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Selection within working memory based on a color retro-cue modulates alpha oscillations

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ABSTRACT

Working Memory (WM) maintains flexible representations. Retrospective cueing studies indicate that selective attention can be directed to memory representations in WM improving performance. While most of the work has explored the neural substrates of orienting attention based on a spatial retro-cue, behavioral studies show that a feature other than location can also improve WM performance. In the present work we explored the oscillatory underpinnings of orienting attention to a relevant representation held in WM guided by a feature value. We recorded EEG data in a group of 36 healthy human subjects (20 females) performing a WM task in which they had to memorize the orientation of four rectangles of different colors. After a maintenance period, a cue was presented indicating the color of the relevant item. We showed that directing attention to a memory item based on its color resulted in a modulation of posterior alpha activity, which appears as more desynchronization in the contralateral than in the ipsilateral hemisphere. Alpha lateralization is considered a neurophysiological marker of external and internal spatial attention. We propose that current findings support the idea that selection of a memory item based on a non-location feature could be accomplished by a spatial attentional mechanism. Moreover, using a centrally presented color retro-cue allowed us to surpass the confounds inherent to the use of spatial retro-cues, supporting that the observed lateralized alpha results from an endogenous attentional mechanism.

Selective attention facilitates processing of relevant information modulating sensory processing areas. Attention to a relevant feature not only improves perception but also working memory (WM). WM maintains flexible representations to which is possible to allocate attention to a relevant item improving WM performance (Lewis-Peacock and Postle 2012; LaRocque et al. 2013; Zokaei et al. 2013, 2014; Heuer and Schubö 2016a; Myers et al. 2017). The benefit of orienting attention to representations already held in WM was revealed by Griffin and Nobre (2003) using an elegant paradigm in which a spatial cue is presented during the retention period indicating which item is likely to be probed (Griffin and Nobre 2003). This is widely known as the retro-cue paradigm, because the cue is provided after the memory set is encoded. Orienting spatial attention in either domain seem to be accomplished via a general top-down mechanism (Gazzaley and Nobre 2012). In this way, a spatial cue, given before (perceptual) or after (memory representation) the memory set, can bias activity in sensory areas processing the relevant item (Capilla et al. 2014; Poch et al. 2014). Specifically, oscillatory alpha band activity seems to be a robust correlate of spatial attention in both domains. In perceptual attention studies, manipulating the relevant hemifield (left vs right), it is widely found that alpha power increases over the ipsilateral cortex to the attended hemifield (Kelly et al. 2006; Rihs et al. 2007; Worden et al. 2000), and decreases (or desynchronization) contralaterally to the attended hemifield (Kelly et al. 2009; Sauseng et al. 2005; Yamagishi et al. 2005). An influential model propose that alpha synchronization is related to the suppression of unattended neural representations, whereas alpha desynchronization is linked to enhancement of neural excitability in cortical areas processing the attended stimulus (Jensen and Mazaheri 2010). This alpha modulation has been also reported in spatial retro-cuing tasks (Poch et al. 2014; Myers et al. 2015; Schneider et al. 2016; Wolff et al. 2017). It is proposed that a transient alpha lateralization reflects the focus of spatial attention, and when an item is selected it changes into a more robust representation and attention is no longer needed (Myers et al. 2017).

While directing attention to a spatial location can enhance perception, selective attention in the perceptual domain can also be guided by non-spatial properties of stimuli (Carrasco, 2011). Although much less studied than spatial attention, it has been shown that allocation of attention to a non-spatial relevant stimulus feature can improve performance and bias cortical areas processing that feature (Treue and Martinez-Trujillo 2007). Some work revealed that feature related neural activity is bias throughout the visual field in a location independent manner (Motter 1994; Treue and Martinez-Trujillo 2007). It has been proposed that this location independent activity represents a map of potential targets. Spatial attention may be allocated to locations containing a relevant feature once a relevant feature has been previously located (Hopf et al. 2004). By this account, selection of an item based on other features, such as color, can be possible by first determining the location that contains that color, and then directing spatial attention to that location. Thus, the selection process would be ultimately based on the location. In favor of this proposal, an ERP experiment found that selecting a target based on non-location features resulted in the modulation of two ERP components (Hopf et al. 2004). An early location independent component, reflected the selection of task relevant features, followed by a later lateralized component (N2pc) reflecting the allocation of spatial attention to the targets location.

