recognition memory effects resulting from two separate attentional manipulations—attentional boost and perceptual degradation—may share a common cause; namely a transient up-regulation of attention at the time of encoding that leads to enhanced memory performance at the time of retrieval. Prior research has demonstrated that inducing two similar transient shifts of attention simultaneously produces redundant performance in memory. In the present study, we sought to evaluate the combined influence of the attentional boost and perceptual degradation on recognition memory. If these two effects share a common cause, then we ought to observe a redundancy in memory performance, such that these two factors interact. Yet, across four experiments we fail to observe such a redundancy in recognition memory. We evaluate these results using the limited resource model of attention and speculate on how combining transient shifts of attention may produce redundant memory performance in the one case, but non-redundant performance in the other case.

KEYWORDS

attention, recognition memory, attentional boost effect, divided attention, degradation effect

Introduction

It is axiomatic that attention plays an important role in remembering—“paying attention” improves remembering, and divided attention undermines remembering (e.g., [Jacoby et al., 1993](#); [Craik et al., 1996](#)). At the same time, attention is a multifaceted construct (e.g., [Posner and Peterson, 1990](#)), and the study of how particular attention processes influence memory is an emerging field of interest. In the present study, we examined the effect of transient shifts of attention on memory encoding, with a particular focus on two distinct effects thought to

be produced by such transient attention shifts: the attentional boost effect and the perceptual degradation effect.

The attentional boost effect

It is well established that engaging in two tasks simultaneously is associated with performance costs (Welford, 1952). These dual task costs are sometimes attributed to attentional resources being limited; use of attentional resources on one task reduces resource availability for a second task (Wickens, 1980). Alternatively, dual task costs have been attributed to a bottleneck occurring at the response selection stage (Pashler, 1994); while one task occupies that processing stage, access for a second task is postponed and thus produces performance costs. Both of these theoretical views have been applied to a wide range of dual task interference effects.

Although dual task performance costs may be the norm, Swallow and Jiang (2010) reported a dual task benefit, where attending to two tasks simultaneously during an encoding phase produced superior memory in a following test phase. In the divided attention trials of their study, participants studied a series of natural images while also performing a secondary detection task. Each natural image was overlaid with a small square for 100 ms—a white square on 20% of trials and a black square on 80% of trials. While studying the images, the secondary task involved detecting white target squares with a button press while ignoring black distractor squares. Importantly, recognition memory of natural images was better on target trials than distractor trials. In fact, recognition on target trials did not differ from a full attention condition in which participants' only task was to remember the natural images. Swallow and Jiang labelled the surprisingly good memory on divided attention target trials the *attentional boost effect* (ABE). They proposed that detecting a target produces a transient up-regulation of attention during an early phase of encoding that enhances memory for items in close spatiotemporal proximity to the target.

Mulligan et al. (2014) subsequently extended the attentional boost procedure to lexical materials. Word frequency effects in recognition are well established, with the usual finding that recognition is better for low than high frequency words (Gorman, 1961). Mulligan et al. noted that low frequency words may attract more attention than high frequency words in an early phase of encoding (Glanzer and Adams, 1990; Criss and Malmberg, 2008). If this is the case, then word frequency effects in recognition could be driven by the same transient up-regulation of attention that produces the ABE. Mulligan et al. reported a pattern of data consistent with this idea—a robust ABE for high frequency but not for low frequency words.

The perceptual degradation effect

Several studies have demonstrated that increased perceptual processing difficulty can result in improved memory (Nairne,

1988; Hirshman and Mulligan, 1991; Hirshman et al., 1994; Mulligan, 1996; Mulligan, 1999; Diemand-Yauman et al., 2011; Rosner et al., 2015; although see Yue et al., 2013), in line with the desirable difficulty principle (Bjork, 1994). One account of these processing difficulty effects is that, like low frequency words and target detection, processing difficulty results in a transient up-regulation of attention that improves memory encoding. For example, Rosner et al. had participants read an intermixed list of clear and blurry words in an incidental study phase. Participants then completed a recognition test for the words they had previously read. Recognition sensitivity was better for blurry than clear words. Rosner et al. suggested that a transient up-regulation of attention may have strengthened memory encoding and consequently improved recognition for blurry items.

The purpose of the present study was to evaluate the relation between perceptual degradation and attentional boost effects on recognition by examining them together. We were particularly interested in whether transient shifts of attention on 'boost' (target present) trials and on blurry trials would be redundant, as appears to be the case for 'boost' and low frequency trials (Mulligan et al., 2014). If target detection and perceptual degradation produce redundant transient shifts of attention, then we should observe a larger ABE for clear than for blurry words.

Experiments 1a and 1b

To measure both the attentional boost and perceptual degradation effects in Experiment 1a, participants read clear and blurry words while monitoring for and responding to target signals. According to Swallow and Jiang (2010), the ABE reflects an up-regulation of attention to items in close spatiotemporal proximity to targets that strengthens memory encoding. Rosner et al. (2015) proposed a similar account for the perceptual degradation effect—a transient up-regulation of attention for blurry items strengthens memory encoding. Our goal was to examine whether these two attention manipulations produce redundant effects on recognition. If so, then the attentional boost effect should be larger for clear than blurry words.

Experiment 1b was conducted as a full attention control condition. Participants read clear and blurry words, but were told nothing about the target and distractor boost signals. In this experiment, we should observe a perceptual degradation effect, but no ABE. Furthermore, performance for the target present trials in Experiment 1a should approximate that of the corresponding full attention condition in Experiment 1b (e.g., Swallow and Jiang, 2010; Mulligan et al., 2014).

Method

Participants

For all experiments in this article, participants were recruited from a pool of undergraduate psychology students at McMaster

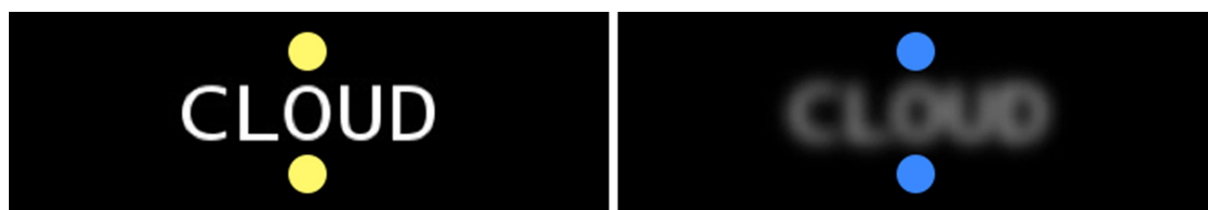


FIGURE 1

An example of a clear and blurry word, including target and distractor coloured dots, used in each of the four experiments.

University. Participants gave informed consent in accordance with the McMaster Research Ethics Board, reported normal or corrected-to-normal vision, and were compensated \$10 CAD or partial course credit. A power analysis conducted using G*Power 3 (Faul et al., 2007) aimed at measuring a large effect size (Cohen, 1988; Mulligan et al., 2014) with power = 0.80 revealed that 20 participants were required. For counterbalancing purposes, we collected data from 24 participants in both experiments. An *a posteriori* sensitivity analysis for a 2×2 repeated measures ANOVA assuming power = 0.80 revealed that we could reliably measure effect sizes larger than $f = 0.41$. Twenty-four undergraduates (20 females) ranging in age from 18 to 23 years ($M = 19.17$, $SD = 1.24$) participated in Experiment 1a. A separate group of 24 undergraduates (17 females) ranging in age from 18 to 22 years ($M = 18.92$, $SD = 1.10$) participated in Experiment 1b.

Apparatus and stimuli

Stimuli were presented on a 24-inch BENQ LCD monitor with a resolution of $1920 \times 1,080$ pixels, using PsychoPy software (Peirce, 2007, 2009). Manual responses were recorded using a QWERTY keyboard. The stimuli consisted of five letter high-frequency nouns (Kučera and Francis, 1967). The words subtended 4.01° of visual angle horizontally and 0.92° vertically. Clear words were presented as text stimuli using PsychoPy. Blurry words were created by applying a Gaussian blur radius of 15 pixels to each word using GNU Image Manipulation Program (GIMP).¹ Rosner et al. (2015) demonstrated that this level of degradation reliably produces perceptual disfluency effects in recognition of single words [see also Xie et al. (2018); Weissgerber et al. (2021) for an interesting recent debate about perceptual disfluency effects in recall of text]. The blurry words were imported into PsychoPy as picture files. On each trial of the study phase, one coloured dot appeared above the word and a second coloured dot appeared below the word. Each dot had a diameter that subtended 1.15° of visual angle, and both dots were either blue or yellow on any given trial. Examples of these stimuli are presented in Figure 1.

¹ gimp.org

Procedure

Participants were seated approximately 50 cm from the computer monitor. Each experiment consisted of a study phase, a distractor phase, and an incidental memory test phase. For Experiments 1a and 1b, the distractor and test phases were identical; the study phases differed slightly, as described below.

In Experiment 1a, the study phase included 10 practice trials and 120 experimental trials. Each trial began with a fixation cross for 200 ms, followed by a word and two coloured dots. The word was either clear or blurry, and both dots were either blue or yellow. The dots were presented for 100 ms, whereas the word remained on screen for 700 ms. Participants were instructed to: (1) read aloud the word; and (2) monitor the colour of the dots—if the dots matched the target colour, they were to press the spacebar.

In Experiment 1b, the study phase was identical to Experiment 1a with the exception that participants were instructed only to read aloud the word on each trial; they were told nothing about the dots that appeared with the words.

Following the study phase, there was a 10-min distractor task that required completion of arithmetic problems. Finally, the test phase involved an incidental recognition test. Each recognition trial began with presentation of a word. Participants were instructed to press the 'A' key for an 'old' response and the 'L' key, for a 'new' response. To assess recollection and familiarity (Rajaram, 1993; Yonelinas and Jacoby, 1995; Yonelinas, 2002) participants also made remember/know judgments following all 'old' responses. If participants 'remembered' seeing the word in the study phase they were to press the 'z' key, whereas if they had a feeling of 'knowing' the word had been presented in the study phase they pressed the '/' key (McCabe and Geraci, 2009). The remember/know procedure was included for exploratory purposes, and recollection and familiarity estimates and analyses are presented in Appendix A, but not in the body of the paper.

Design

The words were drawn from four lists of 60 words (see Appendix B). Of those 240 words, 120 were presented in both the study and test phases ('old' words). The remaining 120 words appeared only in the test phase ('new' words). For both 'old' and 'new' words, half appeared clear and half appeared blurry. This constraint was achieved by assigning one of the four lists to each of the clear 'old', blurry 'old', clear 'new', and blurry 'new'

TABLE 1 Proportions of hits and false alarms for each condition in Experiments 1a, 1b, 2a, and 2b. Standard errors corrected by removing overall between-participant variance are presented in parentheses (Morey, 2008).

Exp.	Clear Words			Blurry Words		
	Target	Distractor	FAs	Target	Distractor	FAs
1a	0.52 (0.02)	0.43 (0.02)	0.27 (0.02)	0.61 (0.03)	0.52 (0.02)	0.28 (0.02)
1b	0.50 (0.03)	0.48 (0.02)	0.27 (0.02)	0.59 (0.03)	0.61 (0.02)	0.28 (0.03)
2a	0.49 (0.02)	0.41 (0.01)	0.24 (0.01)	0.60 (0.03)	0.49 (0.02)	0.28 (0.02)
2b	0.52 (0.02)	0.47 (0.02)	0.31 (0.01)	0.61 (0.02)	0.51 (0.02)	0.31 (0.02)

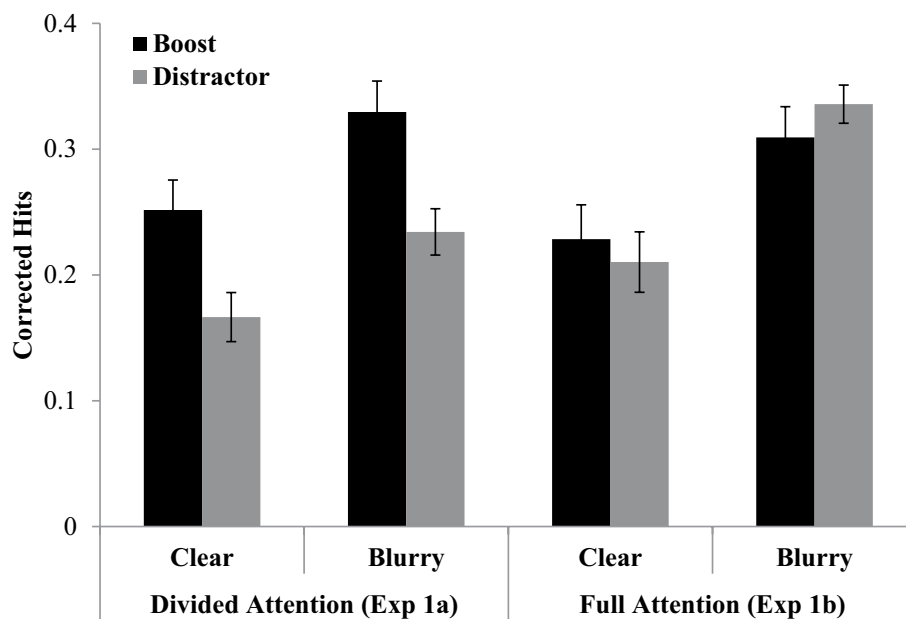


FIGURE 2

Mean corrected hits (hits minus false alarms) for each condition for both Experiment 1a, in which the task involved word reading and signal monitoring, and Experiment 1b, in which the task involved only word reading. Error bars reflect standard errors corrected to remove overall between-subject variation (Morey, 2008).

conditions. The assignment of lists to conditions was counterbalanced across participants such that each list appeared as old/new and clear/blurry an equal number of times. Presentation of words in both the study phase and test phase was randomized. During the test phase, 'old' words appeared as they had appeared in the study phase (i.e., if a word was blurry during the study phase, it was also blurry in the test phase). In both Experiments 1a and 1b, targets occurred on a random 20% of trials and distractors occurred on the other 80% of trials. The assignment of colours (blue/yellow) to target and distractor roles was counterbalanced across participants.

Results

Study phase

For Experiment 1a, target detection sensitivity in the study phase was calculated by subtracting the false alarm rate from the

hit rate, separately for clear and blurry words. There was no difference in sensitivity to boost targets for clear ($M=0.97$) and blurry ($M=0.94$) words ($p>0.05$). For Experiment 1b, participants did not respond to target signals, so no such comparison was conducted.

Test phase

The proportion of 'old' responses for old and new items (i.e., hits and false alarms) for each condition are presented in Table 1. Corrected hit rates (i.e., hits minus false alarms) were computed for each condition and submitted to separate repeated measures analyses of variance (ANOVA) for each experiment. The ANOVAs treated perceptual degradation (clear/blurry) and boost signal (target/distractor) as within-participant factors. Mean corrected hits for each condition are plotted in Figure 2.

Experiment 1a. There was a significant effect of perceptual degradation, $F(1, 23) = 7.46$, $p = 0.01$, $\eta_p^2 = 0.24$,

with better memory for blurry ($M = 0.28$) than clear words ($M = 0.21$). There was also a significant effect of boost signal, $F(1, 23) = 22.23$, $p < 0.001$, $\eta_p^2 = 0.49$, with better memory on target trials ($M = 0.29$) than distractor trials ($M = 0.20$). The interaction between perceptual degradation and boost signal was not significant, $F(1, 23) = 0.08$, $p = 0.79$, $\eta_p^2 = 0.003$. A Bayesian analysis (Wagenmakers, 2007; Masson, 2011) revealed that the posterior probability of the null hypothesis was 0.82 and the posterior probability of rejecting the null hypothesis was 0.16, which constitutes positive evidence for the null hypothesis (see also Raftery, 1995).

Experiment 1b. There was a significant effect of perceptual degradation, $F(1, 23) = 16.56$, $p < 0.001$, $\eta_p^2 = 0.42$, with better memory for blurry ($M = 0.32$) than clear words ($M = 0.22$). No effects involving boost signal were significant, as participants were not asked to detect targets in this experiment.

Comparison of Experiments 1a and 1b. Attention was divided across tasks (naming and target detection) in Experiment 1a and focused on a single task (naming) in Experiment 1b. To compare results across experiments, corrected hits were submitted to a mixed factor ANOVA that treated experiment (1a/1b) as a between-participants factor. This analysis revealed a main effect of perceptual degradation, $F(1, 46) = 14.86$, $p < 0.001$, $\eta_p^2 = 0.24$, with better memory for blurry ($M = 0.30$) than clear words ($M = 0.21$). There was also a significant interaction between experiment and boost signal, $F(1, 46) = 9.70$, $p = 0.003$, $\eta_p^2 = 0.17$. To examine this interaction further, we collapsed across perceptual degradation and compared target and distractor trials across experiments. Corrected hits did not differ across experiments for target trials, $t(45) = 0.49$, $p = 0.62$, $d = 0.14$ (Experiment 1a: $M = 0.29$; Experiment 1b: $M = 0.27$). However, corrected hits for distractor trials were higher in Experiment 1b ($M = 0.27$) than Experiment 1a ($M = 0.20$), $t(45) = 2.08$, $p = 0.04$, $d = 0.60$.

