Feature-based and object-based attention orientation during short-term memory maintenance

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ATTENTION AND SHORT-TERM MEMORY (STM) are interdependent cognitive functions. Studies in the visual domain have revealed that top-down attention can bias STM processing at various stages, including expectation, encoding, maintenance, and retrieval (reviewed in Gazzaley and Nobre 2012). For example, cueing a visual item to be probed retrospectively (retro-cue) during STM maintenance period dramatically improved the performance of the cued item (Landman et al. 2003). Nevertheless, similar mechanisms of attention orientation in the auditory domain were much less explored. During the encoding period of an auditory scene, when attention was directed to an auditory object, the change-detection ability for that object was remarkably enhanced compared with the uncued condition, especially when the scene contained more than four objects (Eramudugolla et al. 2005). Later, Backer and Alain (2012) discovered that during the STM maintenance period, attention could be guided toward one of the maintained sound-object representations through a retro-cue, thereby attenuating the change-deafness, as well.

In a recent study published in The Journal of Neuroscience, Backer et al. (2015) advanced their findings, using electroencephalography (EEG) to explore the neural mechanisms underlying feature-based and object-based attention orientation. Both event-related potentials and neural oscillations explained the behavioral benefits of retro-cues and favored the theory that feature-based and object-based attention orientation were independent.

Attention orientation; retrospective cue; auditory attention; feature-based attention; object-based attention

The authors used event-related potentials (ERPs) and neural oscillations to explain the behavioral benefits. They first implemented spatial principal component analysis (PCA) to reduce the dimensionality of 60 EEG electrodes to three major representative principal components (PCs), which accounted for over 60% of variance in the pooled data from any two of the three conditions (ERPs from informative-spatial, informative-semantic or uninformative trials) across all participants and electrodes. Interestingly, two of the three PCs displayed object-based attention effects; i.e., both informative retro-cues induced differential PC activity compared with the uninformative retro-cues, but no significant difference was observed between the informative-spatial and informative-semantic retro-cues. Instead, the third PC exhibited feature-based attention effects; i.e., the informative-spatial retro-cue induced differential PC activity compared with the informative-semantic retro-cue. Furthermore, when trials were split into fast and slow trials on the basis of reaction time, the feature-specific difference between the informative-semantic and informative-spatial conditions in the third PC showed distinctive patterns in the fast vs. slow trials, indicating that feature-specific processes were dissociable and attention allocated to one feature in an auditory object was not required to influence the processing of another feature in the same object.

Neural oscillations in several frequency bands (alpha: 8–13 Hz; low-beta: 13.5–18 Hz; mid-beta: 18.5–25 Hz; high-beta: 25.5–30 Hz) revealed attention effects, as well. Specifically,
parietal alpha/low-beta/mid-beta event-related desynchronization (ERD) indicated object-based attention effects, and the time periods for these effects were partly overlapped with those for ERP results. Meanwhile, the feature-based attention effects were observed across all frequency bands after \( \sim 1,000 \) ms to the onset of the retro-cues (ERD: semantic \( > \) spatial). These ERD effects were more prominent in the fast trials, indicating that more efficient attention orientation was associated with better performance, and indeed ERD could further explain individual differences in the behavioral (a combined performance measure, accuracy/reaction time) benefit. For alpha/low-beta ERD, the neural-behavioral correlation was observed after both informative retro-cues. However, for mid-beta/high-beta ERD, such correlation was only shown after the semantic retro-cue. Taking these findings together, alpha/low-beta and mid-beta/high-beta oscillations seemed to represent object-based and feature-based (semantic) attention, respectively.

The results reported by Backer et al. (2015) are critical to unravel the neural mechanism underlying auditory attention orientation during STM maintenance, which is in line with previous findings in the visual domain. Additionally, the authors dissociate two kinds of auditory attention orientation (object-based vs. feature-based) through neural activities of both ERPs and ERDs. Coincidentally, in a later issue of *The Journal of Neuroscience*, Katus et al. (2015) reported the use of a retro-cue to spatially orient attention to a tactile object during STM maintenance. These two studies, combined with those visual findings, support the theory of object-based attention across sensory modalities (Shinn-Cunningham 2008) and suggest an amodal attention orientation (see Fig. 1) during STM. It will be interesting to see whether the distinction between object-based and feature-based attention orientation in the auditory domain in Backer et al. still holds in other sensory domains, and to show how the object-based attention orientation will behave if the object consists of features from different sensory modalities, i.e., a multi-modal object (Fig. 1). From Backer et al., it is possible that when attention is cued to an object maintained in STM, some features (which may come from multiple sensory modalities) of this object are strengthened (Fig. 1, darker colored patches), whereas others remain the same (Fig. 1, lighter colored patches). Orienting attention to one feature does not need to facilitate the representation of another feature of the same object (Fig. 1, thicker vs. thinner dashed lines). Moreover, neuroimaging studies in the visual domain have revealed that the general top-down attention orientation is located in the frontoparietal network, largely the intraparietal cortex and superior frontal cortex (Corbetta and Shulman 2002), whereas the feature-based attention is located in subregions of the posterior parietal cortex (PPC) (Greenberg et al. 2010). Given additional evidence on modality-independent control of attention in PPC (Shomstein and Yantis 2006), it is reasonable to hypothesize that the frontoparietal network would control the multimodal object-based attention orientation and that the PPC would direct the feature-based attention orientation, further receiving inputs from different sensory modalities. Future neuroimaging studies, especially in the auditory and tactile domains, will be critical to test this neural hypothesis.