Similarly, recent studies have provided evidence of behavioral benefits using feature retro cues. These studies demonstrated that item prioritization can be accomplished based on either a spatial cue or a non-spatial cue like color or shape (Pertzov et al. 2013; Li and Saiki 2015; Heuer and Schubö 2016b). Additionally, there are recent findings suggesting that as in perception, a feature dimension can be cued while ignoring other dimensions (Ye et al. 2016; Niklaus et al. 2017). Accordingly, it has been proposed that attentional selection within WM based on a non-location feature could be supported by a spatial attentional mechanism (Pertzov et al. 2013). Within WM, location information is believed to be a privileged feature compared to others such as color or shape. Behavioral and neuroimaging studies have shown that while identity features

can be ignored, location is an obligated feature and must be encoded in WM (Poch et al. 2010; Kondo and Saiki 2012; Rajsic and Wilson 2014). In this way, object properties would be necessarily maintained in a retinotopic manner. Thus, selection of an item based on non-location information would result in spatial activity modulation.

What are the neural mechanisms underlying the effect of feature cueing within WM has not been extensively studied yet. We were interested in elucidating how a non-spatial cue, can guide deployment of attention to the representation of a relevant item. Specifically, we aimed to reveal if a color retro-cue would also result in lateralized alpha activity, as has been previously observed in spatial retro-cueing. For this purpose, we recorded electroencephalographic signals while participants had to memorize the orientation of four rectangles of different colors. After a retention period, a color cue was presented indicating which rectangle was going to be probed. In this way, attention is oriented to the representation of the relevant item based on the memory of one of its features (i.e. color). At test, participants had to judge whether the colored rectangle had the same orientation as at encoding. Based on the hypothesis that a color cue would guide attention to the location of the relevant item, lateralized activity was tested comparing ipsilateral and contralateral alpha activity.

METHODS

Participants:

Thirty-six adult subjects [mean age, 20.86, standard deviation (SD), 2.71; range, 22–32 years; 20 females], without any history of neurological or psychiatric illness, volunteered for participation in the study, and gave written consent, in accordance with the Declaration of Helsinki, after the nature of the procedures involved had been explained to them. Participants were right-handed according to the Edinburgh Handedness Inventory (Oldfield 1971) and reported normal or corrected to normal vision. Despite color was critical for performance of the task, participants were not formally tested for normal color vision.

Experimental task:

The experimental task is illustrated in Figure 1A. At the start of each trial, participants first saw a white central fixation cross lasting 1000 ms. This was followed by a sample memory set, consisting of four colored rectangles with different orientations displayed in four locations on a black background. The colors of the rectangles were randomly selected without repetition in each trial from a pool of eight colors. The eight colors were chosen to be distinguishable and with similarly low luminance. The to-be remembered array remained on the screen for 200 ms, in order to discourage participants from making saccadic eye movements to scan the individual items. After a 1000 ms delay interval, participants were presented with a color cue (i.e. retro-cue). The color cue referred to the item to be subsequently probed (validity 100%) (Lepsien et al. 2005; Matsukura et al. 2007). Cues were presented for 200 ms, and were followed by another 1000-ms delay interval. Finally, participants were presented with a single rectangle for 1500 ms, during which they were required to respond. The task was to indicate, by button press, whether the orientation of the probe was the same as at encoding. Following this response period, a blank screen was shown for 1800 ms before the onset of the next trial. A total of 160 trials were presented, of which 80 had retro-cues indicating a left item and 80 a right item.