Discussion

Several findings from these experiments are worth noting. First, the perceptual degradation effect of Rosner et al. (2015) was replicated successfully. Recognition was better for blurry than clear words in both Experiments 1a and 1b. Second, an ABE was observed in Experiment 1a, with better recognition for target trials than for distractor trials (Swallow and Jiang, 2010). Third, recognition of target words in Experiment 1a (divided attention) was similar to that for corresponding words in Experiment 1b (full attention), whereas recognition of distractor words in Experiment 1a (divided attention) was worse than for corresponding words in Experiment 1a (full attention). This result replicates prior studies showing that the attentional boost lifts performance up to the level of full attention performance but not beyond (but see Swallow and Jiang, 2014a; Mulligan and Spataro, 2015). In light of these findings, the key new result is that the ABE was similar in

magnitude for clear and blurry words. This result suggests that the attentional boost and perceptual degradation do not produce redundant effects on recognition (see also Mulligan et al., 2014).

Experiments 2a and 2b

Experiments 2a and 2b aimed to establish the replicability of the key result from Experiment 1a. Experiment 2a was a direct replication of Experiment 1a, with targets occurring on 20% of study phase trials and distractors occurring on 80% of study phase trials. Experiment 2b was identical to Experiment 1a with the exception that targets and distractors each occurred on 50% of study phase trials. Previous research has shown that the ABE does not depend on targets being more rare than distractors (Swallow and Jiang, 2012), yet most studies of the attentional boost have included a higher proportion of distractor than target trials (Swallow and Jiang, 2010, 2011, 2012, 2014a,b; Spataro et al., 2013, 2015; Mulligan et al., 2014; Mulligan and Spataro, 2015). As such, we predicted that an attentional boost should occur in both experiments. The key issue in both experiments was again whether the ABE would be smaller for blurry trials than for clear trials.

Method

Participants

Thirty-six² undergraduates (31 female) ranging in age from 17 to 29 years ($M = 18.36$, $SD = 2.00$) participated in Experiment 2a and 24 undergraduates (18 female) ranging in age from 18 to 25 years ($M = 19.00$, $SD = 1.50$) participated in Experiment 2b. A sensitivity analysis like that conducted in Experiments 1a and 1b revealed that we could reliably measure effect sizes larger than $f = 0.33$ for Experiment 2a, and larger than $f = 0.41$ for Experiment 2b.

Apparatus, stimuli, and procedure

The apparatus, stimuli, and procedure in Experiments 2a and 2b were the same as in Experiment 1a.

Design

The design in Experiment 2a was the same as in Experiment 1a. The design in Experiment 2b was similar to that in Experiment 1a with the exception that there were equal proportions of targets and distractors in the study phase, in contrast to the 0.2/0.8 target/distractor proportions used in Experiments 1a and 2a.

² Multiples of 20 participants were used in all experiments to properly counterbalance the words lists. Our power analysis indicating at least 20 participants were required to measure a large effect size was met in both experiments.

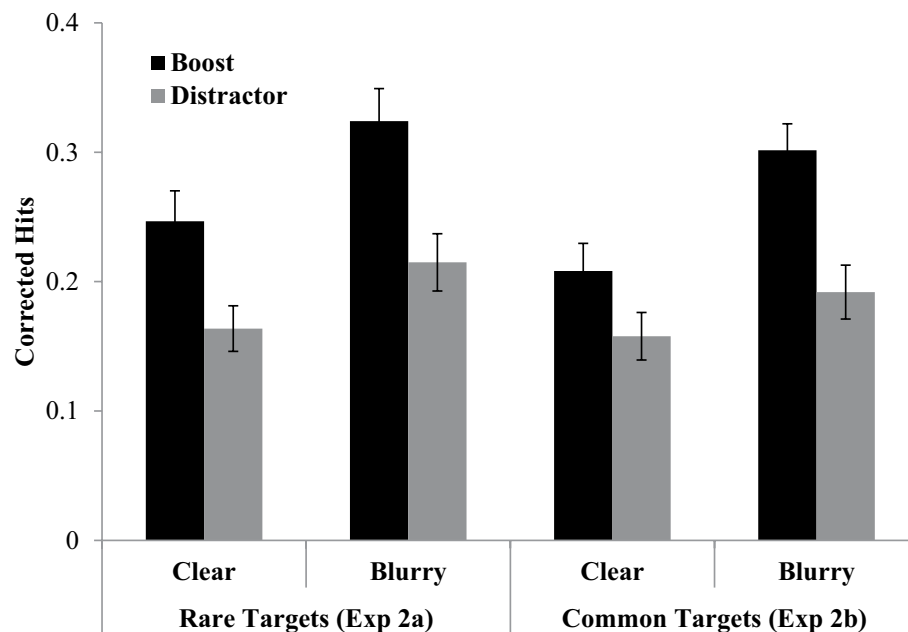


FIGURE 3

Mean corrected hits (hits minus false alarms) for each condition for both Experiment 2a (20% targets) and Experiment 2b (50% targets). Error bars reflect standard errors corrected to remove overall between-subject variation (Morey, 2008).

Results

Study phase

Target detection sensitivity was again measured by subtracting the false alarm rate from the hit rate separately for clear and blurry items. For Experiment 2a, sensitivity did not differ for clear ($M=0.96$) and blurry conditions ($M=0.94$). For Experiment 2b, sensitivity was slightly higher for clear trials ($M=0.91$) than blurry trials ($M=0.88$), $t(23)=2.37$, $p=0.03$, $d=0.48$.

Test phase

For both experiments, corrected hits from the recognition test were submitted to a repeated-measures ANOVA that treated perceptual degradation (clear/blurry) and boost signal (target/distractor) as within-participant factors. Mean corrected hits are presented in Figure 3.

Experiment 2a. There was a main effect of perceptual degradation, $F(1, 35)=7.83$, $p<0.01$, $\eta_p^2=0.18$, with better memory for blurry words ($M=0.27$) than clear words ($M=0.21$). There was also a main effect of boost signal, $F(1, 35)=19.59$, $p<0.001$, $\eta_p^2=0.36$, with better memory for target trials ($M=0.29$) than distractor trials ($M=0.19$). However, these factors did not interact, $F(1, 35)=0.35$, $p=0.56$, $\eta_p^2=0.01$. A Bayesian analysis (Wagenmakers, 2007; Masson, 2011) revealed a posterior probability of the null hypothesis of 0.83 and a posterior probability of the alternative hypothesis of 0.17, indicating positive evidence for the null hypothesis (see also Raftery, 1995). We further explored intraindividual differences in these effects by computing a Pearson correlation coefficient to assess the relation between the perceptual degradation effect and boost

effect across all participants in Experiments 1a and 2a. This correlation was not significant, $r(58)=-0.04$, $p=0.79$.

Experiment 2b. There was a significant effect of perceptual degradation, $F(1, 23)=5.33$, $p=0.03$, $\eta_p^2=0.19$, with better memory for blurry ($M=0.25$) than clear words ($M=0.18$). The effect of boost signal was also significant, $F(1, 23)=23.31$, $p<0.001$, $\eta_p^2=0.50$, with better recognition for target trials ($M=0.25$) than distractor trials ($M=0.17$). There was also a significant interaction between perceptual degradation and boost signal, $F(1, 23)=4.45$, $p=0.05$, $\eta_p^2=0.16$. We explored this interaction further by analyzing boost signal effects separately for clear and blurry items. For clear items, recognition was better for target ($M=0.21$) than distractor ($M=0.16$) trials, $t(23)=2.43$, $p=0.02$, $d=0.49$. For blurry items, the same pattern was observed, with better recognition for target ($M=0.30$) than distractor ($M=0.19$) trials, $t(23)=4.83$, $p<0.001$, $d=0.90$. Critically, the difference in memory sensitivity between targets and distractors was larger for blurry than clear words.

Discussion

The results of Experiment 2a provide a replication of the results of Experiment 1a. There was an effect of both perceptual degradation and attentional boost, however these factors did not interact. The results from Experiment 2b, in which targets occurred on 50% rather than 20% of trials, differed slightly from those of Experiment 1a. In addition to main effects of perceptual degradation and the boost signal, we also observed an interaction between these two factors. This interaction was

driven by a larger ABE for blurry than for clear words. This pattern is not consistent with the idea that perceptual degradation and attentional boost produce redundant effects on recognition memory. If that were the case, then the attentional boost should have been smaller for blurry than clear trials, rather than the reverse.

General discussion

The purpose of this study was to evaluate the combined influence of target detection and perceptual degradation at study on recognition performance. On their own, both target detection (Swallow and Jiang, 2010) and perceptual degradation (Rosner et al., 2015) at study improve recognition memory. It seemed possible that measuring them in the same experiment would produce redundant effects on recognition, with the ABE being smaller for blurry than clear items. Mulligan et al. (2014) reported an effect of this type for word frequency, with the attentional boost being smaller for low than high frequency words. Which they attributed to redundant attention effects of target detection and word frequency on an early phase of encoding. The present study failed to produce evidence for the predicted interaction. Instead, the ABE was no different for clear and blurry words (Experiments 1a and 2a) or larger for blurry than clear words (Experiment 2b). We conclude that perceptual degradation does not interact with the attentional boost in a manner that suggests redundant attention processes on an early phase of encoding.

Yet, the present results do not rule out the idea that perceptual degradation and target detection affect similar attention processes. Consider that encountering either a boost target signal or a blurry word could draw upon the same limited pool of attentional resources (Wickens, 1980). If resource allocation in response to target detection leaves sufficient resources in the pool that resource allocation in response to a blurry word is unaffected, then the effects of these two variables on recognition would be additive, as observed in Experiments 1a and 2a. Alternatively, the allocation of attentional resources from a limited pool could occur at distinct points in time for target detection and perception of a blurry word, which could also produce additive effects of boost signal and perceptual degradation.

Whether an attentional resource account of this type fits with the word frequency findings reported by Mulligan et al. (2014) is unclear. The interaction between attentional boost and word frequency effects reported in that study would imply either that low frequency words draw sufficient resources from the limited pool to compromise the allocation of resources to target detection, and/or that there is substantial overlap in the time course across which resources are drawn in response to low frequency words and target detection. It is worth noting that Prull (2019) did not find an interaction between attentional boost and word frequency. Instead, the magnitude of the ABE was the same for low and high frequency words. To reconcile these results with those reported by Mulligan et al., Prull speculated that perhaps

the low frequency words they used were not orthographically distinct enough from the high frequency words to garner the early allocation of attentional resources in a way that would interfere with boost target detection. An alternative account is that the interaction between target detection and word frequency reflects a form of structural redundancy (Wickens, 1980). By this account, the additive effects of boost signal and perceptual degradation in the present study may occur because there is no structural redundancy between mechanisms required for target detection and the perception of blurry words. Further research on the influence of transient shifts of attention on memory encoding is needed to sort out this issue.

In summary, the present study replicates both the attentional boost and perceptual degradation effects, yet offers no evidence of an interaction that would implicate redundant transient attention mechanisms for these two effects. These results contrast with those reported by Mulligan et al. (2014) in their study of the joint effects of attentional boost and word frequency, and invite additional study of links between transient shifts of attention and long-term memory encoding.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The studies involving human participants were reviewed and approved by McMaster Research Ethics Board. The patients/participants provided their written informed consent to participate in this study.

Author contributions

ML, TR, JO, and BM: conceptualization, methodology. ML: data curation, formal analysis, project administration, software, visualization, and writing – original draft. BM: funding acquisition and supervision. ML and LL: investigation. ML, TR, JO, LL, and BM: writing – review and editing. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fpsyg.2022.1024498/full#supplementary-material>

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Self-referential and social saliency information influences memory following attention orienting

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Self-referential information is a processing priority in individuals. Whether or how self-referential information plays a role in attention orienting by modulating memory encoding during attention orienting is presently unknown. First, we investigated this role with self-referential processing for words. Participants were trained to associate two cues (red and green arrows) with social labels (the words “self” and “other” in Experiment 1). Then, participants performed a cueing task to determine whether various targets were presented at a right or left location. Finally, a recognition task of target items was implemented to examine the influence of arrow cues on memory. Second, given that the difference in social salience also exists between self-and other-referential processing, we investigate whether the same effect as the self-referential processing of words exists for emotional faces with high social salience and regardless of emotional valence (a high and a low social salience in Experiment 2A; and a positive and a negative emotional face in Experiment 2B). The results showed that self-referential and emotional cues, irrespective of their emotional valence, enhance memory for the indicated target objects across experiments. This suggests that automatic prioritization of social salience for self-referential words or emotional faces plays an important role in subsequent cognitive processing through attention orienting to influence memory.

KEYWORDS

self-referential processing, social salience, attention orienting, memory, emotion

Introduction

During the past three decades, many studies have shown that the concept of the self is unique to the individual and is inherently a social construct that serves as a stable anchor for understanding other people (Sui and Gu, 2017). Self-referential information is processed with priority, evinced in the greater recall rate and faster response speed to information (e.g., Rogers et al., 1977). Furthermore, the importance of self-relevant components has been highlighted during perception, such as responding a “self” vs. “other” word (e.g., Sui et al., 2009; Williams et al., 2018), and cognitive processing, such as working memory and decision making (e.g., Yin et al., 2019; see Sui and Humphreys (2015) for a review). Despite a large body of evidence, it remains unknown whether self-referential processing works in a qualitatively distinguishable manner from other-referential processing during attention orienting.

Attention orienting allows us to preferentially process and learn information from our own point of reference (Bayliss and Tipper, 2006) and to understand the other person's inner state by following the orientation of another individual's eye gaze, therefore influencing memory (e.g., Dodd et al., 2012) and affective judgements for the indicated objects (e.g., Bayliss and Tipper, 2006). Although response times (RTs) in attention orienting could also be influenced by arrows as cues, eye gaze, unlike arrows as cues reflects a qualitatively human ability to modulate the depth of encoding for the targets underlying social communication. Specifically, attention orienting by gaze but not arrow cues has been found to enhance memory for the indicated (valid) items even when participants are not explicitly attempting to memorize the items (Dodd et al., 2012). Using a cueing paradigm (Dodd et al., 2012), participants were asked to focus on a word. Then, a memory task was administered. Although the participants were not instructed to memorize the word, an enhanced memory for the indicated word was found by gaze but not arrow cues. This might reflect an incidental episodic memory for the indicated targets facilitated by gaze but not arrow cues in attention orienting. Therefore, to determine whether a qualitatively distinguishable manner is influenced by self-referential processing, it is important to investigate whether the self works to aid the depth of encoding for the targets (i.e., memory) indicated by the cues during attention orienting.

Self-referential processing has been investigated in attention orienting under a cueing paradigm (e.g., Sui et al., 2009; Zhao et al., 2015). Sui et al. (2009) developed a method to modulate the self-referentiality of cues. First, in the training task, participants learn associations between a specific arrow shape and themselves, treating it as a self-referential cue, and between a different arrow shape and a friend, serving as an other-referential cue. Under a subsequent cueing task, the study showed that self-referential arrow cues induce a faster response than other-referential arrow cues when the cue direction and the target location were incongruent at a short cue-target stimulus onset asynchrony (SOA), which indicates that attention more rapidly disengages from the cued spatial location to respond to a target in the self-referential condition.

Zhao et al. (2015) also used the same method to associate cues with the self and others. Participants were first trained to associate two cues (a red and green arrow in Experiment 1A and two different faces in Experiment 1B) with distinct words ("self" and "other") and then used two cues (self-referential and other-referential) and two types of sound (voice and tone as target) in the cueing task. The results found that a large cueing effect could be elicited by self-referential but not other-referential cues on a specific target stimulus (i.e., a voice but not a tone). These findings reflected that attention orienting could be modulated by self-referential processing for words. Interestingly, Zhao et al. (2015), in Experiment 2, also found that self-referential arrow cues and other-referential gaze cues showed the same pattern of attention orienting with commonly used gaze and arrow cues, respectively (cf. Zhao et al., 2014). Self-referential cues could modulate automatic attention orienting by centrally presented cues. However, it remains unknown whether self-reference works in a qualitatively distinguishable manner to influence and modulate accompanying cognitive processing with attention orienting, such as memory. Thus, this study first tested whether self-referential processing for words aids memory for the items indicated by the cues during attention orienting in Experiment 1. Given that individuals are commonly highly familiar with self-referential stimuli such as their face or name, it is possible

that participant memory was enhanced by familiarity rather than the self-referential effect in attention orienting. Based on a previous experimental design to avoid causing a familiarity effect and examine how attention orienting was influenced by self-referential processing (Zhao et al., 2015), participants in a training task were first asked to establish an association between two cues (red and green arrows) and "self" and "other" words (i.e., encoding the relevant arrow stimuli). Previous studies (e.g., Sui et al., 2009; Williams et al., 2018) have shown that self-referential effects exist in "self" versus "other" words. If a low error rate in self-pairs and other pairs were found, the association between arrow cues and "self" and "other" words would be firmly established in the training task. Subsequently, a cueing task using the self-and other-referential arrows required participants to determine whether various targets (a set of meaningless shapes) were presented at a right or left location. Then, a recognition task was implemented to examine the influence of self-and other-referential arrow cues on memory for target shapes during attention orienting. We hypothesized that the number of memorized items indicated by the cues could be enhanced when participants perceived arrow cues associated with "self" words (a high self-referential degree) but not cues associated with "other" words (a low self-referential degree) in Experiment 1.

