REVIEW

# Attention to memory: orienting attention to sound object representations

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Abstract Despite a growing acceptance that attention and memory interact, and that attention can be focused on an active internal mental representation (i.e., reflective attention), there has been a paucity of work focusing on reflective attention to 'sound objects' (i.e., mental representations of actual sound sources in the environment). Further research on the dynamic interactions between auditory attention and memory, as well as its degree of neuroplasticity, is important for understanding how sound objects are represented, maintained, and accessed in the brain. This knowledge can then guide the development of training programs to help individuals with attention and memory problems. This review article focuses on attention to memory with an emphasis on behavioral and neuroimaging studies that have begun to explore the mechanisms that mediate reflective attentional orienting in vision and more recently, in audition. Reflective attention refers to situations in which attention is oriented toward internal representations rather than focused on external stimuli. We propose four general principles underlying attention to short-term memory. Furthermore, we suggest that mechanisms involved in orienting attention to visual object

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representations may also apply for orienting attention to sound object representations.

# Introduction

To date, research on attention has primarily investigated how sustained, selective, or divided attention modulates the processing of sensory information. This is typically achieved by instructing volunteers to attend to stimuli present in the environment (e.g., a vertical bar in a cluttered display or a particular sound in a stream of auditory stimuli). However, throughout the day, thoughts continuously run through our minds, as we reminisce on the past, live in the moment, and plan for the future. Realistically, attention is a balancing act between focusing on events from our external and internal worlds. This notion that attention can be allocated to internal thoughts or representations (reflective attention, Chun & Johnson, 2011; Johnson & Hirst, 1993; Johnson & Johnson, 2009; Johnson, Mitchell, Raye, D'Esposito & Johnson, 2007) has a long standing in psychology and can be traced back to William James' nineteenth century book, Principles of Psychology. In the last decade, there has been a great deal of interest in studying attention to memory during retrieval and recognition processes (Burianova, Ciaramelli, Grady, & Moscovitch, 2012; Cabeza et al., 2011; Ciaramelli, Grady, Levine, Ween, & Moscovitch, 2010; Ciaramelli, Grady, & Moscovitch, 2008; Grillon, Johnson, Krebs, & Huron, 2008) and during visual attention tasks (Nobre et al., 2004; Nobre & Stokes, 2011). Although reflective attention is not a novel concept per se, the development of new experimental paradigms combined with neuroimaging techniques now offer the unique opportunity to test and refine models of attention, which have been developed almost exclusively to account for situations in which attention is focused on external stimuli (termed perceptual attention, Chun & Johnson, 2011).

Reflective attention has been investigated primarily using visual material. Yet, reflective attention may be inherent to audition in general and speech in particular. Since words unfold over time, reflective processing is necessary to attend to and maintain what we perceived in the past; this, in turn, allows us to string words and sentences together into a meaningful discourse. Furthermore, an investigation of auditory reflective attention could have important implications for healthy aging, as well as for a range of mental health issues, since impairment in attentional control to internal states plays a prominent role in dementia (Rosler, Mapstone, Hays-Wicklund, Gitelman, & Weintraub, 2005; Rosler et al., 2000), anxiety disorders (Reinecke et al., 2008), obsessive compulsive disorder (Abramovitch, Dar, Hermesh, & Schweiger, 2012; Armstrong, Sarawgi, & Olatunji, 2012; Arnsten & Rubia, 2012), and depression (Koster, De Raedt, Verschuere, Tibboel, & De Jong, 2009; McNeely, Lau, Christensen, & Alain, 2008; Pelosi et al., 2000), to name a few. For instance, thinking the same anxiety-provoking thought over and over again largely contributes to obsessive compulsive disorder (Amir, Cashman, & Foa, 1997). Therapies for anxiety-related disorders can be imagery-based, in which patients must attend to internal states (e.g., visual: imagining a large spider; auditory/verbal: listening to one's own thoughts), to identify and address anxiety-provoking thought patterns. Recently, there has been a surge in interest in developing a theoretical foundation describing the psychological and neural substrates underlying attention to internal states. In this review, we will explore the notion that attention can be allocated to a representation in short-term memory (STM). First, we will discuss models of auditory attention, followed by a brief summary of perceptual attention in both vision and audition. Finally, we will review studies that have begun to investigate the neural mechanisms that mediate reflective attentional orienting in vision and more recently in audition.

# Models of auditory attention

An overarching goal of attention research is to understand the brain networks and mechanisms underlying selective attention and how these networks/mechanisms interface with other cognitive processes, such as memory and learning. Early classical work on attention aimed to understand how one can selectively attend to one sound or visual object in the midst of other stimuli in the environment. In the auditory domain, this is often illustrated with the cocktail party example (Cherry, 1953): even though several conversations are co-occurring, most listeners can readily focus their attention on one conversation and filter out other, less relevant, conversations. Similar principles apply in the visual domain such that one can selectively attend to certain items in his/her visual surroundings (e.g., the face of a friend sitting across the table) while ignoring other items in the field of view (e.g., the vase of flowers and candle placed on the table).