Several additional issues could be further addressed in follow-up studies with paradigms similar to that of Backer et al. (2015). First, the fate of the uncued items is interesting, because such a topic is still being debated in the visual domain. Some suggest that the uncued representations are removed from the memory buffer (Kuo et al. 2012), whereas others indicate that they are unaffected (Rerko and Oberauer 2013). Further findings in the auditory domain will complement those visual results and help to resolve this issue. Neural oscillations in the alpha band may serve as one candidate of neural markers, since alpha activities have been generally attributed to inhibition of task-irrelevant representations during STM (Jensen et al. 2014). In addition, prestimulus alpha activities associated with the expectation of stimuli have been shown to play causal roles in regulating perception (Romei et al. 2010) and influencing subsequent STM performance (Zanto et al.)

![Fig. 1. Amodal attention orientation during short-term memory (STM). Round patches with different colors indicate features represented in STM (red, visual; blue, auditory; yellow, tactile), and gray round patches depict objects maintained in STM. Orienting attention to a cued object (darker gray) strengthens the representation of this object compared with another uncued object (lighter gray) in STM. However, it may strengthen some features connected to this object (thicker dashed lines) while other features remain (thinner dashed lines). The connection can be bi-directional, i.e., when attention is oriented to one feature; the object representation connected to this feature will be strengthened but may not affect other feature representations from the same object. Overall, the object-based and feature-based attention orientations during STM are independent.](http://jn.physiology.org/lookup/doi/10.1152/jn.00342.2015)
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Second, spatial location has long been recognized as more “special” for attention than other nonspatial features (color, shape, contrast, etc., in the visual domain), because attention operates like a “spotlight” (Tsalk and Lavie 1988). Furthermore, nonspatial visual features per se are not homogeneous, and memory precisions of different features decay with variant speeds (Pasternak and Greenlee 2005). These differences among features may further explain why the informative-spatial retro-cue tends to have greater behavioral benefit than the informative-semantic retro-cue in the study by Backer et al. Future studies with multiple nonspatial auditory retro-cues can test the behavioral benefit and the corresponding neural activity among different auditory features.

Third, attention orientation can be achieved via feedforward or feedback connections (Corbetta and Shulman 2002). Two recent neurophysiological studies in monkeys have revealed that within the visual cortical hierarchy, feedforward processing communicates through higher frequency oscillations (alpha: 40–90 Hz) and feedback processing through lower frequency oscillations (alpha and low-beta) (Bastos et al. 2015; van Kerkoerle et al. 2014). It is notable that in the work of Backer et al., higher frequency oscillations (mid-beta/high-beta, though gamma activities are typically difficult to observe in EEG signals) represent feature-based attention orientation and lower frequency oscillations (alpha/low-beta) represent object-based attention orientation. Given the frequency–specific directions of connection (feedforward vs. feedback) (Bastos et al. 2015; van Kerkoerle et al. 2014), is there any relationship between the feature-based/object-based attention orientation and the directions of information transfer? It will be noteworthy to see how the feedforward/feedback processing contributes to the feature-based/object-based attention orientation.

Many more aspects from the study of Backer et al. (2015) are worth investigating: for example, manipulating STM load in the task to see how the burden of STM influences attention orientation, using an auditory retro-cue to avoid extra switching processes between different sensory modalities, or implementing a contralateral retro-cue to induce a contralateral delay activity that is widely used in visual STM studies (Luck and Vogel 2013), as well as the tactile STM study mentioned (Katus et al. 2015). To conclude, the study by Backer et al. opens up new ideas about the research on interaction between attention and STM, which is at the core of cognition.

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Y.K. conception and design of research; Y.K. interpreted results of experiments; Y.K. prepared figures; Y.K. drafted manuscript; Y.K. edited and revised manuscript; Y.K. approved final version of manuscript.

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