Second, there is a possibility that a difference between self-and other-referential processing is also reflected in the level of social salience (Sui et al., 2012; Scheller and Sui, 2022). Social salience is inherent in self-referential as well as emotional information such as what is attractive or dangerous. Some studies have shown that self-referential (e.g., Sui et al., 2009) as well as emotional information modulate attention orienting (e.g., Lassalle and Itier, 2015) and memory performance (e.g., Tyng et al., 2017). Other studies suggest the differential role of self-referential and emotional processing (Stolte et al., 2017). To determine whether the social salience of stimuli can influence accompanying cognitive processing with attention orienting, we addressed whether another person's emotional faces with high social salience, which is defined by the valence and emotional arousal of an experience (Alger and Payne, 2016), had the same influence on cognitive processing during attention orienting as the self-relevant words. The level of social salience for perceiving another person's emotional face determines how we perceive and attend to the world, and how we behave. For example, happy faces are friendly related stimuli, and fearful faces are threat stimuli, both of which may present higher levels of social salience and be more subjected to attentional biases [A review for Yiend (2010)]. Thus, in Experiment 2A, two cues (red and green arrows) were associated with faces with a happy and a neutral face with a straight gaze in the training task. If a low error rate was found for both positive and neutral face pairs, the association between arrow cues and positive and neutral faces was firmly established in the training task. Then, the cueing task and the recognition task were implemented. However, this experiment cannot exclude the possibility that the difference in memory performance under the recognition task might be explained by only positive emotional valence of the word "self" and happy faces.

In Experiment 2B, we manipulated two cues (red and green arrows) so that they were associated with a positive and a negative emotional face (i.e., a happy and a fearful face) in the training task. If a low error rate were found for both positive and negative emotional face pairs, the association between arrow cues and positive and negative emotional faces would be firmly established in the training

task. Moreover, given that both emotional faces have a high magnitude of social salience, we presumed a large difference in emotional valence but a similar degree of social salience between happy and fearful faces with a straight gaze. Thus, if the magnitude of social salience but not positive emotional valence manifests a qualitatively different function to modulate participants' cognitive processing during attention orienting, we hypothesized that the number of memorized items indicated by the cues could be enhanced when participants perceived arrow cues associated with happy faces (a high magnitude of social salience and a positive emotional valence) but not cues associated with neutral faces (a low magnitude of social salience degree and a neutral emotional valence) in Experiment 2A and no difference between when participants perceived cues associated with happy (a high magnitude of social salience degree and a positive emotional valence) and fearful faces (a high magnitude of social salience and a negative emotional valence) in Experiment 2B.

Experiment 1

The purpose of Experiment 1 was to determine whether self-referential processing of words can aid in influencing memory during attention orienting. In the training task, participants were first trained to associate arrow cues and two different words representing “self” or “other” words. To this end, a cueing paradigm was implemented, in which using the arrows associated with “self” and “other” words as cues required participants to determine whether various targets were presented at a right or left location. Finally, the recognition task was used to examine the effect of self-referential processing on memory, even when participants did not attempt to memorize items (i.e., target shapes under the cueing task). We hypothesized that the number of memorized items indicated by the cues could be enhanced when participants perceived arrow cues associated with “self” words but not cues associated with “other” words.

Materials and methods

Participants

Fifty-four Japanese students (mean age \pm SD, 21.3 ± 0.47 years; 25 males) participated in Experiment 1. The effect size in a comparable previous study (Experiment 3 in Dodd et al., 2012) was 0.1 (62 participants). With a desired power (0.95) for detecting the effect size ($f = 0.21$) at an alpha level of 0.05, we needed a minimum sample of 52 participants, which was calculated by G*Power (Faul et al., 2007). The dominant hand of the participants was evaluated by the Edinburgh Handedness Inventory (Oldfield, 1971). All participants were right-handed. There was no overlap in participants across experiments, and all participants reported normal colour vision and normal or corrected-to-normal visual acuity. This study was approved by the local ethics committee, and all procedures complied with the ethical standards of the 1964 Declaration of Helsinki regarding the treatment of human participants in research. This study was not preregistered.

Stimuli

To compare our results with those of a previous study (Zhao et al., 2015), we used the same stimuli as those in the training task. In the training task, the stimuli used were illustrated. A red or green arrow (8.3°

wide \times 3.0° high) was displayed above the fixation cross, and a “self” (自分) or “other” (他人) (6.8° wide \times 3.0° high) word was presented below the fixation cross. The red and green arrows implemented in the cueing task were the same as those implemented in the training task.

In the cueing and recognition task, the target stimuli were drawn from the set of novel meaningless closed shape contours ($3.8^\circ \sim 3.9^\circ$ wide \times $3.2^\circ \sim 5.8^\circ$ high) developed by Endo et al. (2003), which were difficult to verbalize. All stimulus contours were drawn with black outlines and a white background. According to the perceptual preference score (Endo et al., 2003), we divided 64 shape stimuli into four sets, for which there was no difference in perceptual preference (Supplementary Result S1; Supplementary Table S1). We used two sets (one set with the self-referential arrow condition and the other set with the other-referential arrow condition) in the cueing task and the other two sets (one was paired with the self-referential set and the other one was paired with the other-referential set as a novel item) in the recognition task, and these assignments were counterbalanced across participants in the cueing task. The centre of the shape stimuli appeared 9.6° to the left or the right of the cue.

Apparatus

The stimuli and fixation icons were created by Photoshop on a Windows computer. Presentation software (Neurobehavioral Systems) was used to present the stimuli and control the program. Stimuli were presented on a 19-inch Dell monitor with a screen resolution of $1,024 \times 768$ pixels and a refresh rate of 60 Hz. A chin and headrest were used to maintain the fixed viewing distance between the monitor and participants at approximately 57 cm. Participants used a keypad to respond.

Procedure

First, all participants were instructed to complete two tasks in the experiment: a training task and a cueing task. In the training task, the participants were instructed to associate two arrows, a red arrow and a green arrow, with “self” and “other,” respectively, and then they performed the cueing task using the self-and other-referential arrows. After two tasks, the participants were given instructions to complete a recognition task. The participants did not know that they needed to perform a recognition task until they completed the cueing task.

Training task. The participants were instructed to associate self-and other-referential information (the word “self” [自分] or “other” [他人]) with different colour arrows (a red or a green arrow) (Figure 1A). As shown in Figure 1B, training trials began with a fixation cross at the centre of the screen presented for 600 ms. Then, the training stimulus (a red arrow or a green arrow) with an assigned or unassigned word was shown for 100 ms. We manipulated one of two different patterns between two colour arrows and the words (i.e., a red arrow associated with “self” and a green arrow associated with “other; a green arrow associated with “self” and a red arrow associated with “other”) for each participant. The participants were asked to judge whether the association between the arrow and the assigned word was correct. Specifically, although four stimulus pairs were included in total (a red arrow and self, a green arrow and other, a green arrow and self, a red arrow and other), we requested that the participants push a button only for the two correct stimulus pairs (e.g., a red arrow and self and a green arrow and other) as quickly and accurately as possible, but the other stimulus pairs (e.g., a green arrow and self and a red arrow and other) were requested to not push a

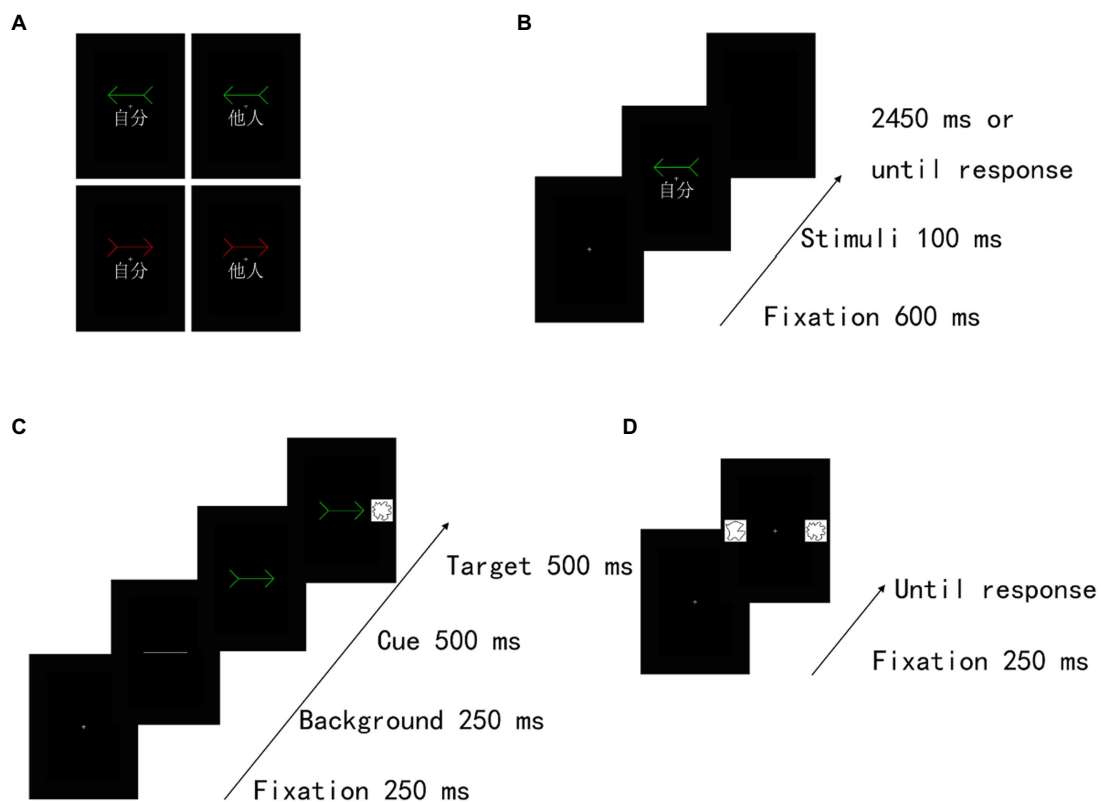


FIGURE 1

Experimental task structure in Experiment 1. (A) Examples of self-and-other-arrow pair stimuli. Illustration of stimuli presented in the (B) training task, (C) cueing task and (D) recognition task. Two different colour arrows (i.e., red and green) were associated with the "self" or "other" words in the training task. Subsequently, a cueing task and a recognition task were implemented. In the cueing task, the participants were instructed to indicate as quickly and accurately as possible whether the target was presented on the left or right side by pressing the corresponding key (judge the location of the target). The target was equally likely to be presented on the same (valid cue condition) or opposite (invalid cue condition) side of the cue stimulus. The task consisted of 4 conditions, including valid and invalid conditions with self-and other-referential cues. In the recognition task, the participants were instructed to choose which of two shapes was displayed regardless of the location of the target in the cueing task. The recognition task consisted of 4 conditions, validity in the cueing task (valid and invalid cue condition) × self referentially in the cueing task (self-and other-reference conditions). The familiar shape was presented on the same (valid cue condition) or opposite (invalid cue condition) side as the self-or other-referential arrow cue in the cueing task.

button. Moreover, across participants, the assignments of these patterns (a red arrow and self, a green arrow and other, a green arrow and self, a red arrow and other) were counterbalanced. A block of 64 trials was performed with the self-related stimuli and other-related stimuli occurring equally often in a randomized order. Thirty-two practice trials preceded the experimental trials.

Cueing task

After the training task, a cueing task was immediately implemented. To ensure an effective orienting effect and interaction with memory, the procedure of the cueing task was based on the previous studies (Dodd et al., 2012). In the cueing task, the same arrow stimuli were used for the self-and other-referential cues; the stimulus presentation sequence in the cueing task is shown in Figure 1C. Each trial began with the appearance of a fixation cross for 250 ms at the centre of the screen, and then a transverse white line was presented for 250 ms at this location as a background. Subsequently, a cue stimulus pointing right or left (red or green arrow) was presented in the centre of the screen; the SOA between a cue event and a target event was 500 ms. A shape target stimulus was displayed to the left or the right spatial location of the cue for 500 ms. Two different sets of shape stimuli were used in the self-and

other-referential cue conditions. The participants were instructed to indicate as quickly and accurately as possible whether the target was presented on the left or right side by pressing the corresponding key. Then, the reaction time (RT) to localize the target was recorded in each trial. The cue and the target remained present until response or until 2,500 ms had elapsed. The target was equally likely to be presented on the same (valid cue condition) or opposite (invalid cue condition) side of the cue stimulus. The central cues were uninformative and did not predict the target spatial location, and the participants were requested to keep their fixating screen centre. Similar to a previous study (Dodd et al., 2012), the task consisted of one block of 32 trials. Eight trials were performed under each condition. Each condition was presented in a pseudorandomized order.

Recognition task

Consistent with a previous study (Dodd et al., 2012), a memory task started immediately following the cueing task. Thus, after the cueing task, a recognition task started immediately with a short instruction. As shown in Figures 1D, a trial began with the appearance of a fixation cross for 250 ms at the centre of the screen. Then, two shapes were presented on either side of a black background.

Specifically, one was drawn from two sets of shape stimuli presented in the cueing task, and the other was a novel stimulus drawn from another two sets. The participants were instructed to respond regarding which one of two shapes was displayed regardless of the location of the target in the cueing task. The task consisted of one block of 32 trials. Eight trials were included under each condition. Each trial was presented in a pseudorandom order.

Data analysis

For the training task, we measured total error rates (TERs), including omission and commission errors, to assess the strength of the association between arrows and self-or other-referential words using a cut-off of 10% error. Consistent with a previous study (Zhao et al., 2015), the participants were instructed to respond correctly on at least 58 trials in each block. RTs became stable after nearly 60 training trials, comparable to the results reported by Sui et al. (2009). Thus, we suggest that if the participants respond correctly on at least 58 trials in each block, then they have effectively learned the association between the “self” or “other” words and arrows stimuli. We excluded trials with abnormal RTs that were shorter than 150 ms or longer than 1,000 ms (0.9% of the trials). For each participant, the mean RTs and accuracy between self-and other-referential arrow conditions were analysed using a paired *t* test. The TERs of three (two males and one female) participants were greater than 10% and were excluded from the analysis. Thus, the association between arrow cues and “self” and “other” words was firmly established in the remaining participants.

In the cueing task, we excluded RTs that were shorter than 150 ms or longer than 1,000 ms (0.43% of the trials) and incorrect responses from RT analysis (0.06% of the trials). The error rates showed a floor effect because of a low rate of incorrect responses. Hence, we did not analyse the error data. The mean RT differences were analysed using a repeated-measures analysis of variance (ANOVA) with cue (self-and other-referential arrows) and validity (valid and invalid) as the within-participant factors. The resultant perceptual preferences of items were not different among cue type (self-referential cue or other-referential cue) and validity (valid or invalid) conditions under the cueing task in the remaining 51 participants (see [Supplementary Table S2; Supplementary Results S2](#)).

In the recognition task, the mean differences in accuracy rate for memorized items were analysed using a repeated-measures ANOVA with cue (self-and other-referential arrows) and validity (valid and invalid) as the within-participant factors. Then, to determine whether self-referential processing enhances or inhibits memory for items during attention orienting and memory performance under each

condition, we examined whether the accuracy rate significantly differed from chance level (50%) using one-sample *t* tests.

Results and discussion

Training task

The remaining 51 participants responded significantly faster to the arrow associated with the “self” word than to the arrow associated with the “other” word (mean \pm SD, self: 523 ms \pm 73.40 vs. other: 565 ms \pm 77.28; CI: 95% confidence interval, self: 502.7–544.4 ms vs. other: 543.4–587.3 ms), $t(50) = -6.15$, $p < 0.001$, although the error rates were not significantly different between conditions (mean \pm SD, self: 0.21 \pm 0.11% vs. other: 0.43 \pm 0.12%; CI: 95% confidence interval, self: 0–0.43% vs. other: 0.18–0.68%), $t(50) = -1.36$, $p = 0.18$. Self-referential information has a stronger processing priority than other-referential information.

Cueing task

[Table 1](#) and [Figure 2](#) show the mean RTs and error rates under each condition. We explored the validity effect using a 2 (cue type: self, other) \times 2 (validity: valid, invalid) repeated-measures ANOVA. The analysis did not show a significant main effect of cue type, $F(1, 50) = 2.04$, $p = 0.16$, $\eta_p^2 = 0.04$, or a significant cue type \times validity interaction, $F(1, 50) = 0.83$, $p = 0.37$, $\eta_p^2 = 0.02$; however, we found a significant main effect of validity, $F(1, 50) = 10.25$, $p = 0.02$, $\eta_p^2 = 0.17$, indicating that the RTs were faster in the valid condition than in the invalid condition.

Recognition task

The effect of self-referential processing was explored using a 2 (cue type: self and other) \times 2 (validity: valid and invalid) repeated-measures ANOVA ([Table 1](#) and [Figure 2](#)). The analysis revealed a significant main effect of validity, $F(1, 50) = 10.78$, $p = 0.002$, $\eta_p^2 = 0.18$, indicating that accuracy for memory was higher in the valid condition than in the invalid condition; however, we did not find a significant main effect of cue type, $F(1, 50) = 0.58$, $p = 0.45$, $\eta_p^2 = 0.012$. Notably, the cue type \times validity interaction was significant, $F(1, 50) = 5.19$, $p = 0.03$, $\eta_p^2 = 0.09$. *Post hoc t* tests found that the accuracy for memory was significantly greater for the valid condition than for the invalid condition for the self-referential arrow ($p = 0.001$) but not for the other-referential arrow ($p = 0.81$). The results indicated that the memory for the cued items was enhanced during attention orienting when using arrow cues associated with a “self” word.