Some theories based on data from visual attention tasks have characterized attention in spatial or frequency terms, likening it to a "spotlight" or "filter" that moves around, applying processing resources to whatever falls within a selected spatial region (Brefczynski & DeYoe, 1999; LaBerge, 1983; McMains & Somers, 2004). Other accounts of visual attention discuss resource allocation on the basis of perceptual objects, in which attending to a particular object enhances processing of all features of that object (Chen & Cave, 2008; Duncan, 1980, 1984; Egly, Driver, & Rafal, 1994; Hecht, Abbs, & Vecera, 2008; Shomstein & Yantis, 2002; Valdes-Sosa, Bobes, Rodriguez, & Pinilla, 1998). Objects are the mental representations of subsets of incoming sensory information that are grouped together and kept distinct from other subsets (Duncan, 1984). The object-based account of visual attention has received considerable support from behavioral (e.g., Baylis & Driver, 1993; Egly et al., 1994) and neuroimaging studies using functional magnetic resonance imaging (fMRI) (e.g., O'Craven, Downing, & Kanwisher, 1999; Yantis & Serences, 2003) or scalp recording of event-related potentials (ERPs) (e.g., Valdes-Sosa et al., 1998). Evidence from neuroimaging studies has shown that attention allocated to a visual object facilitated the processing of all features that belong to that object.

A similar object-based account has been proposed as one putative mechanism by which auditory information is selected for further processing (Alain & Arnott, 2000; Shinn-Cunningham, 2008). Originally, the model was presented as an alternative to the feature-based account, which posits that the similarity between task-relevant and task-irrelevant stimuli drives attention effects on performance and brain activity. For instance, in early and now classical studies, it was found that performance in shadowing a particular message was facilitated by increasing the physical difference between two co-occurring stories by either varying the voice of the speakers (Spieth et al. 1954) or their spatial locations (Treisman, 1964). Subsequent studies measuring auditory event-related potentials (ERPs) have revealed feature-specific attention enhancement in auditory cortical fields (e.g., Alho et al., 1987a; Alho, Tottola, Reinikainen, Sams, & Naatanen, 1987b; Hansen & Hillyard, 1983; Hillyard, Hink, Schwent, & Picton, 1973; Woldorff et al., 1993; Woods & Alain, 2001; Woods et al., 1991, 1994), which is consistent with the feature-based account of attention.

However, in these early studies, it was often not possible to distinguish feature- and object-based attention effects because the stimuli were presented at a high rate and the task-relevant and task-irrelevant sounds differed markedly in either pitch and/or location thereby promoting auditory stream segregation and the perception of co-occurring sound sources (i.e., perceptual objects). Therefore, how do we dissociate the feature-based from the object-based account if sound objects are distinguished by their defining acoustic features? One strategy to differentiate between feature- and object-based attentional accounts is to pit the grouping of stimuli into perceptual objects against the physical proximity of features. Using such a strategy, Alain et al. showed enhanced attention-related neural activity in a situation designed to promote auditory stream segregation (Alain, Achim, & Richer, 1993; Arnott & Alain, 2002; Alain & Woods, 1993, 1994). More importantly, performance improved and attention-related neural activity was larger when a distant stream of distracters was moved closer in frequency to another stream of distracter sounds that was nearer to the task-relevant stream (Arnott & Alain, 2002; Alain & Woods, 1993, 1994). Hence, it appears that sound objects form the basic unit for attentional selection and that perceptual grouping can override physical similarity effects during selective listening.

Using a different approach, Gamble and Luck (2011) measured auditory ERPs while listeners were presented with two clearly distinguishable sound objects occurring in the left and right hemispace simultaneously. Participants indicated whether a predefined target was present or absent. They found an increased negativity between 200 and 400 ms that was maximum at anterior and contralateral electrodes to the target location (termed N2ac), which was followed by a posterior contralateral positivity. These results suggest that auditory attention can be quickly deployed to a sound object's location. More importantly, these findings suggest that ERPs may provide a useful tool for studying the deployment of auditory attention in reallife situations in which multiple sound sources are simultaneously active in the environment. This is an important issue to address, given that auditory perception often occurs in a densely cluttered, rapidly changing acoustic environment, where multiple sound objects compete for attention.

