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

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RUNNING HEAD: Orienting attention during short-term memory
Abstract

Top-down attention biases the short-term memory (STM) processing at multiple stages. Orienting attention during the maintenance period of STM by a retrospective cue (retro-cue) strengthens the representation of the cued item and improves the subsequent STM performance. In a recent paper, Backer and colleagues extended these findings from the visual to the auditory domain, and combined electroencephalography to dissociate neural mechanisms underlying feature-based and object-based attention orientation. Both event related potentials (ERPs) and neural oscillations explained the behavioral benefits of retro-cues, and favored the theory that feature-based and object-based attention orientation were independent.

KEYWORDS: Attention orientation; retrospective cue; auditory attention; feature-based attention; object-based attention
Attention and short-term memory (STM) are inter-dependent 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 directing attention to an auditory object, the change detection ability for that object was remarkably enhanced as compared with the uncued condition, especially when the scene contained more than four objects (Eramudugolla et al., 2005). Later, Backer and Alain 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 (Backer and Alain, 2012).

In a recent study published in The Journal of Neuroscience, Backer et al. advanced their findings, using electroencephalography (EEG) to explore the neural mechanisms underlying the orientation of attention in the auditory domain (Backer et al., 2015). They again used a delayed matching-to-sample task with auditory scenes as stimuli. The auditory scene consisted of four different sounds simultaneously presented at four different locations. Each sound was obtained from one semantic category (non-speech human, animal, music, or man-made object) and presented at one free-field location (-90°, -30°, +30°, +90°). Therefore, two features (semantic and spatial) together formed
one auditory object. During the STM delay period, a visual retro-cue directed attention
to one object (Informative) or divided attention among the four objects (Uninformative).
Informative retro-cues were further separated into two kinds: the Informative-Spatial
retro-cue leading to a judgment if the category of the cued location changed (semantic
decision), and the Informative-Semantic retro-cue leading to a judgment if the location
of the cued category changed (spatial decision). The Uninformative trials were also
divided into two kinds (spatial and semantic) and grouped with the related Informative
trials together to form spatial/semantic blocks. All retro-cues were valid, and they
enhanced the STM task performance, reminiscent of those situations in the visual
domain. Compared with the Uninformative retro-cues, both Informative-Spatial and
Informative-Semantic retro-cues shortened the reaction time, yet only the Informative-
Spatial retro-cue increased the accuracy.

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
principle 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 based on 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 were 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) 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 ERP results. Meanwhile, the feature-based attention effects were observed across all frequency bands after ~1000 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. Taken together, alpha/low-beta and mid-beta/high-beta oscillations seemed to represent object-based and feature-based (semantic) attention respectively.

The result in Backer et al. is 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. use a retro-cue to spatially orient attention to a tactile object during STM maintenance (Katus et al., 2015). 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 Figure 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 (Figure 1). From Backer et al., it is possible that when cueing attention to an object maintained in STM, some features (may come from multiple sensory modalities) of this object are strengthened (Figure 1, darker colored patches) while others remain the same (Figure 1, lighter colored patches). Orienting attention to one feature does not need to facilitate the representation of another feature of the same object (Figure 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 fronto-parietal network, largely the intraparietal cortex and superior frontal cortex (Corbetta and Shulman, 2002), while the feature-based attention is located in sub-regions of the posterior parietal cortex (PPC) (Greenberg et al., 2010). Given extra evidence on modality-independent control of attention in PPC (Shomstein and Yantis, 2006), it is reasonable to hypothesize that the fronto-parietal network would control the multi-modal object-based attention
orientation, and 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 similar paradigms to Backer et al. First, the fate of the uncued items is interesting as such a topic is still being debated in the visual domain. Some suggest that the uncued representations are removed out of 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, pre-stimulus 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., 2014). Note that in Backer et al. the alpha power prior to the spatial retro-cue seems stronger than the semantic situation, which may suggest different levels of expectation to the two kinds of retro-cues, and these neural differences might potentially explain the behavioral differences in the two retro-cue conditions.

Second, spatial location has long been recognized as more “special” for attention than other non-spatial features (color, shape, contrast, etc. in the visual domain), as attention operates like a “spotlight” (Tsai and Lavie, 1988). Furthermore, non-spatial 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 Backer et al. Future studies with multiple non-spatial 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 (gamma, 40-90 Hz) and feedback processing through lower frequency oscillations (alpha and low-beta) (van Kerkoerle et al., 2014; Bastos et al., 2015). It is notable that in 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) (van Kerkoerle et al., 2014; Bastos et al., 2015), 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 Backer et al.’s study are worth investigating, for example, manipulating STM load in the task to see how the burden of STM influences attention orientation, or 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 (CDA) 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.

GRANTS
Y. Ku was supported by the National Institute of Health Grants (5R01AG030395), China National Key Fundamental Research (973) Program (2013CB329501), and Shanghai Committee of Science and Technology (15ZR1410600).

DISCLOSURES
No conflicts of interest, financial or otherwise, are declared by the author.

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Figure 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 grey round patches depict objects maintained in STM. Orienting attention to a cued object (darker grey) strengthen the representation of this object compared with other uncued object (lighter grey) 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.