TABLE 1 Mean response times (ms) in the cueing task and mean accuracy (%) in the recognition task as a function of cue and validity in Experiment 1.

Cue and validity	Cueing task				Recognition task		
	<i>M</i>	SEM	%E (SD)	CI	<i>M</i>	SEM	CI
Self-relevant arrow							
Valid	322.1	7.6	0.49 (2.4)	306.6–337.6	59.1	2.9	53.2–64.9
Invalid	329.7	7.8	0 (0)	313.8–345.6	45.6	2.5	40.5–50.6
Other-relevant arrow							
Valid	323.9	8.3	0.49 (2.4)	307.2–340.7	54.7	2.5	49.7–59.6
Invalid	338.6	9.5	0.49 (2.4)	319.3–357.8	53.9	2.9	48.0–59.8

M, mean; SEM, standard error of the mean; SD, standard deviation; %E, percent error rate; CI, 95% confidence interval.

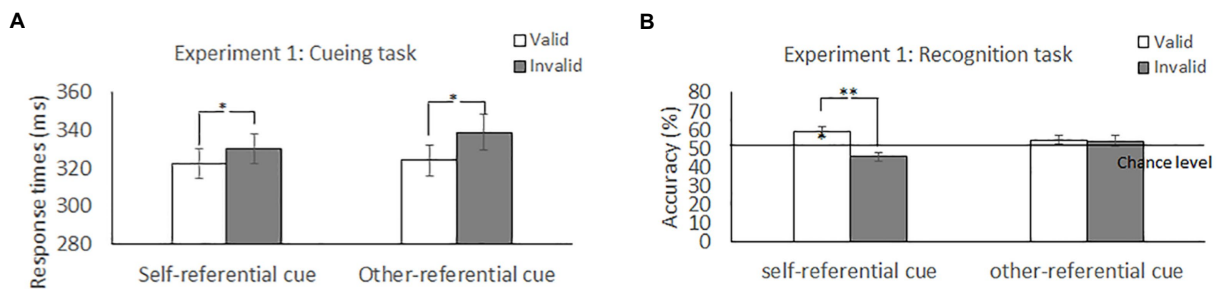


FIGURE 2
Mean difference in response times in the cueing task and accuracy in the recognition task to self- and other-referential arrow cues in Experiment 1.
** $p < 0.01$; * $p < 0.05$.

Accuracy was also significantly higher than chance level for the valid condition when paired with a self-referential arrow cue [$t(50) = 3.09, p = 0.003$] but not when paired with other conditions [all $t(50) < 1.88, p > 0.05$]. The results indicated that memory performance was above chance level only when using arrow cues associated with a “self” word.

Discussion

In the training task, the remaining participants almost always responded correctly ($> 90\%$) and on at least 58 trials with arrows associated with words. The association was firmly established between arrow cues and (“self” and “other”) words. Additionally, participants responded faster to the arrows associated with “self” than to those associated with “other.” Consistent with previous studies (Zhao et al., 2018), a stronger processing priority was found for self-referential cues than for other-referential cues (arrows). In the cueing task, no significant difference in RTs to the target items was found between self- and other-referential cues. Participants reliably oriented their attention to the cued direction irrespective of self- and other-referential cues. In the recognition task, memorizing items presented at valid locations was higher than that presented at invalid locations when paired with a self-referential arrow cue but not when paired with an other-referential arrow cue. The memory for the cued items may be enhanced by self-referential processing even when participants did not attempt to memorize items following attention orienting. Given a potential difference between self and other words in the level of social salience, Experiment 2 investigated whether the social salience of the stimulus is self-relevant and can enhance memory during attention orienting.

Experiment 2

The purpose of Experiment 2 was to determine whether the social salience of the stimulus is only self-relevant and can enhance memory during attention orienting.

Experiment 2A

In Experiment 2A, participants were first asked to associate arrow cues with two different faces representing a happy or neutral

emotion in the training task. To this end, a cueing paradigm was implemented, in which using the arrows associated with happy and neutral emotions as cues required the participants to determine whether various targets were presented at a right or left location. Finally, a recognition task was used to examine the effect of a cue associated with a happy face on memory even when participants did not attempt to memorize items during attention orienting. We hypothesized that the number of memorized items indicated by the cues could be enhanced when participants perceived arrow cues associated with happy faces (a high magnitude of social salience degree and a positive emotional valence) but not cues associated with neutral faces (a low magnitude of social salience degree and a neutral emotional valence).

Materials and methods

Participants

A different cohort of 54 naïve participants (mean age \pm SD, 21.3 ± 1.52 ; 26 males) participated in Experiment 2A. All participants provided written informed consent before participating in the experiment, and all reported normal colour vision and normal or corrected-to-normal visual acuity.

Stimuli, apparatus, procedure, and analysis

The stimuli and procedure were identical to those in Experiment 1, except that we presented two emotional faces (happy and neutral) (3.8° wide \times 4.6° high) with a straight gaze that was associated with a red arrow and a green arrow. The face stimuli (female, AF01; male, AM11) were taken from the Karolinska Directed Emotional Faces (KDEF) database of faces (Lundqvist et al., 1998). Both female and male emotional faces were displayed to all participants. Thus, the assignments of the patterns between two emotional faces, including female and male happy faces, female and male neutral faces, and red and green arrows, were counterbalanced across participants. Moreover, the emotional arousal of happy faces is 3.80 ± 1.85 SD, and that of neutral faces is 2.31 ± 1.47 SD (Goeleven et al., 2008). Thus, the level of social salience was different between happy and neutral faces. In the training task (Figure 3A), we excluded RTs that were shorter than 150 ms or longer than 1,000 ms (2.56% of the trials) from the analysis. The TER of one female participant's data was greater than 10% in at least one block, and her data were excluded from the analysis. For the remaining participants, the results showed that

the association was firmly established between arrow cues and emotion (happy and neutral faces).

Furthermore, in the cueing task (Figure 3B), we excluded RTs that were shorter than 150 ms or longer than 1,000 ms (0.12% of the trials) and incorrect responses (0.47% of the trials) from the analysis. Accuracy scores indicated a floor effect because of a low rate of incorrect responses. Hence, we did not analyse the error data. For the assigned target items under the cueing task, we confirmed no significant difference in perceptual preference among conditions under the cueing task in the remaining 53 participants (see Supplementary Table S3; Supplementary Results S3).

Results

Training task

The remaining 53 participants responded significantly faster to the arrow associated with a happy face than to the arrow associated with a neutral face (mean ± SD, happy face: 565 ms ± 99.37 vs. neutral face: 609 ms ± 77.05; CI: 95% confidence interval, happy face: 538.9–592.0 ms vs. neutral face: 587.5–630.4 ms), $t(52) = -6.46, p < 0.001$. Moreover, there was a significantly lower error rate in response to the arrow associated with a happy face than to the arrow associated with a neutral face (mean ± SD, happy: 0.06 ± 0.04% vs. neutral: 0.32 ± 0.10%; CI: 95% confidence interval, happy face: 0–0.14% vs. neutral

face: 0.12–0.52%), $t(52) = -2.44, p = 0.019$. A cue associated with a happy face had a stronger processing priority than a cue associated with a neutral face.

Cueing task

Table 2 and Figure 4 show the mean RTs and error rates for each condition. We explored the validity effect using a 2 (cue type: happy, neutral) × 2 (validity: valid, invalid) repeated-measures ANOVA. The analysis did not show a significant main effect of cue type, $F(1, 52) = 2.37, p = 0.13, \eta_p^2 = 0.04$, or a significant cue type × validity interaction, $F(1, 52) = 0.10, p = 0.75, \eta_p^2 = 0.002$; however, there was a significant main effect of validity, $F(1, 52) = 7.39, p = 0.009, \eta_p^2 = 0.12$, indicating that RTs were faster in valid conditions than in invalid conditions. Both arrows associated with a happy face and a neutral face reliably oriented attention in the cued direction.

Recognition task

We explored the validity effect using a 2 (cue type: happy and neutral) × 2 (validity: valid and invalid) repeated-measures ANOVA (Table 2 and Figure 4). The analysis did not show a significant main effect of cue type, $F(1, 52) = 0.57, p = 0.46, \eta_p^2 = 0.01$, or validity, $F(1, 52) = 3.45, p = 0.07, \eta_p^2 = 0.06$. Notably, there was a significant interaction between cue type and validity, $F(1, 52) = 4.31, p = 0.04, \eta_p^2 = 0.08$. The accuracy for memory was significantly greater under

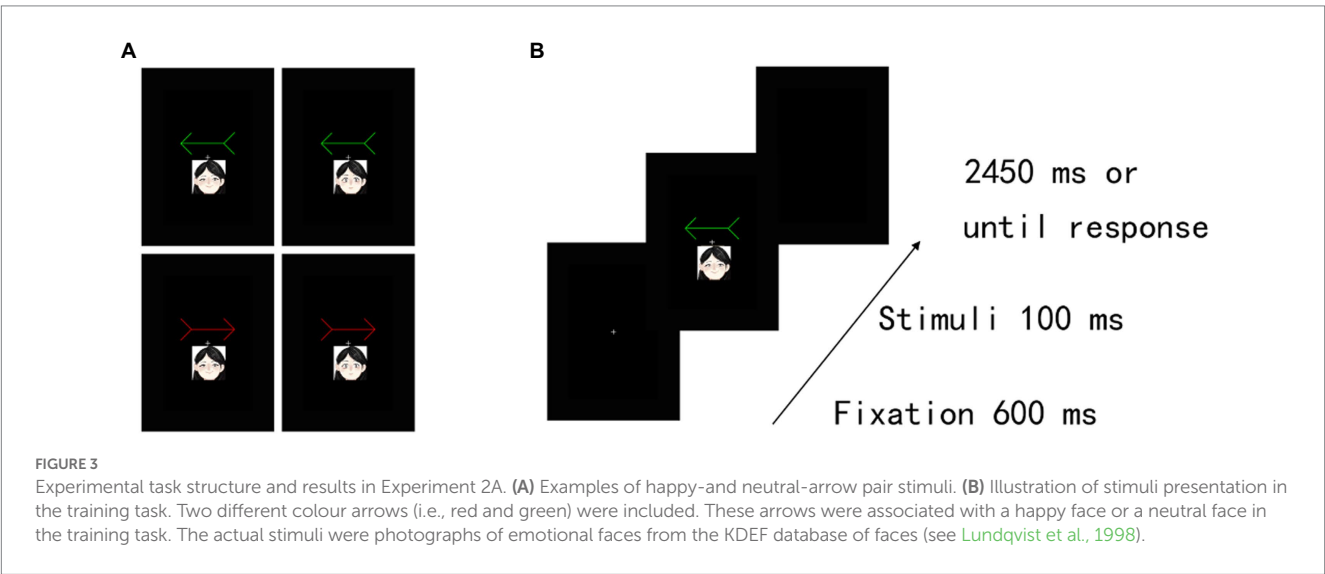


TABLE 2 Mean response times (ms) in the cueing task and mean accuracy (%) in the recognition task as a function of cue and validity in Experiment 2A.

Cue and validity	Cueing task			Recognition task		
	M (SEM)	%E (SD)	CI	M	SEM	CI
Happy arrow						
Valid	318.5 (6.8)	0.94 (5.3)	304.8–332.2	62.5	2.5	57.4–67.6
Invalid	328.8 (7.0)	0.34 (1.7)	314.6–342.9	53.5	2.9	47.7–59.4
Neutral arrow						
Valid	324.9 (6.1)	0.47 (2.4)	312.5–337.2	55.9	2.5	50.8–61.0
Invalid	332.3 (8.2)	0.24 (0.23)	315.7–349.0	56.1	2.5	50.2–62.1

M, mean; SEM, standard error of the mean; SD, standard deviation; %E, percent error rate; CI, 95% confidence interval.

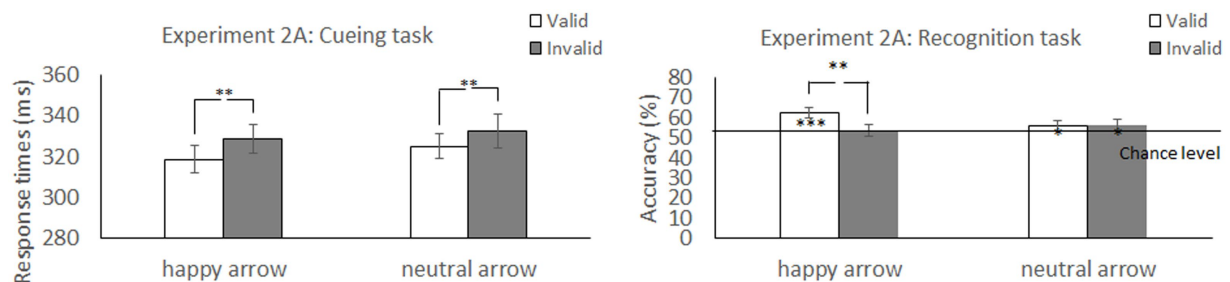


FIGURE 4
Mean difference in response times in the cueing task and accuracy in the recognition task to happy face-associated and neutral face-associated arrow cues. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

the valid condition than under the invalid condition when a happy face was associated with a cue ($t(52) = 2.77, p = 0.008$) but not when a neutral face was associated with a cue ($t(52) = -0.07, p = 0.94$). The results indicated that the memory for the cued items was enhanced during attention orienting when using arrow cues associated with a happy face.

The accuracy for memorizing items was also significantly higher than chance level for the valid condition [$t(52) = 4.96, p < 0.001$] but not for the invalid condition [$t(52) = 1.22, p = 0.23$] when paired with the arrow associated with a happy face. When paired with the arrow associated with a neutral face, accuracy was significantly higher than chance level for the valid [$t(52) = 2.31, p = 0.025$] and invalid conditions [$t(52) = 2.07, p = 0.044$]. The results indicated that memory performance was above chance level under both valid and invalid conditions when using arrow cues associated with a neutral face.

Experiment 2B

Although Experiment 2A showed that the memory for the cued items was enhanced only when using arrow cues associated with a happy face but not a neutral face during attention orienting, the difference between happy and neutral faces exists not only in social salience but also in emotional valence. Thus, Experiment 2B examined whether the phenomenon was influenced only by positive emotional valence during attention orienting. Participants were trained to associate arrow cues (red and green arrows) and two different emotional stimuli representing a positive and a negative emotion (i.e., happy and fearful faces) prior to a cueing and a recognition task. We hypothesized that the number of memorized items indicated by the cues could be enhanced when participants perceived cues associated with happy (a high magnitude of social salience degree and a positive emotional valence) and fearful faces (a high magnitude of social salience degree and a negative emotional valence).

Materials methods

Participants

A different cohort of 54 naïve participants (mean age \pm SD, 21.9 ± 3.3 ; 31 males) participated in Experiment 2B. All participants provided written informed consent before participating in the

experiment, and all reported normal colour vision and normal or corrected-to-normal visual acuity.

Stimuli, apparatus, procedure, and analysis

The stimuli and procedure were identical to those in Experiment 1, except that we presented two emotion faces (happy and fearful), each with a straight gaze, to be associated with a red and a green arrow. The Emotional arousal of score for the happy face was 3.80 ± 1.85 SD, and that of the fearful faces was 3.83 ± 1.66 SD (Goeleven et al., 2008). Thus, the level of social salience was similar for happy and neutral faces. In the training task (Figure 5A), we excluded RTs that were shorter than 150 ms or longer than 1,000 ms from the analysis (3.22% of the trials). The TERs of four (4 males) participants' data were greater than 10% in at least one block, and their data were excluded from analysis. The results for the remaining participants showed that the association was firmly established between arrow cues and "self" and "other" words. Moreover, in the cueing task (Figure 5B), we excluded RTs that were shorter than 150 ms or longer than 1,000 ms (0.38% of the trials) and incorrect responses (0.44% of the trials) from the analysis. Accuracy scores existed for a floor effect because of a low rate of incorrect responses in the cueing task. Hence, we did not analyse the error data. For the assigned target items under the cueing task, we confirmed no significant difference in perceptual preference among conditions in the remaining 50 participants (see Supplementary Table S4; Supplementary Results S4).

Results

Training task

The remaining 50 participants responded significantly faster to an arrow associated with a happy face than to an arrow associated with a fearful face (mean \pm SD, happy: $597 \text{ ms} \pm 99.99$, fearful: $654 \text{ ms} \pm 81.72$; CI: 95% confidence interval, happy face: $570.7\text{--}623.5 \text{ ms}$ vs. fearful face: $630.2\text{--}677.2 \text{ ms}$), $t(49) = -8.151, p < 0.001$. Moreover, a significantly lower error rate was observed when responding to an arrow associated with a happy face than to an arrow associated with a fearful face (mean \pm SD, happy face: $0.28 \pm 0.10\%$ vs. fearful face: $0.84 \pm 0.14\%$; CI: 95% confidence interval, happy face: $0.08\text{--}0.48\%$ vs. fearful face: $0.56\text{--}1.13\%$), $t(49) = -3.397, p = 0.001$. A cue associated with a happy face has a stronger processing priority than a cue associated with a fearful face.