Figure 1 illustrates a schematic of the object-based account of auditory attention. First, incoming concurrent sounds' low-level properties (e.g., spectrotemporal structure, location, onset, etc.) are analyzed, leading to the formation of object representations. Behavioral and EEG studies, which demonstrated that sequential (Cusack, Carlyon, & Robertson, 2000; Snyder, Alain, & Picton, 2006) and concurrent sound segregation (Alain & Izenberg, 2003; Dyson, Alain, & He, 2005) can occur independently



Fig. 1 Schematic representation of the object-based model of auditory attention, based on Alain et al. (Alain & Arnott, 2000; Alain & Bernstein, 2008). Concurrent sounds, represented by the four sets of sound waves, enter the ears. These concurrent sounds are subsequently transformed into sound object representations (indicated by the lighter shading of the sound wave sets), which coexist in auditory short-term memory. Both bottom-up salience (e.g., loudness) and top-down processes (e.g., attention [perceptual or reflective], familiarity, and schemata) determine which sound(s) lie in the focus of attention and which fall to the background; thicker arrows indicate greater bottom-up or top-down salience. In this example, the purple sound is the most salient. Note that the weights assigned by top-down control processes can dynamically change in accordance with our goals. Through top-down reflective attention, we are able to selectively attend to object representations, even in the absence of relevant external stimulation. We can use various metrics (e.g., performance, EEG, and fMRI) to understand how auditory object representations can be selectively accessed from and maintained in short-term memory

of a listener's attention, provided evidence for pre-attentive segmentation of incoming acoustic data into sound objects. These "sound objects" or "streams", derived from a preattentive segmentation of the auditory scene, form the basic units of attention (Alain & Arnott, 2000; Shinn-Cunningham, 2008). In addition to the studies mentioned earlier, more recent behavioral evidence supports the hypothesis that objects, instead of features, serve as the foremost organizational principle in auditory memory (Dyson & Ishfaq, 2008). In their study, Dyson and Ishfaq (2008) presented listeners two sounds (a noise and a tone) in the same location at the same time, and found that participants performed better when they retrieved two features from one object rather than one feature from each object. The authors concluded that auditory information is organized into objects within auditory STM.

Once the auditory scene has been partitioned into its sound objects, a selection process allows one to focus his/ her attention on a particular object and switch his/her attention from one object representation to another. Importantly, both bottom-up (i.e., stimulus salience) and top-down (i.e., internal goals) demands compete to determine which object(s) in our surroundings are attended (Corbetta, Kincade, & Shulman, 2002; Mazaheri, DiQuattro, Bengson, & Geng, 2011; Santangelo & Spence, 2008; Serences et al., 2005). To date, the importance of bottomup and top-down attentional interactions during auditory scene analysis has been documented using relatively simple stimulus sequences in which transient events usually occur successively (Alain & Woods, 1994; Best, Gallun, Ihlefeld, & Shinn-Cunningham, 2006; Mayer, Harrington, Stephen, Adair, & Lee, 2007; Mayer, Harrington, Adair, & Lee, 2006; Salmi, Rinne, Koistinen, Salonen, & Alho, 2009). A key assumption of the object-based account is that attention can be selectively oriented in a top-down manner to one of several object representations that coexist in STM-even in the absence of relevant external stimuli. In other words, objects can be reflectively attended. Understanding the neural mechanisms and time course that mediate this process would allow us to further elucidate the inner workings of auditory attention.

# **Perceptual attention**

Attention is commonly studied from a perceptual<sup>1</sup> perspective, in which observers or listeners are presented with a cue (e.g., light or sound) to a particular location, visual item, or sound stream prior to the presentation of visual or auditory stimuli (e.g., Posner cuing and visual search paradigms) (Posner, 1980; Posner, Snyder, & Davidson, 1980). In visual and auditory spatial attention tasks, the cue can either be exogenous (e.g., light or sound at the target location) or endogenous (e.g., arrow pointing toward the target location). Because participants receive an attentional cue before the task-relevant stimuli are presented, selective attention primes the perceptual system prior to the presentation of the incoming stimuli. Typically, participants perform better (e.g., faster response times) on trials in which a cue orients attention to a task-relevant object or location (valid cue) than on trials where attention is misled toward a task-irrelevant object or location (invalid cue) or on trials in which a cue is not provided (Posner et al., 1980). In the auditory domain, such cuing prior to a predefined target has been shown to improve performance in responding to lateralized sounds (Mondor and Amirault, 1998), reduced thresholds in detecting a signal embedded in noise (Hubner & Hafter, 1995; Huang, Xu, Wu, & Li, 2010) and eliminated change deafness in complex auditory scenes (Backer & Alain, unpublished data, Eramudugolla,

Irvine, McAnally, Martin, & Mattingley, 2005). There is also evidence that attention can be cued to a particular point in time (for a review see Lange, 2013), as evidenced by improved target detection (Sanders & Astheimer, 2008) and decreased attentional blink (Shen & Alain, 2011, 2012) when a target occurred at the cued temporal interval within a sequence of stimuli.

The mechanisms involved in the deployment of attention to a cued item can be assessed by examining brain activity during the cue period (i.e., the interval between the cue and the onset of the target or stream of sounds)specifically, comparing brain activity between conditions in which attention is directed to one feature or another (e.g., vision: location vs. color; audition: location vs. pitch) that defined either the likely incoming target or the sound stream to be attended. In this way, both featurespecific and domain-general activities involved in attentional control can be identified. Studies using such a design in conjunction with fMRI have identified a frontoparietal network involved in the deployment of attention to a cued item within an array of visual items (Corbetta & Shulman, 2002; Corbetta et al., 2002; Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Giesbrecht, Woldorff, Song, & Mangun, 2003; Hopfinger, Buonocore, & Mangun, 2000; Shulman et al., 1999) or to a sound stream in the midst of competing sounds (Hill & Miller, 2010; Shomstein & Yantis, 2004, 2006). A similar frontal-parietal network has been reported when attention switches between locations in both the auditory and visual modalities (Salmi, Rinne, Degerman, Salonen, & Alho, 2007; Shomstein & Yantis, 2004; Smith, Hsieh, Saberi, & Hickok, 2010), sound locations (left vs. right ear), or sound identities (male vs. female voice) (Shomstein & Yantis, 2006). The network that mediates voluntary control of auditory attention encompasses several brain areas that vary among studies and tasks. These include, but are not limited to, the inferior and superior frontal gyri, dorsal precentral sulcus, inferior parietal sulcus, superior parietal lobule, and auditory cortex. Some of the areas (e.g., anterior cingulate, frontal eye fields, superior parietal lobule) involved in orienting auditory spatial attention are similar to those observed during the orientation of visual spatial attention, suggesting that control of spatial attention may be supported by a combination of supramodal and modality-specific brain mechanisms (Wu, Weissman, Roberts, & Woldorff, 2007). This network varies as a function of the feature to be attended, with location recruiting the parietal cortex to a greater extent and attention to pitch recruiting the inferior frontal gyrus (Hill & Miller, 2010) and resembles the network observed during auditory working memory for sound location and sound identity (e.g., Alain, He, & Grady, 2008; Leung & Alain, 2011; Rama et al., 2004).

<sup>&</sup>lt;sup>1</sup> Recall that we are using the term "perceptual" to refer to attention to ongoing, external stimuli (per Chun & Johnson, 2011).

### **Reflective attention**

In contrast to perceptual processing, reflective attentional processing (Chun & Johnson, 2011; Johnson & Hirst, 1993) refers to selectively orienting attention to representations in STM or retrieved from long-term memory either in the absence of external stimuli or in the presence of unrelated external stimuli (e.g., thinking about an earlier conversation while the TV is currently on). In our opinion, reflective attention is an active process, whereas we consider "STM" as a passive storage system. The contents of STM can dynamically change, as a result of reflective attentional processes and other executive processes that discard representations from or add representations to STM or otherwise manipulate representations within STM. In vision, reflective processing has been studied using a variant of the delayed match-to-sample or change detection paradigm in which a cue appears during the retention interval (i.e., retro-cue). In these paradigms, a visual scene or memory array (e.g., photograph or array of items) is presented, followed by a blank retention interval, during which the participant must rehearse and maintain the memory array's contents. After this retention interval, the participant views a memory probe, which can include one or more items. If the probe comprises one item, the participant indicates if that item was present or absent or if the probe's location matched its original position within the original memory array. If the probe includes multiple items, the participant reports whether the memory probe is an exact match to the original memory array. In such paradigms, the retro-cue presented during the retention interval retrospectively directs the participant's attention to a particular object representation held within STM, thereby engaging the brain in reflective attentional processing. Thus, in the context of STM, reflective attentional processing relies on top-down controlled processes to rehearse (Baddeley, 1992) the retro-cued object. In this way, reflective processing is thought to involve dynamic manipulation and prioritization of co-existing object representations within STM.

# Visual reflective attention

Most of the research on reflective attention has been done in vision. As we describe in the following section, four *processing principles* consistently emerge from these studies.

1. Attention can be guided to visual object representations.

This is evidenced by a behavioral advantage on informative retro-cue trials as compared to trials with no cues or non-informative retro-cues (Griffin & Nobre, 2003; Kuo, Stokes, & Nobre, 2012; Landman, Spekreijse, & Lamme, 2003; Lepsien, Griffin, Devlin, & Nobre, 2005; Lepsien, Thornton, & Nobre, 2011; Lepsien & Nobre, 2006, 2007; Makovski, Sussman, & Jiang, 2008; Matsukura, Luck, & Vecera, et al. 2007; Nobre, Griffin, & Rao, 2007; Nobre et al., 2004; Sligte et al., 2008, 2009). Furthermore, prestimulus cues (as used in perceptual attention studies) and informative retro-cues presented after 1,500 ms of memory retention (i.e., post-iconic memory) have resulted in a comparable behavioral advantage on delayed match-to-sample tasks (Griffin & Nobre, 2003; Nobre et al., 2004), in which the number of items in the memory array did not exceed working memory capacity (i.e., usually up to three or four items) (Cowan, 2001; Vogel & Machizawa, 2004).