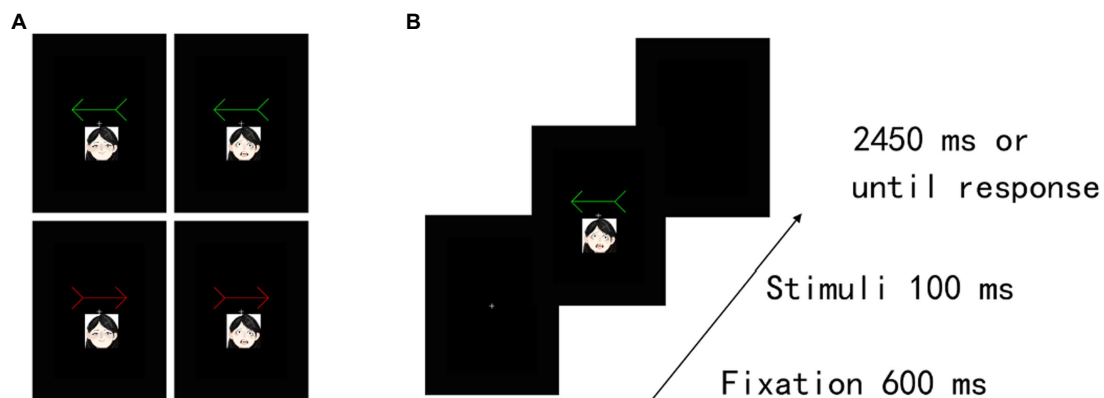


FIGURE 5

Experimental task structure and results in Experiment 2B. (A) Examples of happy- and fearful-arrow pair stimuli. (B) Illustration of stimuli presentation in the training task. The actual stimuli were photographs of emotional faces from the KDEF database of faces (see Lundqvist et al., 1998).

TABLE 3 Mean response times (ms) in the cueing task and mean accuracy (%) in the recognition task as a function of cue and validity in Experiment 2B.

Cue and Validity	Cueing task			Recognition task		
	M (SEM)	%E (SD)	CI	M	SEM	CI
Happy arrow						
Valid	311.3 (5.7)	0.5 (2.4)	299.7–322.9	54.8	2.4	50.2–59.8
Invalid	322.7 (6.9)	0 (0)	308.6–336.7	50.0	2.8	44.3–55.7
Fearful arrow						
Valid	307.1 (6.1)	0.5 (2.4)	294.8–319.4	55.3	2.5	50.2–60.3
Invalid	331.1 (6.4)	0.75 (3.9)	318.2–344.1	48.5	3.1	42.3–54.7

M, mean; SEM, standard error of the mean; SD, standard deviation; %E, percent error rate; CI, 95% confidence interval.

Cueing task

Table 3 shows the mean RTs and error rates for each condition. We explored the validity effect using a 2 (cue type: happy and fearful) \times 2 (validity: valid and invalid) repeated-measures ANOVA. The analysis did not show a significant main effect of cue type, $F(1, 49) = 0.299$, $p = 0.587$, $\eta_p^2 = 0.006$. Notably, there was a significant cue type \times validity interaction, $F(1, 49) = 4.23$, $p = 0.045$, $\eta_p^2 = 0.08$, and a main effect of validity, $F(1, 49) = 14.28$, $p < 0.001$, $\eta_p^2 = 0.23$, indicating that RTs were faster in valid conditions than in invalid conditions. The *post hoc* test revealed significantly shorter RTs for the valid condition than for the invalid condition for both an arrow cue associated with a happy face ($p = 0.026$) and an arrow cue associated with a fearful face ($p < 0.001$). There was no significant simple main effect of cue type under either valid ($p = 0.37$) or invalid conditions ($p = 0.11$). Both arrows associated with a happy and a fearful face reliably oriented attention to the cued direction, although the latter had a larger effect on attention orienting.

Recognition task

We explored the validity effect using a 2 (cue type: happy and fearful) \times 2 (validity: valid and invalid) repeated-measures ANOVA (Table 3 and Figure 6). The analysis revealed a significant main effect of validity, $F(1, 49) = 5.35$, $p = 0.025$, $\eta_p^2 = 0.09$, indicating that memory performance was higher in the valid condition than in the invalid condition; however, we did not show a significant main effect of cue

type, $F(1, 49) = 0.06$, $p = 0.80$, $\eta_p^2 = 0.001$, or a significant cue type \times validity interaction, $F(1, 49) = 0.11$, $p = 0.74$, $\eta_p^2 = 0.002$. The results indicated that memory for the cued items was enhanced during attention orienting when using arrow cues associated with a happy or a fearful face.

We found that accuracy was significantly higher than chance level for the valid condition [$t(49) = 2.11$, $p = 0.04$; $t(49) = 2.10$, $p = 0.04$] but not for the invalid condition [$t(49) < 0.001$, $p = 1.0$; $t(49) = -0.49$, $p = 0.63$] when using arrows associated with both happy and fearful faces as cues. The results indicated that memory performance was above chance level under valid conditions when using arrow cues associated with a happy face or a fearful face.

Discussion

For the training task, the remaining participants almost always responded correctly (>90%) to arrows associated with emotional faces (“happy” and “neutral”) in Experiment 2A and (“happy” and “fearful”) in Experiment 2B. The association of arrow cues with face stimuli was firmly established, as shown in Experiment 1. A faster and more accurate response to the arrows associated with happy faces than to those associated with neutral faces in Experiment 2A and to those associated with fearful faces in Experiment 2B. Compared with neutral and negative facial expressions, participants were more sensitive to positive emotion. Consistent with this result, a previous

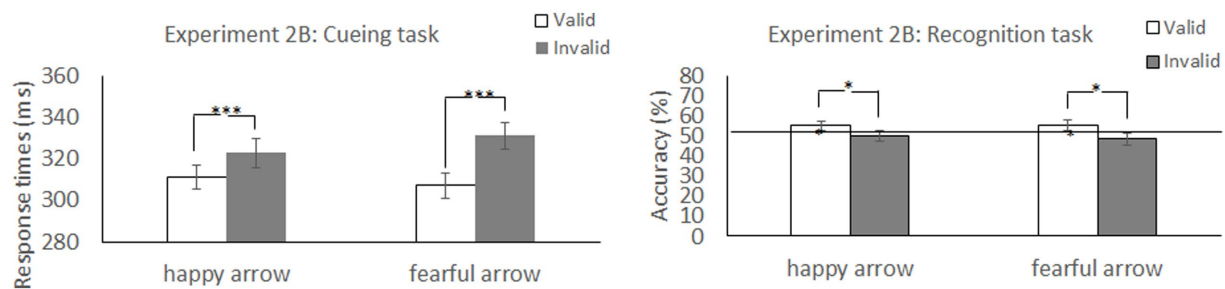


FIGURE 6

Mean difference in response times in the cueing task and accuracy in the recognition task to happy face-associated and fearful face-associated arrow cues. *** $p < 0.001$; * $p < 0.05$.

study suggests a high level of asymmetry in the recognition and categorization among emotional signals (Leppänen and Hietanen, 2004). Specifically, compared with neutral and fearful faces, happy faces include low-level features, making them visually more salient (e.g., Hess et al., 1997) and resulting in an enhanced response to a happy face.

In the cueing task, no significant difference in the cueing effect was found between cue types in Experiment 2A (cues associated with a happy or a neutral face). Although a greater magnitude of cueing effect (i.e., invalid versus valid conditions) was shown when using arrows associated with fearful rather than happy faces as cues ($p = 0.045$) in Experiment 2B (Supplementary Results S5), the *post hoc* analysis for significant interaction did not reveal any clear difference between cue types under either valid or invalid conditions. This finding is consistent with a previous report that the cueing effect triggered by gaze direction is not influenced by static emotional faces, including neutral, happy and fearful faces (e.g., Hietanen and Leppänen, 2003), although an enhanced cueing effect by gaze direction was reported when using dynamic emotional faces compared with neutral faces (e.g., Uono et al., 2009; Lassalle and Itier, 2015). Moreover, a greater cueing effect was found for a fearful face than for a happy face when using a threatening stimulus as a target, whereas this greater cueing effect for fearful faces disappeared when using a pleasant stimulus as a target (Friesen et al., 2011; Kuhn and Tipples, 2011). Cueing effects could be influenced by emotional faces depending on participants' goals. A set of meaningless shapes used as targets might obscure the difference in magnitude in the cueing effect between emotional faces.

Importantly, an interaction for accuracy was found in the recognition task. The results of Experiment 2A showed that memory performance for items was enhanced at valid locations but was not inhibited at invalid locations when the arrow associated with a happy face was used as a cue but not when a neutral face was used as a cue. Moreover, the results of Experiment 2B showed that memory performance for items presented at valid locations was enhanced but not inhibited at invalid locations when the arrows associated with happy or fearful faces were used as cues. When participants perceived stimuli associated with others' happy or fearful faces with a straight gaze, either the positive or negative emotional valence of these emotional faces could enhance memory encoding during attention orienting. Thus, we suggest that during attention orienting, the memory for the cued items was enhanced

only when using arrow cues associated with the magnitude of social salience regardless of emotional valence.

General discussion

Following the firm establishment of the associations between specific stimuli (words and emotional faces) and arrow cues in the training task, the cueing task did not show a difference in the cueing effect between arrow cues associated with a high and a low magnitude of social salience stimulus, although both cues induced attention orienting (i.e., RTs were facilitated in valid conditions rather than in invalid conditions). Sui et al. (2009) investigated whether attention orienting was influenced by self-referential cues. The results showed more rapid attentional disengagement from the cued location to capture a target when using self-vs. friend-arrow cues with a short SOA. Zhao et al. (2015) implemented two types of targets (voice and tone) to examine the priority of self-referential processing during attention orienting. A facilitated cueing effect on the voice target relative to the tone target induced by self-referential but not other-referential cues. We proposed the possibility that the number of trials was not enough to detect the effect of self-referential processing and emotional processing in the present cueing task. To avoid a ceiling effect in memory, we used a small number of trials for each condition (i.e., 8 trials). Participants could see each target stimulus once in the cueing task. Previous studies including a large number of trials for each condition (e.g., 48 trials in Zhao et al., 2015) showed a significant behavioural difference in the cueing effect between self-and other-referential cues. Moreover, compared with these previous study settings (various SOAs and types of targets), a relatively simple design of the present cueing paradigm was used and may cause difficulties in distinguishing the difference in the cueing effect. However, this paradigm can effectively induce differences in memory performance during the subsequent recognition task.

Notably, an interaction for the accuracy was found in the recognition task. Given a different level of social salience for self-vs. other-referential processing (Sui et al., 2012; Scheller and Sui, 2022) and another person's emotional face [A reviewer for Yiend (2010)], the recognition task suggested that the prioritization of social salience could facilitate memory following attention orienting. Previous studies (Bayliss and Tipper, 2006; Dodd et al., 2012) have shown an enhanced depth of encoding for valid targets, including incidental

episodic memory and affective judgement, under gaze cues but not arrow cues. A qualitative difference exists between gaze and arrow cues. In contrast with arrows, the importance of other people's eye gaze could modulate one's own performance and influence one's understanding of others' intentions and interests. Based on these findings, in the present study, it can be interpreted that directional cues have been qualitatively modulated for the depth of encoding for valid targets by both social salience for self-referential words and emotional faces during attention orienting. We propose that the arrow stimuli associated with the high priority of social salience might trigger a qualitatively different behavioural performance for the depth of encoding for valid targets that is similar to that elicited by social cues (i.e., eye gaze) during the cueing task to memorize items due to the experiences that the participant had during the training task.

Given that this study examined social salience for self-referential words and emotional faces and that an interaction with attention orienting subsequently modulated the depth of memory encoding for the valid targets, our findings suggest that social salience was influenced by not only information associated with self-relevant stimuli (e.g., "self" words) but also the contained degree of salience in non self-relevant emotion stimuli (e.g., a happy face with a straight gaze); thus, social salience could also act as a modulator of processing information in social environments. Additionally, it would be useful to understand the importance of social salience as a potential mechanism underlying gaze-triggered attention orienting because a phenomenon similar to that observed with eye gaze was shown with self-referential and emotional arrow cues to facilitate the depth of memory encoding for valid targets during attention orienting. Additionally, given individuals can learn to associate reward with a colour, and subsequently prioritize this colour in the absence of said reward in a later task (e.g., [Anderson et al., 2011](#)), future research should examine whether not only social salience for self-referential words and emotional faces can also trigger an enhanced phenomenon (e.g., memory reward etc.).

The present findings might provide a clue for understanding how to prioritize the selection of relevant information in the environment, and then affect the depth of memory encoding. Some researchers (a review for [Santangelo et al., 2015](#)) have shown that memory can be modulated by the perceptual and semantic saliency of objects during the encoding of natural scenes. For example, the representation of short-term memory was enhanced by emotional information ([Buttafuoco et al., 2018](#)) and semantic congruence ([Almadori et al., 2021](#)). The present study showed that the depth of memory encoding for valid targets could be modulated by the social salience of the cue associated with self-referential words and emotional faces through attention orienting. This suggests that a cue stimulus (e.g., arrow and gaze) can orient one's attention to an object in the environment and that intrinsic and/or experience-dependent semantic salience of the cue also influences the depth of memory encoding of the attended object. This extended mechanism might play an important role in learning about the social world under joint attention with (e.g., gaze and pointing gesture) or without other individuals (e.g., arrow and schematic gaze), resulting in individual differences in long-term memory representation.

The current findings also have implications for understanding impaired social attention in individuals with autism spectrum

disorder (ASD). The impairment in social attention orienting (e.g., gaze-triggered orienting) has been characterized in individuals with ASD (e.g., [Ristic et al., 2005](#); [Goldberg et al., 2008](#); [Marotta et al., 2013](#)). However, most experimental evidence has reported generally intact gaze-triggered orienting in ASD (a review by [Nation and Penny, 2008](#)). Some researchers have recently highlighted the importance of a self-relevant component during attention orienting in individuals with typical development (TD) and ASD. For example, [Zhao et al. \(2018\)](#) showed that individuals with ASD exhibit intact self-referential processing but that self-referential processing affects the attention orienting of individuals with ASD in atypical patterns from that of TD individuals. Thus, one promising area of future research is the investigation of the impact of the social salience of cues for words and emotional faces on memory following attention orienting in individuals with ASD. The use of our paradigm may provide a possible design to explain atypical social attention orienting in individuals with ASD. For example, impaired social attention orienting might be influenced by atypical sensitivity to social salience in individuals with ASD.

The present study has some limitations that should be addressed. First, the accuracy is overall very close to chance level. Given a two-alternative forced choice task was implemented in recognition task, future research should use a Yes-No discrimination task and the d' prime analyse for measuring sensitivity and response bias, and also incorporate participants' confidence ratings following each trial in the recognition task to evaluate their response confidence. Second, the participants' biasing was influenced by the colours of the arrows. Although the RT of the social salience of word/emotion type was not influenced by the colour of the arrow in the cueing task across experiments, memory of the social salience of word/emotion type was influenced by the effects of the colour of the arrow in the recognition task in Experiments 1 and 2B but not in Experiment 2A ([Supplementary Results S6](#)). Moreover, although the assignments of these colour patterns across participants were counterbalanced in all experiments, future research may need to investigate individuals' preference scores for colours as a covariate to avoid participants' biasing influenced by arrow colours. Finally, we did not use a neutral condition (e.g., no-cue condition) at baseline. A small number of trials were used for each condition (i.e., 8 trials) to avoid a ceiling effect in memory. Thus, future research may need to use a baseline condition in which the neural cues involve no spatial information, such as no-cue arrow, to determine how the depth of memory encoding for the valid target (i.e., facilitate or inhibit memory) was influenced by social salience of the cue associated with self-referential words and emotional faces.

Taken together, Experiments 1 and 2 provide the first evidence that the salience of social information works during attention orienting. Although a difference has been shown between self-referential processing and emotional processing in behaviour performance (e.g., no behavioural correlation between the self-referential bias and the emotional bias effects in [Stolte et al., 2017](#)), our results showed that the arrow stimuli associated with high social salience in Experiment 1 (self-referential information) and in Experiment 2A (emotional faces) might trigger a similar behavioural effect during a cueing task, facilitating the depth of memory encoding for valid targets due to the experiences of the participant during training. These findings suggest that a high degree of social salience for self-reference and emotional faces was

found to facilitate the depth of memory encoding for the valid targets following attention orienting. In future research, we should investigate how self-referential processing and emotional processing are intertwined for social interaction (e.g., the depth of memory encoding under joint attention).

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/[Supplementary material](#).

Ethics statement

The studies involving human participants were reviewed and approved by the local ethics committee of Kyoto University Graduate School and Faculty of Medicine. The patients/participants provided their written informed consent to participate in this study.