2. The number of items presented within the array (i.e., set size) affects how retro-cues are used and consequently modulate performance.

Specifically, when set size is within STM capacity limits, informative retro-cues can result in the prioritization of the cued item(s) over the uncued items; however, the uncued items can still be retrieved (Astle, Summerfield, Griffin, & Nobre, 2012). Conversely, when set size exceeds capacity limits, informative retro-cues may lead to performance benefits over neutral cues, due to discarding the uncued items from STM thereby reducing the number of items to maintain (Astle et al., 2012) and protecting them from decay (Matsukura et al., 2007).

3. While perceptual and reflective attention rely on overlapping processes and networks, there are some additional processes, related to imagery and search within memory, that are specific to reflective attention.

Recent studies have also begun to compare the time course (using ERPs) and neural networks (using fMRI) involved in perceptual and reflective attentional processing. Both perceptual and reflective processing require attentional control to select and maintain the relevant item(s), while ignoring irrelevant distracting stimuli, either externally in the environment or internally in STM. Thus, it is not surprising that, at least in vision, both types of attention generate comparable neural correlates (Henseler, Kruger, Dechent, & Gruber, 2011; Nobre et al., 2004; Nee & Jonides, 2009; Roth, Johnson, Raye, & Constable, 2009). Griffin and Nobre (2003) compared ERPs when attention was oriented to an external stimulus or to an internal spatial representation. For both pre- and retro-cues, the direction of attention (left or right) modulated the sensory evoked responses ( $\sim 120$  ms) and generated a fronto-central negativity (360-480 ms), such that these ERPs were enhanced contralateral to the attended visual field. The similarity in timing and amplitude distribution between pre- and retrocue conditions suggests substantial overlap between neural

correlates associated with perceptual and reflective attention during visual scene analysis.

However, there is also evidence of ERP signatures that are specific to reflective attention. In Griffin and Nobre's (2003) study, retro-cues, but not pre-cues, generated an early frontal modulation followed by an ERP parietal effect. In a subsequent study, Kuo, Rao, Lepsien, and Nobre (2009) used the contralateral delay activity (CDA) to investigate whether orienting attention to a representation in memory acts by reducing memory load. The CDA is a sustained, negative potential observed in posterior parietal and lateral occipital electrodes contralateral to the attended hemifield; the CDA amplitude reflects the number of items being maintained in visual STM (Vogel & Machizawa, 2004). Kuo et al. (2009) showed that orienting attention to a given spatial representation via a retro-cue facilitates performance and reduces CDA amplitude. This CDA effect suggests that reflective attention to a specific representation can reduce memory load (Kuo et al., 2012), such that task-irrelevant representations are discarded from STM.

Nobre et al. (2007) also described a negative deflection that peaks at about 320 ms after the onset of the probe (N3<sub>RS</sub>) at fronto-central regions. The amplitude and duration of the N3<sub>RS</sub> systematically increased with visual STM load in neutral retro-cue trials. When spatial retro-cues were provided (indicating only one item to maintain), this "retro-search" (N3<sub>RS</sub>) component was absent. These findings suggest that the influence of top-down attentional biases extends to mnemonic functions, and, specifically, that searching for items within visual STM can be under flexible voluntary control. A follow-up study (Kuo et al., 2009) compared ERPs when participants searched for a visual target in either a stimulus array or a mental representation of a stimulus array in visual STM. They replicated the N3<sub>RS</sub> effect for search within visual STM, as well as showing an N2pc effect for both perceptual and reflective search. The N2pc is an early ( $\sim 240-300$  ms) posterior negativity that is thought to index the deployment of spatial attention toward a target (Hopf et al., 2000). However, it remains to be determined whether these reflective-specific ERP effects, especially the N3<sub>RS</sub>, are modality-specific or whether they index more general supramodal mnemonic processes.

Similarly, several visual fMRI studies have identified brain regions that are specific to or activated more strongly during reflective, as compared to perceptual, processing. These generally include the dorsolateral (Nobre et al., 2004; Roth et al., 2009), ventrolateral (Nee & Jonides, 2009; Nobre et al., 2004), and rostrolateral prefrontal cortex (Henseler et al., 2011), bilateral inferior frontal cortex (Roth et al., 2009), insula (Nobre et al., 2004), and left temporal cortex (Roth et al., 2009). Nobre et al. (2004) also found that the precuneus and bilateral intraparietal

sulcus were more strongly activated during reflective processing (i.e., on retro-cue trials) than during perceptual attention (i.e., on pre-stimulus cue trials). Prefrontal activity during reflective attention has been attributed to increased attentional control needed to search for and select a particular object representation from several co-existing objects in STM (Griffin & Nobre, 2003; Nobre et al., 2004). The parietal, especially precuneus, activity sensitive to reflective processing is thought to index mental imagery that may have aided selection of the object representation in the retro-cued position (Nobre et al., 2004).