Author contributions

SZ: Conceptualization, Formal analysis, Writing Original Draft, Review & Editing; SU: Conceptualization, Writing Original Draft, Review & Editing; RH and SY: Conceptualization, MT: Conceptualization, Supervision. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fpsyg.2023.1092512/full#supplementary-material>

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Improving memory for unusual events with wakeful reactivation

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Memory consists of multiple processes, from encoding information, consolidating it into short- and long- term memory, and later retrieving relevant information. Targeted memory reactivation is an experimental method during which sensory components of a multisensory representation (such as sounds or odors) are 'reactivated', facilitating the later retrieval of unisensory attributes. We examined whether novel and unpredicted events benefit from reactivation to a greater degree than normal stimuli. We presented participants with everyday objects, and 'tagged' these objects with sounds (e.g., animals and their matching sounds) at different screen locations. 'Oddballs' were created by presenting unusual objects and sounds (e.g., a unicorn with a heartbeat sound). During a short reactivation phase, participants listened to a replay of normal and oddball sounds. Participants were then tested on their memory for visual and spatial information in the absence of sounds. Participants were better at remembering the oddball objects compared to normal ones. Importantly, participants were also better at recalling the locations of oddball objects whose sounds were reactivated, compared to objects whose sounds that were not presented again. These results suggest that episodic memory benefits from associating objects with unusual cues, and that reactivating those cues strengthen the entire multisensory representation, resulting in enhanced memory for unisensory attributes.

KEYWORDS

episodic memory, multisensory memory, memory reactivation, memory tagging, consolidation

Introduction

Which memories do we remember and which do we forget? Can we influence this process by rendering certain events and objects more memorable? Memory consists of multiple processes, from encoding information, consolidating it into short- and long-term memory, and later retrieving relevant information. Classical research revealed that maintaining the same context when first encountering information and later retrieving it enhances memory (Tulving and Thomspon, 1973). One form of context is multisensory information, where multisensory encoding improves later retrieval of the *unisensory details* of these memories, such as better remembering images previously presented with sounds (Thelen and Murray, 2013; Thelen et al., 2015; Duarte et al., 2022; but see Pecher and Zeelenberg, 2022). The benefits of multisensory memory can arise from several mechanisms: One proposed mechanism is "redintegration," whereby semantic multisensory representations are created during encoding, and later activated by their unisensory stimuli (Von Kriegstein and Giraud, 2006; Shams and Seitz, 2008; Shams et al., 2011). Another possibility is that multisensory representations modify the unisensory

representations themselves, rendering them more precise and accessible for retrieval (Shams and Seitz, 2008; Shams et al., 2011).

Following the encoding of new knowledge or skill, a consolidation process occurs whereby information is transferred over time into long-term memory. The consolidation process is considered an off-line memory process during which memories are strengthened, occurring at wake and sleep after learning. An emerging approach termed *targeted memory reactivation* (TMR) reveals that when sensory components of the multisensory representation (such as sounds or odors) are “reactivated” during sleep, a replay of associated memories occurs, facilitating the later retrieval of the entire memory representation (Rudoy et al., 2009; Oudiette and Paller, 2013). In one of the original studies (Oudiette and Paller, 2013), the procedure consisted of a learning period, whereby participants were presented with visual images and their matching sounds (e.g., cat-“meow”) appearing at different locations on a computer screen. Participants were instructed to learn the locations of the objects. The visual images had different values associated with them, with half of the images having a high value and half a low value. Following learning, half of the participants went to sleep in the lab, and were unknowingly exposed to the sounds from the learning phase. During a test phase the next day, all participants were better at recalling the location of the high-value images compared to low-value images. Importantly, for participants who experienced the reactivation of sounds, the low-value images associated with reactivated cues were better remembered compared to low-value images not associated with such cues. This finding reveals that “weaker” memories – events with initial lower memory strength – particularly benefit from reactivating their unisensory components (Oudiette et al., 2013; Oudiette and Paller, 2013). Studies across a range of domains have shown that TMR can be beneficial not only for episodic memory, but for language and skill learning as well (Rudoy et al., 2009; Antony et al., 2013; Hu et al., 2020; Laurino et al., 2022).

Are some memories reactivated while others not? Do some memories benefit from reactivation to a greater degree than others? *Memory tagging* refers to the process whereby new information is tagged for its potential importance or value. Memories tagged as valuable are thought to be rehearsed over time, with underlying neural circuits being strengthened, and certain events rendered more memorable (Oudiette et al., 2013). Tagging is influenced by multiple factors, such as attention, intention, emotion and reward. One potent form is *novelty-based tagging*, whereby novel attributes associated with an object (e.g., a visual image paired with a novel sound rather than a repeating sound), enhances object memory. The “oddball” is thought to trigger an attentional mechanism, resulting in enhanced object processing (Kim and McAuley, 2013; Cohen Hoffing and Seitz, 2015; Liao et al., 2016). Cowan et al. (2021) further propose that memory tagging enhances consolidation, whereby *goal-relevant* information, considered particularly rewarding or valuable for achieving one’s goals, is “tagged” for future consolidation. Another type of memory tagged for consolidation are “weaker” memories – information that is initially weakly encoded or learned (Tambini et al., 2017; Schapiro et al., 2018; Denis et al., 2021).

Memories tagged for consolidation may be the ones that benefit the most from TMR. Events and objects that are novel and unpredicted may be a good candidate for TMR, as they signal a rapid change in the environment, making them both salient and valuable in deciphering a new situation. However, novel stimuli

may be also “weaker,” as they are not easily encoded into pre-existing schemas, and may need further processing. To test this hypothesis, we compare the influence of reactivation on novel versus normal (predicted) stimuli, and test memory for different attributes of the multisensory representation.

Sensory cues

What types of sensory cues are most beneficial for TMR? Sensory cues strongly associated with memories are particularly beneficial, such as semantically-associated visuals and sounds (e.g., cat-“meow”; Oudiette et al., 2013). Sound melodies matched to simple action patterns are also helpful (Antony et al., 2013). New associations between senses can also be formed during a short learning period (Rasch et al., 2007; Vargas et al., 2019), especially with potent stimuli such as odor. In their seminal study, Rasch et al. (2007) presented participants a single scent of a rose when learning the locations of objects. During sleep, half of the participants were presented with the rose scent. During a memory test, participants were presented with objects without the odor, and asked to recall the locations of the objects. These participants showed improved spatial memory compared to participants who did not experience the reactivation of the single odor. These findings suggest that the odor served as a context-cue for all objects. Yet, in most studies, the test phase includes the presentation of the reactivated sensory cue, serving as a potent retrieval cue. This leaves open the question of whether reactivation alone can modify the multisensory representation, modifying its components such that it is easier to freely recall them, even in the absence of reactivated cues. We address this question in our study.

Wakeful TMR

Memory improvement also occurs when sensory cues are reactivated during a resting period, and not just sleep (Oudiette et al., 2013; Tambini et al., 2017). For example, after participants learnt the locations of objects, they performed a simple repetitive task whereby some visual objects appeared. This visual reactivation during another task resulted in improved memory for the locations of the objects (Tambini et al., 2017). The authors suggest that reactivation benefits memory consolidation during times in which the hippocampus is not engaged in coding novel information, such as a restful period or sleep. However, the conditions that enable successful TMR during wakefulness are not yet clear, as other studies have not found such a benefit (Rudoy et al., 2009; Diekelmann et al., 2011; Schreiner and Rasch, 2015). For example, vocabulary learning was enhanced when words were reactivated during sleep, but not during active and passive waking (Schreiner and Rasch, 2015). Diekelmann et al. (2011) suggest that TMR is not a unitary phenomena, but rather underlied by different mechanisms and brain areas operating during sleep and wakefulness. One proposal is that reactivation during sleep stabilizes and strengthens memories, while reactivation during wakefulness does the opposite by destabilizing memories, allowing newer and more relevant information to override these memories. We theorize that unusual events alert us to changing environmental circumstances and expectations, and that wakeful reactivation can be particularly beneficial in modifying these memories.

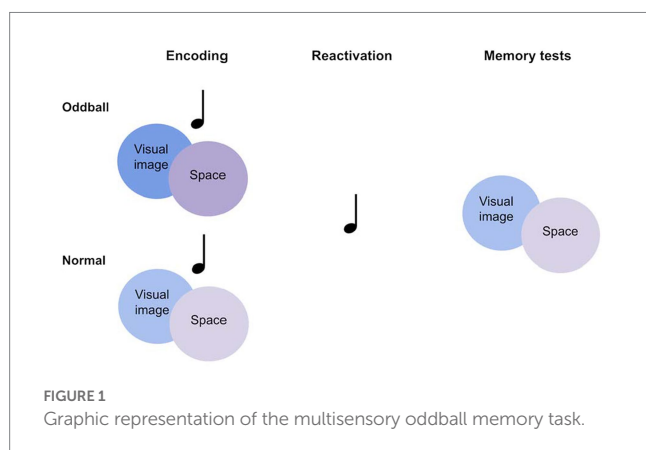
To address this theory, we tested the following hypotheses: Wakeful reactivation of novel and unusual events will enhance encoding of these events compared to normal events, in line with previous research (Hunt and McDaniel, 1993). Importantly, memory for unusual events will be improved by coupling these events with sensory cues during encoding, and later reactivating these cues. By forming a rich multisensory representation, reactivating a component of this representation will benefit memory for other components as the entire multisensory representation is strengthened. While prior studies tested memory in the presence of the sensory cues that were reactivated during sleep or wakefulness, we test visual memory without sound cues, hypothesizing that the shared multisensory representation is evoked. We conducted two experiments in which participants were first presented with audiovisual objects at different locations, followed by a replay of sounds. Participants were then tested on their memory for visual and spatial information in the absence of sounds. This method addresses the question of whether reactivation in one sensory modality leads to memory benefits in another modality. In Experiment 1, audiovisual objects consisted of everyday objects coupled with their corresponding sounds, with “oddball” objects consisting of unusual objects and sounds. In Experiment 2, everyday objects were coupled with repeating sounds, with “oddballs” created by associating certain objects with an irregular sound. During both experiments, participants completed a cognitive ability task in computerized form (Raven’s Advanced Progressive Matrices) to further test the possible relations between memory improvement and cognitive ability (see Figure 1).

Experiment 1: Audiovisual tagging

Method

Participants

A total of 78 participants were run. Nine participants were removed due to exhibiting no correct responses in some conditions during the memory test phase (thus creating a missing design), resulting in 69 participants. All participants had normal or corrected-to-normal visual acuity and received course credit for a 1-h session. All participants gave written informed consent, approved by the University of California, Riverside Human Research Review Board.



Apparatus and stimuli

An Apple Mac Mini running Matlab (MathWorks, Natick, MA, United States) and Psychophysics Toolbox Version 3.014 (Brainard, 1997; Pelli and Vision, 1997) was used for stimuli generation and experiment control. Stimuli were presented on a ViewSonic PF817 monitor with a 1,600 × 1,200 resolution, and a refresh rate of 100 Hz.

Design

A 2×2 within-participants design was employed with the following factors: *Stimuli* (oddball/normal) and *Reactivation* (yes/no). We created an *oddball memory task*, consisting of three parts: Encoding, reactivation, and memory tests (see Figure 2). All of the tasks were performed successively within a single session.

Encoding phase

We created *audiovisual tagging*:

- *Normal* visual stimuli appeared with their matching sounds, such as animals with their vocals, and musical instruments with their notes. Stimuli belonged to seven categories, each category consisting of 12 images, for a total of 98 trials (see [Supplementary Appendix I](#) for full stimuli description).
- *Oddballs* were created by presenting a mismatching object for each category (e.g., animals: *unicorn*, musical instruments: *gramophone*). These objects were also paired with mismatched sounds (e.g., unicorn—heartbeat sound, gramophone—kissing sound). Each category included two oddballs, resulting in a total of 14 oddball trials.

Overall there were 112 trials. Participants were presented with a stream of visual and auditory stimuli. Each image (normal or oddball) appeared randomly either to the left or right of a fixation point for 1,200 ms. Each normal sound appeared at the onset of the visual image for 400 ms. In contrast, an oddball sound was repeated three times to reinforce the sound, with no pause between sounds.

We created two oddball conditions:

- *Category oddballs* ($N=56$). Stimuli presentation was as follows: There were two presentation blocks, with the seven categories appearing in successive order (e.g., category 1–category 2, etc.). The order of the categories was chosen randomly for each presentation. Overall, each category consisted of 16 images, 14 normal images, and 2 oddballs. The images for each category presentation were also chosen randomly, with each image appearing once during encoding. However, the number of images for each category presentation was varied. There are seven possible options to split images (e.g., 7–9, 10–6, 11–5, etc.), and each category was randomly associated with an option. This meant that participants could not predict the length of each category. The oddball image appeared randomly during the category presentation, with the constraint that it did not appear in the first two places. The intention was that the oddball will “pop-out” from the category (following the method of Cohen Hoffing and Seitz, 2015). Each category appeared in one location of the screen (either left or right to the fixation point) chosen randomly.
- *Random oddballs* ($N=22$). Another approach was to present oddballs randomly, so that the distinct perceptual features of the stimuli will pop-out regardless of category. Oddballs appeared



amidst random objects—images were randomly chosen from the seven categories – and changed location on each trial, with the constraint that an oddball was preceded by at least three normal stimuli. All other presentation attributes were similar to those of the *category oddballs* condition.

In both conditions, to ensure participants engaged with the stimuli, they were asked to perform two successive tasks: (i) Judge whether the category of the present object matched that of the previous one ($n-1$ task), pressing 3 for the same category, and 4 for a different category. (ii) To verify our oddball stimuli, participants were then asked to indicate for each sound whether it was surprising or not, pressing the spacebar if the sound was surprising.

The conditions were run sequentially across two academic quarters. We recruited available participants for each condition, with a non-optimal end result of an unequal number of participants between conditions. Importantly, though, this is a within-participant study, enabling a direct comparison of the main *reactivation* manipulation, as will be described shortly.

Cognitive ability task

Participants completed an abridged version of Raven's advanced progressive matrices in computerized form (12 questions; based on Kubricht et al., 2017), with questions presented in order of increased complexity. There was a time limit of 12 min, after which the study proceeded to the next part automatically. Participants were presented with 2 practice trials prior to completing the test questions. The score is calculated as percent correct.

Reactivation phase

Participants were presented with a stream of 84 sounds *via* headphones. Each sound appeared for 400 ms, with a short pause between sounds that lasted 400 ms. The sounds appeared in random order for each participant. The following sounds were reactivated:

- *Re-activated oddballs*: one oddball sound per category was randomly chosen for each participant, with each sound repeating three times (21 presentations in total).
- *Re-activated normal stimuli*: three normal sounds per category were randomly chosen for each participant, with each sound repeating three times (63 presentations in total).

During the sound presentation, participants were asked to complete simple word puzzles, with the following instructions: "You will hear a series of sounds. You will also complete a word search on paper. Please keep your headphones on during the entire part." The word puzzles consisted of a list of words, for example, geography words, and participants were asked to find the words in a big table of letters (see [Supplementary Appendix I](#) for an example). There was no semantic overlap between the puzzle words and the sounds presented during the memory phases. This phase lasted approximately 5 min. Recognition accuracy was measured.

Recognition test

Images appeared at the middle of the screen without sound. Participants judged each image as "old" or "new." There were five stimuli conditions, totaling 112 trials:

- *Re-activated oddballs* (seven trials): Oddballs presented during encoding, and whose sounds were presented later again.
- *Non-reactivated oddballs* (seven trials): Oddballs presented during encoding only.
- *Re-activated normal images* (21 trials): Normal stimuli presented during encoding, and whose sounds were presented later again.
- *Non-reactivated normal images* (21 trials): Normal stimuli presented during encoding only.
- New images that did not appear during the encoding phase (56 trials).

Each image appeared until the participant responded. To capture different forms of recognition memory, participants answered using a *confidence scale*. The instructions were as follows: "You will see a series of pictures. Half of the pictures appeared in Part I (Old pictures), and half will appear for the first time (New pictures). For each picture, please answer whether the picture new or old? Press 1-Old Remember, 2-Old Familiar, 3-New."

Location test

If participants indicated that an image was "old," they were asked to recall the original location of the image during encoding using a second confidence scale. We hypothesized that object memory and object-location memory may be differently sensitive to the experimental manipulation, and therefore assessed confidence separately for location recall as well. The instructions were as follows: "If the picture is Old, did it appear in the Left or Right side? Press 1—Left remember, 2—Left familiar, 3—Right familiar, and 4—Right remember." Location accuracy was measured.

Statistical analyses were conducted with the programming language R, with the tidyverse package (v1.3.2; Wickham et al., 2019), ggplot2 (v3.3.6; Wickham, 2016), colorspace (v2.0–3; Zeileis et al., 2020), apex (v1.1–1; Singmann, 2022), emmeans (v1.7.5; Lenth, 2017), and psycho (v0.6.1, Makowski, 2018). We examined accuracy (e.g., percent correct). Outliers were determined as values below $Q1 - 1.5$ IQR, and above $Q3 + 1.5$ IQR across conditions, and were excluded from further analysis. For full descriptive statistics of the encoding phase, see [Supplementary Appendix II](#).

Results

Recognition test

We first examined whether tagging led to an improvement in memorization of the images. To address this, we examined accuracy (e.g., percent correct) in the recognition test (see [Figure 3](#)). We further calculated signal detection measures— d' -prime (sensitivity) and c (criterion) to account for possible response biases. A within-participant Analysis of Variance (ANOVA) was conducted for d' -prime, followed by planned contrasts with *stimuli* (oddball/normal) and *reactivation* (yes/no) factors. There was a significant main effect of *stimuli*, $F(1, 68) = 48.987$, $p < 0.0001$, following a Greenhouse–Geisser correction for departure from sphericity. Pairwise contrasts with holm adjustment for multiple comparisons reveal that participants were more accurate at recognizing oddballs than normal stimuli, mean difference = 10.832, $t(68) = 10.832$, $p < 0.0001$. The *reactivation* factor was non-significant, $F(1, 68) = 0.65$, $p = 0.4$. These

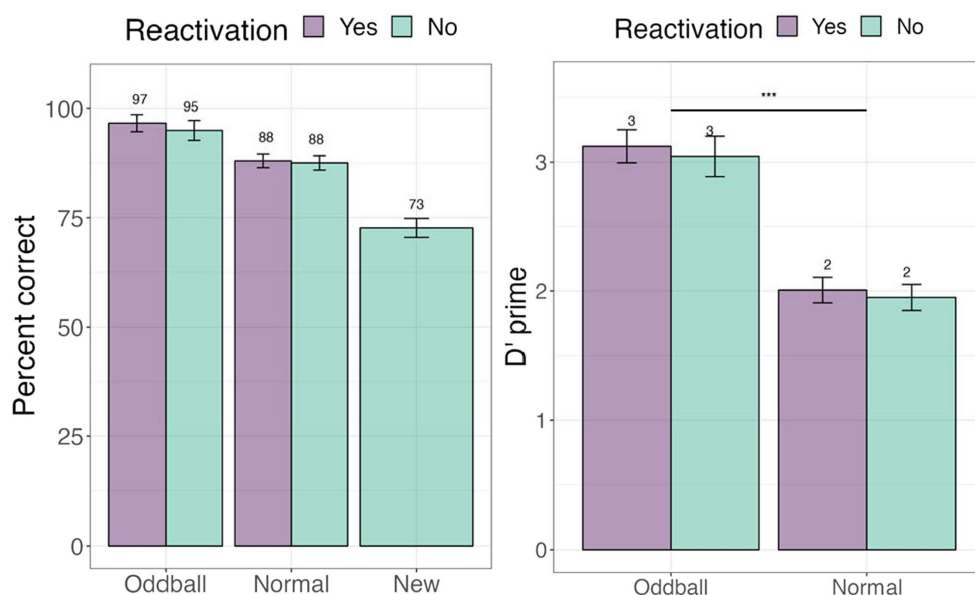


FIGURE 3

Percent correct and d'-prime values for the visual recognition test in Experiment 1. ***The significance of $0 < 0.001$. Error bars represent standard errors of the mean.

results establish our memory task as successful in creating highly memorable audiovisual oddballs. For full descriptive statistics see [Supplementary Appendix III](#).

Recognition confidence

To ascertain whether there were differences between stimuli with different levels of memory quality (stimuli that participants explicitly remembered versus were only familiar with), we conducted a 3×2 ANOVA, with *stimuli* (oddball/normal), *reactivation* (yes/no), and *confidence* (remember/familiar) factors. We note that 19 participants were removed from this analysis due to missing values (not all conditions had “remember” or “familiar” responses). There was a significant *stimuli* \times *confidence* effect, $F(1, 49) = 72.36$, $p < 0.0001$, with participants showing greater accuracy for remembered oddballs compared to remembered normal stimuli, or any familiar stimuli. Pairwise contrasts with holm correction reveal that participants were more accurate at recalling the location of “remember” oddballs compared to “familiar” oddballs, mean difference = 19.3, $t(49) = 4$, $p = 0.0006$. Similarly, they were better at recalling “remember” oddballs compared to “remember” normal images, mean difference = 10.27, $t(49) = 10.27$, $p = 0.0001$ (see [Figure 4](#)). This result suggests that accuracy and self-report confidence are well matched in this task, with accuracy largely based on recollection-based recognition memory rather than familiarity ([Yonelinas et al., 2022](#)). The *reactivation* factor was non-significant, $F(1, 49) = 0.44$, $p = 0.5$. *Stimuli* \times *reactivation* interaction was non-significant as well, $F(1, 49) = 0.59$, $p = 0.45$.

Location test

We next examined performance on the location task to test whether tagging improved contextual knowledge of the stimuli (see [Figure 5](#)). Only trials with correct answers on the recognition test were considered. A 2×2 ANOVA with *stimuli* and *reactivation* factors

revealed a significant *stimuli by reactivation* interaction, $F(1, 68) = 4.13$, $p = 0.046$, following a Greenhouse–Geisser correction. Participants were better at recalling the location of *reactivated oddballs* compared to *non-reactivated oddballs* in the subsequent absence of sounds, mean difference = 7.74, $t(68) = 2.5$, $p = 0.015$. This finding is consistent with our hypothesis that reactivation will benefit spatial memory for oddballs.

Oddball conditions

We performed a 3×2 mixed ANOVA with a between-participants factor—*oddball condition* (category oddballs/random oddballs), and two within-participant factors—*stimuli* (oddball/normal) and *reactivation* (yes/no), with location accuracy as the dependent variable. There was a significant *condition* \times *stimuli* \times *reactivation* effect, $F(1, 67) = 8.15$, $p = 0.019$. Computing a two-way interaction for each condition level revealed a statistically significant interaction of stimuli and reactivation for *random oddballs*, $F(1, 67) = 25.479$, $p < 0.001$, with participants worse at recalling the locations of *random oddballs* that were not reactivated compared to those that were reactivated (see [Figure 6](#)). This result suggests that oddballs attract the most attention when they cannot easily be tied to a familiar stimuli category, and that reactivating the oddball events *via* sound improved spatial memory.

Location confidence

To ascertain whether there were differences between stimuli with different levels of memory quality, we conducted a 3×2 ANOVA, with *stimuli* (oddball/normal), *reactivation* (yes/no), and *confidence* (remember/familiar) factors. We note that 20 participants were removed from this analysis due to missing values (not all conditions had “remember” or “familiar” responses). There was a significant *stimuli* effect, $F(1, 49) = 5.06$, $p = 0.028$, with participants being more accurate at recalling oddball locations than normal

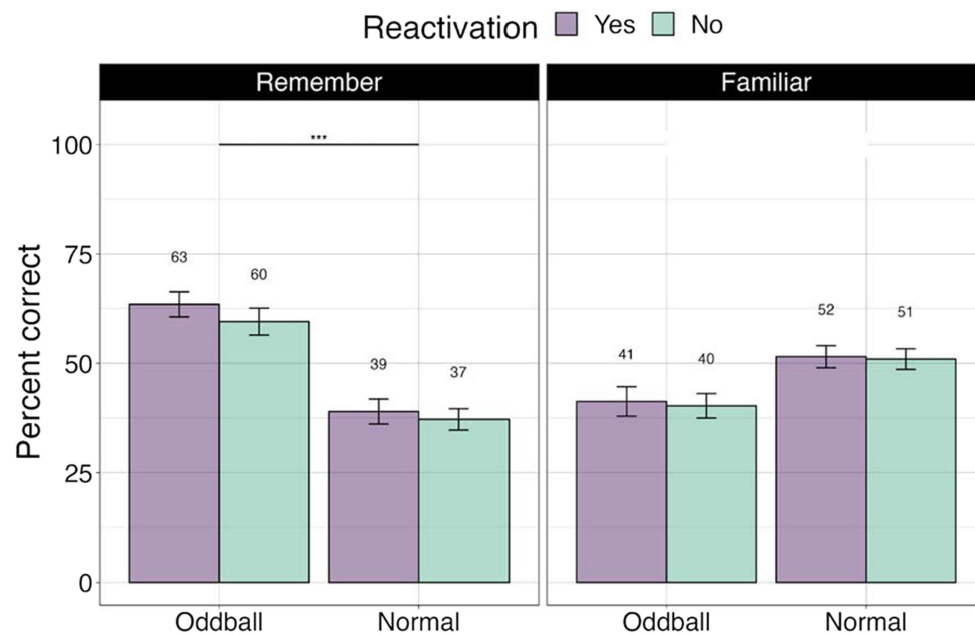


FIGURE 4

Percent correct for the visual recognition test by self-reported confidence levels in Experiment 1. ***The significance of $0 < 0.001$. Error bars represent standard errors of the mean.

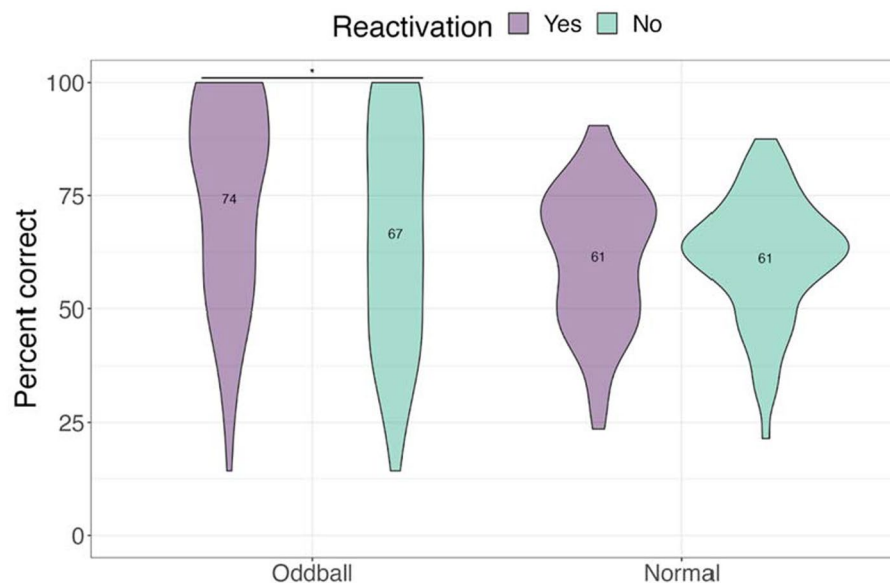


FIGURE 5

Mean accuracy for the location test in Experiment 1. The violin plot is a mirrored density plot with the kernel density estimates on each side (a violin plot combines boxplot and density plots into a single plot). *The significance of $p < 0.05$.

stimuli locations. Importantly, there was a significant *confidence* effect, $F(1, 49) = 29.73$, $p < 0.0001$. Pairwise contrasts with holm correction reveal that participants were more accurate at recalling the location of “remember” oddballs compared to “familiar” oddballs, mean difference = 12.5, $t(49) = 3.46$, $p = 0.0045$. Similarly, they were better at recalling “remember” normal images compared to “familiar” normal images, mean difference = 14.35, $t(49) = 4.8$, $p = 0.0001$ (see Figure 7).

Cognitive ability

There were no meaningful correlations between general cognitive ability measured as accuracy on Raven’s advanced progressive matrices, sensitivity (d') in the recognition test, and accuracy in the location test. This suggests that the oddball memory task is tapping semantics and long-term memory, while general cognitive ability is associated with working memory ability (Süß et al., 2002; Pahor et al., 2022). See Supplementary Appendix IV for full descriptive statistics (Figure 7).

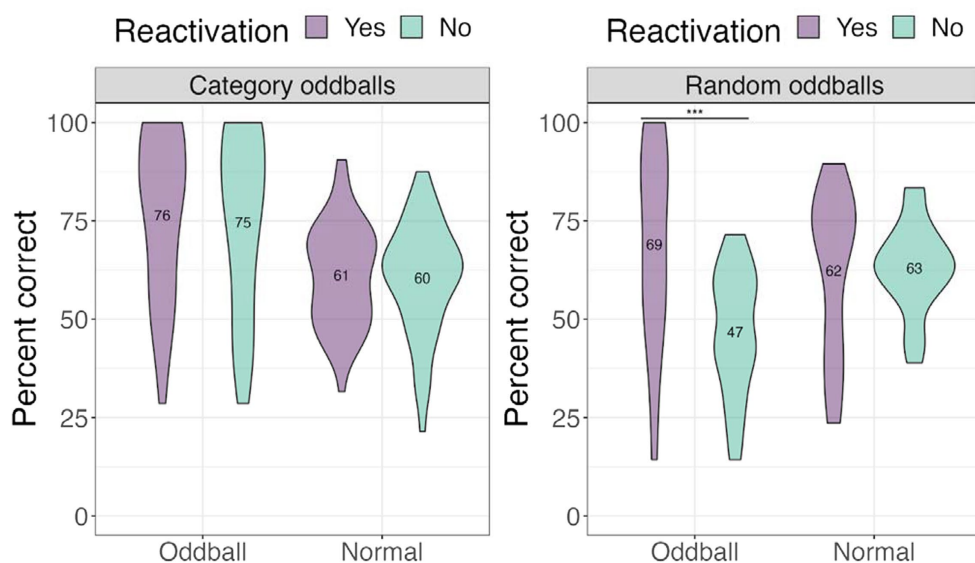


FIGURE 6

Percent correct for the location test for different oddball conditions in Experiment 1. ***The significance of $p < 0.001$.

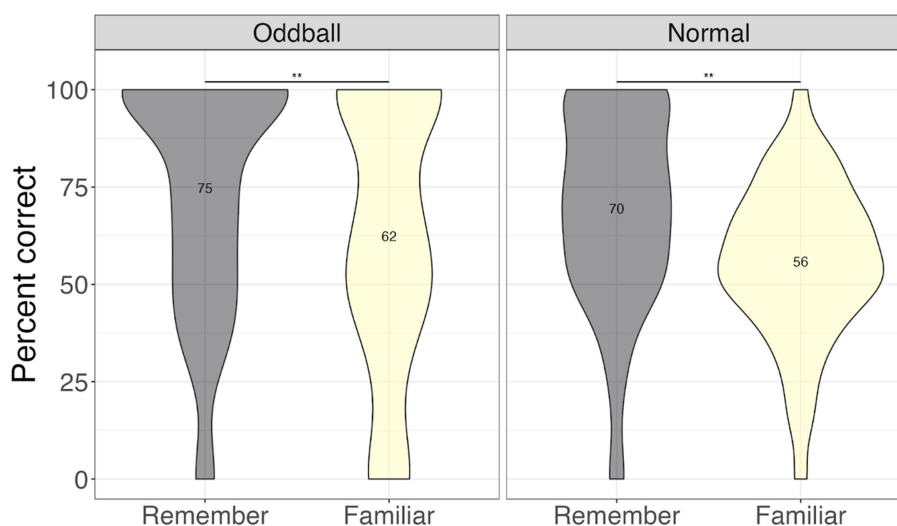


FIGURE 7

Percent correct for location test by self-reported confidence levels in Experiment 1.

Summary

When presented with normal or oddball audiovisual events, participants were better at remembering oddballs on a recognition test. Performance was particularly high, perhaps creating a ceiling effect for any other condition differences to occur. High recognition is mostly due to explicit recognition of the event, and not just mere familiarity, as evident in self-report confidence ratings.

The critical finding of this study is that participants better remembered the location of objects whose associated sounds were reactivated during a wakeful consolidation period, compared to objects whose sounds were not reactivated. Even though object location was encoded incidentally during the first phase, sound

reactivation boosted memory for this attribute. Our results further suggest that an encoding stage with random presentation of images compared to one where images appeared in chunked categories yielded a memory benefit for the oddballs, presumably because they were particularly noticeable in the former presentation. Together, these results suggest that memory is improved for rare audiovisual events, and that reactivating a sensory component of the event is enough to enhance memory for other associated attributes.

A key attribute of our memory task is a reliance on existing semantic associations in the case of normal events, with oddballs created by associating a mismatching sound to a rare category member. To better understand what characteristics of the stimuli are necessary to find this effect, we Experiment 2 examines whether sound oddballs in a perceptual

stream are enough to form a multisensory representation that can be later evoked during reactivation and retrieval.

Experiment 2: Sound tagging

Participants

A total of 46 participants were run. All participants had normal or corrected-to-normal visual acuity and received course credit for 1-h session. All participants gave written informed consent, as approved by the University of California, Riverside Human Research Review Board.

Apparatus and stimuli

Similar to experiment 1.

Design

A within-participants design was employed with *Stimuli* (reactivated oddball /oddball/normal) as factor. We created a second version of the oddball memory task, consisting of three parts: Encoding, reactivation, and memory tests.

Encoding phase

We created *sound tagging*, whereby visual stimuli appeared with the same repetitive sound (“pop”) for a total of 84 trials. Oddballs were created by pairing a subset of normal visual images with a unique mismatched sound (e.g., “heartbeat”) to create a “pop-out” effect. Each oddball image was paired with a unique mismatched sound, with a total of 28 trials. Each image appeared either to the left or right of a fixation point for 1,200 ms. If the sound was a normal one it appeared once for 400 ms. If the sound was an oddball, it repeated three times in order to reinforce this event. Categories appeared successively, so that the 16 images of the same category appeared successively, before moving on to the next category. Participants performed the same tasks as in Experiment 1.

Reactivation phase

Participants were presented with a stream of sounds *via* headphones. Each sound appeared for 400 ms, with a short pause of 400 ms. Two sounds per category were randomly chosen for each participant, resulting in 14 oddballs. Since tagging consisted of sounds alone (as opposed to sounds and images), we sought to strengthen reactivation effects by repeating each sound 6 times, for the total of 84 trials. Sounds appeared in random order for each participant.

Recognition test

Images appeared at the middle of the screen without sound. Participants judged stimuli as “old” or “new” with the same *confidence scale* as in Experiment 1.

There were four stimuli conditions, totaling 112 trials. The following stimuli appeared during the test:

- *Reactivated oddballs*: Images whose sounds appeared during reactivation (14 trials)
- *Non-reactivated oddballs*: Images that appeared during encoding, but their sounds did not appear during reactivation (14 trials).
- *Non-reactivated normal images*: Images that appeared during the encoding phase (28 trials).
- *New*: Images that did not appear during the encoding phase (56 trials).