4. Reflectively attending to different stimulus features or categories modulates the neural activity wherein the representation lies.

In the visual studies discussed above, all used spatial retro-cues to orient reflective attention to object representations. Yet, both the visual and auditory domains are thought to involve at least two parallel processing streams: the ventral ("What") stream and the dorsal ("Where") stream (Alain, Arnott, Hevenor, Graham, & Grady, 2001; Arnott & Alain, 2011; Rauschecker & Tian, 2000; Romanski et al., 1999; Ungerleider, Galkin, & Mishkin, 1983). While many studies in both vision and audition have examined how the attended feature modulates brain activity related to perceptual attention (Cristescu, Devlin, & Nobre, 2006; Krumbholz, Eickhoff, & Fink, 2007), visual researchers have only recently begun to investigate how reflective attention to different stimulus features or attributes affects brain activity (Johnson & Johnson, 2009; Han, Berg, Oh, Samaras, & Leung, 2013; Lepsien et al., 2011; Lepsien & Nobre, 2007; Oh & Leung, 2010). For instance, Lepsien and Nobre (2007) presented participants with two stimuli on each trial (1 face and 1 scene), followed by a non-spatial retro-cue that directed attention to either the face or scene stimulus. After a delay, a second retro-cue, instructing participants to keep maintaining the current representation or to switch their attention to the originally uncued representations, was presented. After another delay, a single-item probe stimulus was presented, and participants judged if the probe matched one of the items in the array. The retro-cued stimulus category (i.e., face or scene) modulated STM maintenance-related activity in the fusiform gyrus and parahippocampal gyrus, reflecting the task-relevant stimulus category to maintain (Lepsien & Nobre, 2007). This feature-specific activity may index selection of the reflectively attended representation, while the commonly observed frontal and parietal activity may reflect an attentional control network, which provides executive control of the search within STM for the retro-cued item. However, since these studies typically used retro-cues that were predictive of the probe's category, another possibility is that the feature-specific activity

may reflect anticipation of the upcoming probe stimulus, rather than selective maintenance of the retro-cued representation (Lepsien et al., 2011). Further research is necessary to dissociate these two possibilities. Also, future studies could use complementary techniques, such as simultaneous EEG-fMRI or a beamforming analysis on neuromagnetic data from magnetoencephalography, to reveal how the fronto-parietal network and the featurespecific activity interact across time.

# Auditory reflective attention

To date, most of the research on reflective attention has used visual stimuli. However, there have been a few attempts to examine auditory reflective attention. Investigating reflective attention in audition provides an opportunity to understand how sounds, especially concurrent sounds, are represented in and selectively accessed from STM-a question that auditory scientists have been struggling with for decades. In a behavioral study, we adapted the visual retro-cue delayed match-to-sample task described above to the auditory domain (Backer & Alain, 2012). Participants heard a pair of auditory scenes (composed of three realistic, concurrent sounds, e.g., dog bark, violin tone, human sneeze, each presented in a different location), separated by a 2- or 4-s silent retention interval. On some trials, the two scenes were identical, and on other trials, two sounds switched locations. Participants indicated by pressing a button whether the two scenes were the same or different and identified which two sounds switched locations, if they did notice a change. Also, on each trial, we presented either an informative pre-stimulus cue, an informative retro-cue (occurring at different time points within the retention interval), or no cue. All pre-stimulus and retro-cues were endogenous spatial cues, directing attention to a particular location of a sound that would be involved in the location switch on Change trials. As was reported in previous visual retro-cue paradigms (Griffin & Nobre, 2003; Nobre et al., 2004), participants were faster and more accurate on retro-cued than on uncued trials. Importantly, all retro-cues presented up to 4 s of memory retention enhanced performance to the same extent, suggesting that sound object representations are available for attentional selection for at least 4 s after the external stimulus disappears. Notably, these findings extended visual retro-cue benefits to the auditory domain, suggesting that there may be a supramodal aspect, in addition to a modality-specific component, mediating reflective attentional orienting. Also, it has often been assumed that, as in vision, the concurrent events composing an auditory scene can be unambiguously segregated and identified. The objectbased account relies on this assumption, since to selectively attend to one of several sound object representations in STM, these sound sources must be clearly segregated to form objects in the first place. The results from our study demonstrated unequivocally for the first time using complex, meaningful stimuli that attention can indeed be oriented to one of several sound object representations (Backer & Alain, 2012). Additional studies are needed to further understand the neural correlates of attention to sound object representations that emerge from complex listening environments where multiple sound sources are simultaneously active. In doing so, these studies have the potential of elucidating how concurrent sounds are represented in and manipulated within STM.