Location test

If participants indicated that an image was “old,” they were asked to recall the original location of the image using the same *confidence scale* as in Experiment 1.

Results

Recognition test

We tested whether tagging led to an improvement in memorization of the images. Percent accuracy was calculated. We further calculated d' -prime (sensitivity) and c (criterion) measures (see [Figure 8](#)). A within-participant Analysis of Variance (ANOVA) was conducted with *stimuli* (reactivated oddball /oddball/normal) factor. We note that unlike the analysis used in Experiment 1, we did not have a separate reactivation factor, but instead compared the three stimuli types employed in Experiment 2's design. There was a significant main effect of stimuli, $F(1, 45) = 16.397, p = 0.0002$. Pairwise contrasts among stimuli with holm adjustment for multiple comparisons revealed that participants were better at recognizing normal to oddball images, $t(45) = -4.6, p = 0.0001$. For full descriptive statistics see [Supplementary Appendix III](#).

Recognition confidence

We conducted a 3×2 ANOVA, with *stimuli* (reactivated oddball /oddball/normal), and *confidence* (remember/familiar) factors. Fourteen participants were removed from this analysis due to missing values. There was a significant *stimuli* effect as found in the previous analysis, $F(2, 62) = 11.44, p < 0.0001$. Importantly, there was a significant *confidence* effect, $F(1, 31) = 112.62, p < 0.0001$. Participants were far more accurate for remembered compared familiar stimuli, mean difference = 36.5, $t(49) = 10.6, p < 0.0001$ (see [Figure 9](#)).

Location test

A one-way ANOVA revealed no significant differences across stimuli conditions (see [Figure 10](#)).

Location confidence

We next examined accuracy and self-rated confidence level. we conducted a 3×2 ANOVA, with *stimuli* (reactivated oddball /oddball/normal) and *confidence* (remember/familiar) as factors. We note that 15 participants were removed from this analysis due to missing values (not all conditions had “remember” or “familiar”

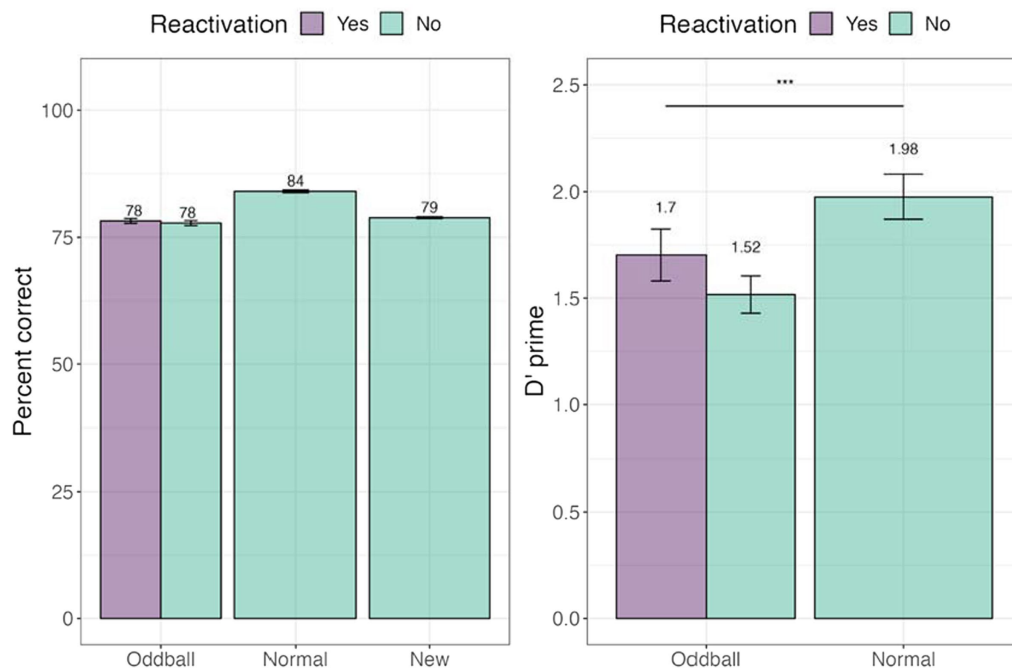


FIGURE 8

Percent correct and d' -prime for the visual recognition task in Experiment 2. ***The significance of $p < 0.001$. Error bars represent standard errors of the mean.

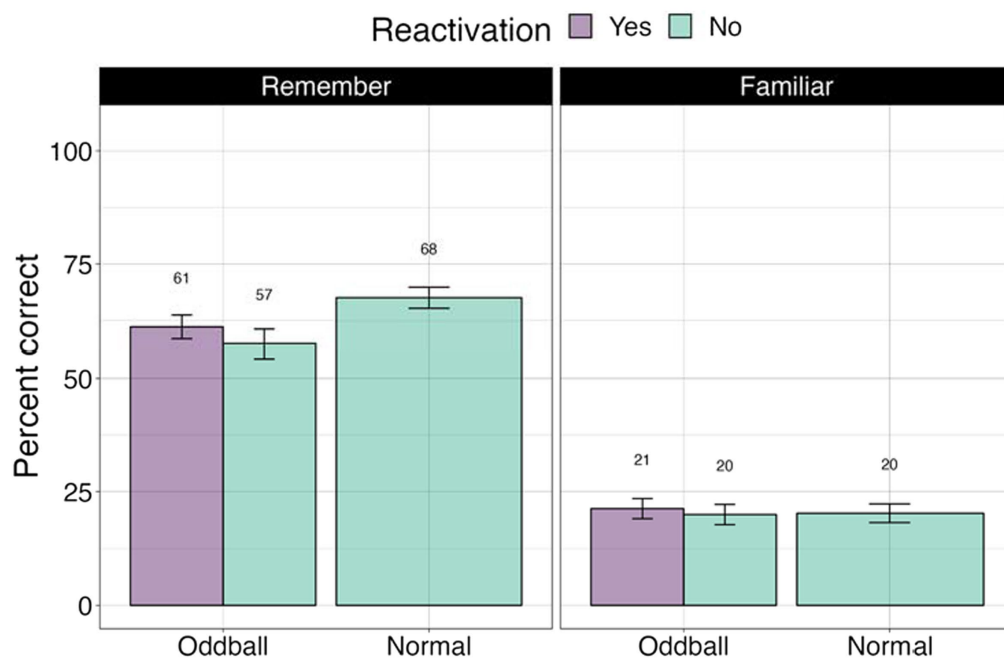


FIGURE 9

Percent correct for the visual recognition test by self-reported confidence levels in Experiment 2.

responses). There was a significant *confidence* effect, $F(2, 60) = 26.948$, $p < 0.0001$. Pairwise contrasts with holm correction reveal that participants were more accurate at recalling the location of “remember” of all stimuli types compared to “familiar” stimuli, mean

difference = 12.5, $t(49) = 3.46$, $p = 0.0045$. Participants were also specifically better at recalling “remember” normal images compared to “familiar” normal images, mean difference = 19, $t(30) = 5.19$, $p < 0.0001$ (see Figure 11).

Cognitive ability

Similarly to Experiment 1, there are no meaningful correlations between general cognitive ability measured as accuracy on Raven's advanced progressive matrices, sensitivity (d' prime) in the recognition test, and accuracy in the location test.

Summary

When participants were presented with visual images associated with a regular repeating sound or an oddball sound, they were better at remembering the normal images. Participants were also better at remembering normal images they rated as “remember” compared to those rated as “familiar,” suggesting a high association between memory accuracy and confidence ratings. This finding is different from results obtained in Experiment 1. We attribute this to a possible floor effect, whereby the memory task as a whole was difficult,

suppressing possible benefits for sound tagging. One option is to make auditory encoding easier, for example, by presenting a complex sound that varies in several dimensions, such as loudness and pitch, from the normal sounds. A second option is to create an easier-to-learn association, such as pairing an image with a short mismatched melody. Another option is to utilize more potent sensory cues, such as odors that may trigger stronger attentional and emotional processing. These possibilities can be pursued in future studies.

Discussion

We remember events and objects by their multisensory attributes—what things looked like, how they sound, where they were, how they made us feel. One way to strengthen memory is to replay parts of events (Oudiette et al., 2013). We propose that when retrieving information about these events shortly later, other sensory attributes are more easily accessed. In our study, participants were presented with a series of everyday objects and their sounds, with some objects having an unusual visual and auditory characteristic to render it more memorable. We found that reactivating one attribute (sound) of a particularly memorable event (an “oddball”) enhances memory for another attribute (location). Improved memory for spatial information occurred even though this information was encoded incidentally during initial presentation. A memory benefit occurred when oddball stimuli appeared randomly as opposed to being part of a sequence (e.g., a sequence of animals), presumably rendering the oddballs even more salient.

This study demonstrates the benefit of sensory reactivation during wakefulness and not sleep. Most studies exploring target memory reactivation focus on reactivation during sleep, when memory replay and consolidation processes often occur. Several studies suggest that reactivation can take place during wakeful periods as well (Oudiette et al., 2013; Tambini et al., 2017). Mednick et al. (2011) suggested that the brain seeks to opportunistically engage in consolidation processes

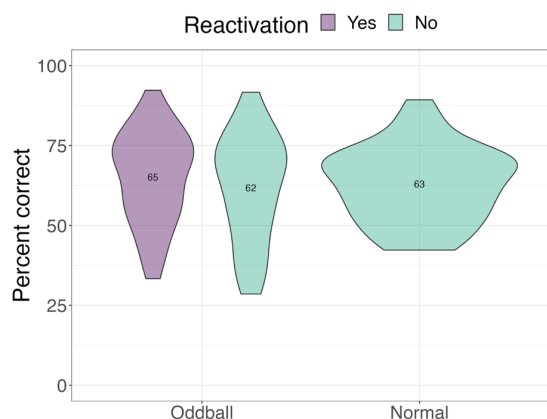


FIGURE 10
Mean accuracy for the visual recognition task in Experiment 2.

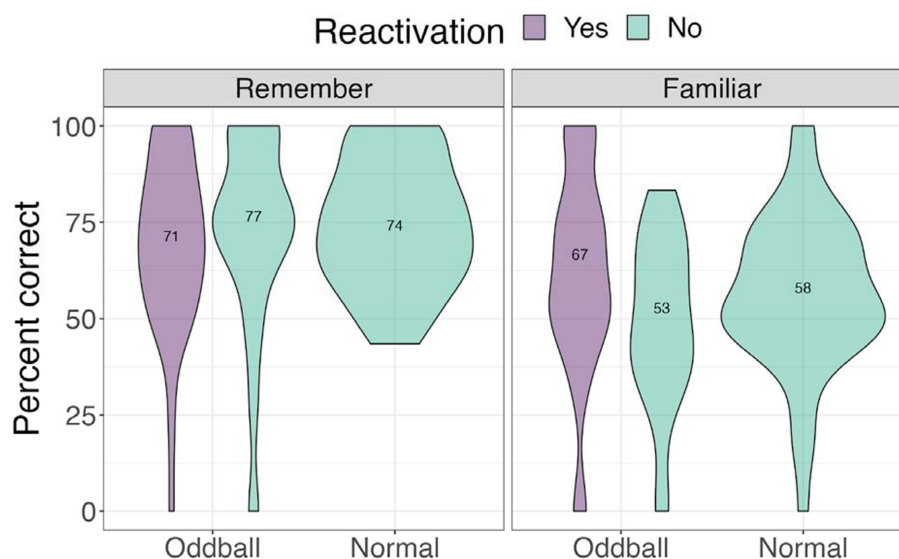


FIGURE 11
Mean accuracy for the visual recognition by different confidence levels task in Experiment 2.

during periods of reduced interference from external stimuli, whether during sleep or restful moments during the day. This is thought to be related to processing in the hippocampus, where when it is not involved in coding new events, consolidation of previous events occurs.

An interesting question is whether the same or different structures are involved in memory reactivation during wakefulness compared to sleep. A recent study on rat learning reveals that different structures support the creation of long-term object recognition representations (Sawangjit et al., 2022). During sleep, the hippocampus forms context-dependent representations, whereby different sensory attributes are binded together. During wakefulness, context-independent representations are formed by extra-hippocampal, striatal, and cortical regions. The hippocampus may also be forming parallel representations, if free from encoding new events. Wakeful reactivation may be particularly beneficial for attention-grabbing oddball events, where the object itself is of immediate interest. In contrast, reactivation during sleep boosts memory for event context, where context-representations are strengthened by hippocampal activation.

Another suggestion is that wakeful reactivation can work well for semantic tagging by capitalizing on existing long-term memories, whereas sensory tagging and reactivation (as in Experiment 2) requires sleep to strengthen new representations.

It is important to note that the time-course of TMR is not well addressed in our study. While, we assessed TMR in participants tested immediately after the wakeful reactivation, prior studies employed longer delays between reactivation and testing, for example, ~10 min (Oudiette et al., 2013), and 24 h (Tambini et al., 2017). The time interval between reactivation and test may be affecting different consolidation processes: At a shorter delay, short-term representations are modified, while at a longer delay, hippocampal representations are modified. Further research will be required to understand how changing the delays between encoding, reactivation and tests of recall impact results in our paradigm.

While previous studies presented information in the same modality during encoding, reactivation and test, we took a different approach, presenting *different sensory attributes of the same event* across encoding, reactivation and test. The memory benefits observed in this study support *dual coding* models proposing that multisensory stimuli are encoded by multiple systems, notably the visual and verbal systems (Clark and Paibio, 1991). Once a multisensory representation is formed, it can be accessed by its different unisensory components, either through direct links between sensory cortices, or *via* links to the same semantic representation (Driver and Noesselt, 2008; Shams and Seitz, 2008). We expand this framework by demonstrating that reactivating one sensory component during a consolidation period strengthens the entire multisensory representation, evident in superior memory for other sensory components.

Audiovisual tagging evokes existing long-term semantic representations. In this form of tagging, most objects appeared with their corresponding sounds (for example, animals with their vocals, and objects with the sound they omit). Oddballs were created by presenting some objects with mismatching sounds, with the aim of creating a deviation from existing associations. Reactivating mismatched sounds improved memory for oddball locations, compared to oddballs that were not reactivated. Wakeful reactivation

is hence effective at modifying an oddball memory, a salient object with weaker context. In contrast, in a second experiment utilizing *sound tagging*, oddballs were created by capitalizing on a well-known perceptual mechanism, whereby irregular events draw attention. While most objects appeared with a single repeating sound, oddballs appeared with a unique novel sound. Here, no effect was found for reactivation on memory performance. One possibility is that wakeful reactivation is not effective in the complete absence of semantics, and reactivation during sleep may be needed to create new contextual representations. Another possibility is that overall low object recognition prevented a reactivation difference to manifest for object locations. In order to create stronger tagging, a future study can employ more complex sounds, a different sensory cue, or repeated stimuli presentations.

A limitation of Experiment 1 is an unequal number of participants between conditions. However, the conditions themselves each consisted of a within-participant design, allowing a direct comparison of the effect of reactivation on memory performance of the same sample of participants.

An exciting potential of TMR research is the potential to improve episodic memory in aging and amnesia with memory reactivation interventions (Fernández et al., 2022). While episodic memory tends to decline with age, MCI is characterized by a notable episodic memory impairment, without compromising everyday functioning. Fernández et al. (2022) found a benefit of a *reactivation intervention* on associative memory: Three groups of participants—adults, older adults, and MCI patients—learned new face-name pairs. After a day, half of the participants of each group were presented again with faces and the first letters of their names (to encourage active retrieval), while the other half did not. A day later, participants were tested on their memory for the face-name pairs. Across all groups, participants who underwent the reactivation intervention showed improved associative memory compared to the control condition. The memory benefit was particularly pronounced for MCI patients, who showed better memory for the face-name pairs, as well as memory for single faces or names. Reactivation is hence most potent for participants with the weakest memories. While reactivation is helpful for participants with varying degrees of episodic memory impairments originating in the function of the hippocampus, it may be that utilizing non-hippocampal representations can be even more effective. Future studies could target single-item memory, for example, reactivating oddball events such as an unusual name. Participants with a memory deficit or decline are hypothesized to show improved memory for such oddballs following wakeful reactivation, relaying on relatively intact non-hippocampal areas.

In conclusion, we tested the hypothesis that memories could be strengthened by coupling exposure events with sensory cues (either in a single or multiple modalities), and later reactivating these cues when participants are awake. One possible application of these results are ways to benefit memory for novel events. Such events could be new or unconventional educational material, new scientific findings, or new words in a language, such as technology-related words. These pieces of information could potentially be paired with different sensory cues, with these cues presented again during daily activities (such as listening to sounds when walking) to consolidate information. An exciting possibility is that TMR can be used in interventions to benefit those with memory

concerns, such as older adults with memory declines. While future research in the field is certainly required, the beauty of multisensory memory interventions is that they are relatively simple to deploy and have shown some effectiveness to aid in memory encoding, consolidation, and recall.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The studies involving human participants were reviewed and approved by University of California Riverside, Human Subjects Review Board. The patients/participants provided their written informed consent to participate in this study.

Author contributions

All authors designed the research. AG created and ran the experiments, analyzed the data, and wrote the manuscript with input

from AS and LS. All authors contributed to the article and approved the submitted version.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fpsyg.2023.1092408/full#supplementary-material>

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