There have also been other studies that have attempted to compare reflective attention between auditory and visual modalities. For instance, Johnson et al. (2005; Experiment 4) used fMRI to examine whether reflective attention to auditory and visual information (i.e., spoken and written words) relies on the same neural substrates. On each trial, one stimulus was presented: either a word (which could be a new word or the same word that was presented on the previous trial) or a dot or beep (for visual and auditory blocks, respectively). The dot and beep stimuli instructed the participant to think back on ("refresh") the word that was just presented on the previous trial. Left prefrontal regions were activated during refreshing (relative to perceiving) both visual and auditory words, whereas activity in auditory and visual cortex was evident when refreshing (but to lesser extent than perceiving) a word presented in the corresponding sensory modality (Johnson et al., 2005). These results suggest both supramodal and modality-specific aspects of reflective attention (i.e., refreshing).

In another study, Buchsbaum, Olsen, Koch, and Berman (2005) investigated the neural correlates of selectively maintaining auditory or visual verbal information, again using spoken and written words and fMRI to focus on the superior temporal cortex. Although the authors did not frame their study in terms of retro-cuing or reflective attention, it can be construed as such. On each trial, participants were presented sets of spoken and written words. After the words were presented, a retro-cue appeared, instructing participants to rehearse the spoken words or the written words. After a long (11 s) delay, participants said out loud the words that they were rehearsing. During the early part (first 4-5 s) of the maintenance period, auditoryspecific activity was observed in left superior temporal gyrus and sulcus that the authors likened to an echoic or sensory memory store; this activity was also functionally connected with ventrolateral prefrontal cortex (Buchsbaum et al., 2005). However, sustained activity in a portion of the posterior superior temporal cortex (Spt) was unspecific to modality, was functionally coupled with dorsal motor and superior frontal regions, and reflected a phonological or articulatory rehearsal process (Buchsbaum et al., 2005). These results, in conjunction with Johnson et al's (2005)

results, suggest that reflective attention interacts first with the veridical stimulus representation in a modality-specific fashion, followed by a supramodal transformation of this information into an articulatory or phonological code, assuming both visual and auditory representations can be verbalized. More research is needed to directly test this hypothesis.

# Neural oscillations: a new metric for reflective attention

The ERP studies reviewed above used signal averaging techniques applied in the time domain, which reveal several deflections peaking at various latencies and locations over the scalp, as has been the traditional approach to EEG data analysis over the past few decades. However, EEG following sensory stimulation can also be examined in the frequency domain. In the time-frequency analysis of the EEG data, the time waveform is converted into a frequency spectrum using the discrete Fourier transform (Bertrand and Tallon-Baudry, 2000; Picton, 2010). This approach complements the analysis in the time domain and allows for examination of EEG oscillations that occur at various times and frequencies (Bertrand & Tallon-Baudry, 2000; Yuval-Greenberg & Deouell, 2007). A time-frequency analysis generally results in two metrics: spectral power and inter-trial phase coherence; however, here we will focus on spectral power, which is the amplitude of a response within a given frequency band relative to a baseline period (expressed in decibels [dB]). Spectral power is a useful metric because it can show activity that is both phase-locked to a given stimulus (evoked activity) and not phase-locked (induced activity); in contrast, ERPs reveal only slow-frequency ( $\sim 1-20$  Hz, depending on filter settings), evoked activity, since induced activity is "lost" during trial averaging.

Oscillatory activity is thought to reflect the synchronous firing of neural ensembles that enables both short- (cortical to cortical) and long-range (sub-cortical to cortical) communication (Alain & Ross, 2008; Kaiser & Lutzenberger, 2003). These brain rhythms are implicated in a wide variety of perceptual and cognitive (especially attention and memory) tasks, with different frequency bands playing different roles (Fan et al., 2007). Here, we will briefly describe theta (4–7 Hz), alpha (8–12 Hz), beta (13–29 Hz), and gamma (30–100 Hz) activity, and how each of these frequency bands relates to attention and memory.

Increased theta power, especially in temporal regions, has been observed during lexical and semantic decision tasks, in which lexical or semantic information is retrieved from long-term memory, in both vision (Bastiaansen, Oostenveld, Jensen, & Hagoort, 2008; Bastiaansen, van der Linden, Ter Keurs, Dijkstra, & Hagoort, 2005; Hald, Bastiaansen, & Hagoort, 2006) and audition (Bastiaansen et al., 2008; Shahin, Picton, & Miller, 2009). Theta oscillations are also often observed in visual memory tasks (e.g., Cashdollar et al., 2009; Tesche & Karhu, 2000), and they are thought to reflect configural-relational binding of information by the hippocampus and prefrontal cortex (Olsen, Rondina Ii, Riggs, Meltzer, & Ryan, 2013).

Enhanced alpha activity has been implicated as a suppression mechanism of distracting or irrelevant stimuli during selective attention (Fan et al., 2007; Foxe & Snyder, 2011). Specifically, enhanced alpha power is thought to index inhibition of unattended object representations (i.e., distracters) in STM (Hamidi, Slagter, Tononi, & Postle, 2009; Jensen & Mazaheri, 2010; Jokisch & Jensen, 2007; Sauseng et al., 2005; Sauseng et al., 2009; Shahin & Pitt, 2012). For example, studies that examined the deployment of spatial attention to external stimuli showed that alpha suppression (aka desynchronization; i.e., a decrease in alpha power relative to baseline) occurs in occipito-parietal regions contralateral to the attended hemifield, while alpha enhancement occurs ipsilateral to the attended hemifield. This lateralized alpha effect has been revealed in both visual (Rihs, Michel, & Thut, 2009; Worden, Foxe, Wang, & Simpson, 2000) and auditory (Banerjee, Snyder, Molholm, & Foxe, 2011; Kerlin, Shahin, & Miller, 2010; Muller and Weisz, 2012) spatial attention, suggesting a supramodal mechanism. However, it is unknown if reflective attention to locations of internal object representations results in similar alpha effects. Furthermore, multiple visual STM studies have shown that alpha power increases with memory load during retention (Schack & Klimesch, 2002; Tuladhar, ter Huurne, Schoffelen, Maris, Oostenveld, & Jensen, 2007). This alpha effect has been localized to parieto-occipital regions and may reflect the disengagement of task-irrelevant neural processes so that processing resources can be reallocated to memory maintenance as load increases (Jensen, Gelfand, Kounios, & Lisman, 2002; Schack & Klimesch, 2002; Sauseng et al., 2009; Tuladhar et al., 2007). Similarly, during an auditory Sternberg task, alpha (right prefrontal) and beta (right temporal) oscillations increased monotonically with load and were shown to reflect attentional control during the maintenance interval and the formation of object representations, respectively (Leiberg, Kaiser, & Lutzenberger, 2006a). Similarly, other auditory studies have postulated that beta oscillations play a role in binding sound representations across time, allowing words to be linked together into a coherent sentence stored in STM (Bastiaansen, Magyari, & Hagoort, 2010; Shahin & Pitt, 2012).

Stronger gamma band activity has been associated with maintenance of visual (Axmacher et al., 2007; Jokisch and Jensen, 2007; Tallon-Baudry, Bertrand, Peronnet, & Pernier, 1998) or auditory (Kaiser & Bertrand, 2003; Kaiser & Lutzenberger, 2003; Kaiser, Lutzenberger, Decker, Wibral,

Rahm, 2009a; Kaiser, Rahm, & Lutzenberger, 2009b; Kaiser, Ripper, Birbaumer, & Lutzenberger, 2003; Leiberg et al. 2006a; Leiberg, Lutzenberger, Kaiser, 2006b; Lutzenberger, Ripper, Busse, Birbaumer, & Kaiser, 2002) objects within the focus of attention. For instance, Jokisch et al. (2007) presented participants with a visual "What" and "Where" STM task, in which they had to remember the identity or orientation of face stimuli. Maintenance of identity (ventral stream) resulted in stronger alpha activity over dorsal regions, relative to face orientation, suggesting inhibition of the task-irrelevant feature. However, retention of face orientations was related to greater gamma enhancement over dorsal regions, relative to face identity. In another study, auditory and visual stimuli were presented concurrently, and participants attended to either the auditory or visual stimulus. Attending to a particular stimulus modality led to enhanced gamma activity in the attended modality's sensory cortex and suppressed gamma in the unattended modality's sensory cortex (Sokolov & Nezlina, 2004). Taken together, these studies demonstrate that brain oscillations play an important role in perceptual attention and memory maintenance. However, future studies in both audition and vision are needed to compare neural oscillations during perceptual and reflective attention. This comparison will result in a deeper understanding of how object representations in memory are selectively processed and maintained.

#### **Concluding remarks**

Attention plays a critical role in all aspects of perception, cognition, and action. Traditionally, the study of attention has focused on how we can direct and focus our attention on external visual, auditory, or tactile stimuli. However, in the last decade, research has turned toward understanding how attention may be directed to internal memory representations. While research in the visual domain has begun to explore how object representations are selectively accessed through top-down attention (i.e., reflective attention), this has yet to be addressed in the auditory domain. Consequently, a better understanding of the brain mechanisms that govern selective attention will invariably have important implications for many clinical populations, including patients with mild cognitive impairment, patients suffering from traumatic brain injury, as well as children with learning disabilities and attention deficit disorders.

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