EEG recording and preprocessing:

Data were acquired using a Biosemi Active Two system with 128 electrodes. Additional EOG – vertical and horizontal- electrodes and a tip-nose reference were also recorded. The data was digitalized at a sampling rate of 2048 Hz and filtered between 0.16 Hz and 100 Hz. The data were offline re-referenced to tip nose and down-sampled to 250 Hz in MATLAB using Fieldtrip (www.fieldtriptoolbox.org). Subsequent analyses were also carried with Fieldtrip toolbox.

Time-frequency analysis:

The EEG signal was preprocessed before time-frequency analysis. Only correct trials were included in the analysis. Analysis were done considering only 61 posterior electrodes. The signal

was epoched from 2400 ms before cue onset to 2000 ms after cue onset. Epochs were visually inspected for artifacts. A mean of 6.11% (SD=3.99%) epochs were rejected, which led to a total of 4428 trials for subsequent analysis. The eye blinks component was extracted out of the signal using Independent Component Analysis ('runica' EEGLab implemented in Fieldtrip.) Time-frequency representations of individual trials were then calculated using Morlet's wavelet analysis with a wavelet width set to 7. Trials were then averaged for each condition –right and left- and normalized to decibels using a baseline of 300 ms before memory array presentation ($10 \cdot \log_{10} (\text{power}/\text{baseline})$). Subsequently, contralateral and ipsilateral to the attended representation activity was calculated, by collapsing the left condition electrodes with a mirrored version of right condition electrodes. Contralateral activity is then represented in right electrodes by averaging right electrodes of the left condition with left electrodes of the right condition. In analog way, ipsilateral activity is represented in left electrodes.

Lateralized alpha activity was then tested for significance. Statistical analysis was performed using non-parametric cluster analysis as implemented in fieldtrip (<http://www.fieldtriptoolbox.org>) (Maris and Oostenveld 2007) which controls for Type error I. First, time-frequency data were average in the alpha range (8-12 Hz). A t-test was then computed for each sensor-time point. P-values below 0.05 were used to form clusters of adjacent time points and electrodes. A minimum of two channels were used to form a cluster. Cluster-level statistic was calculated by summing t-values within a cluster. Significance of the cluster statistic was evaluated by a permutation test. The permutation distribution was obtained by randomly assigning the data to two subsets and calculating the maximum cluster statistic. A histogram of cluster statistics was obtained by repeating the previous step 1000 times. Cluster p-value is then obtained as the proportion of randomizations that are above the observed cluster-level statistic.

RESULTS

The mean task accuracy was 0.82 (SD=0.13), and the mean reaction time was 643 ms (SD=136.48).

Time-frequency representations revealed oscillatory alpha activity (8-12 Hz) desynchronization after cue presentation peaking around 400 ms post cue onset (Figure 1B) after which, alpha resynchronized again reaching a maximum at 900 ms. Importantly, ipsilateral and contralateral electrodes were not equally modulated. Specifically, as shown in the topography of alpha band activity, contralateral electrodes were more desynchronized than its homologues in the ipsilateral cortex (Figure 1C). Significance of alpha lateralization was tested by means of a non-parametrical statistical analysis which revealed a significant cluster ($p=0.032$) of occipito-ventral electrodes in the temporal window from 580 to 960 ms after retro-cue presentation (Figure 1D).

Although the scope of this work was the attentional modulation in the alpha band, attentional modulation in other bands was also investigated. Specifically, time-frequency representations showed more gamma (30-70 Hz) and beta band activity (15-30 Hz) in contralateral electrodes than in ipsilateral ones (Figure 1B). However, this difference did not reach statistical significance ($p=0.48$ for beta band and $p=0.37$ for gamma band).

DISCUSSION

In the present work we explored the oscillatory underpinnings of orienting attention to a relevant representation held in WM guided by a feature value. By comparing ipsilateral and contralateral alpha activity, we showed that orienting attention toward and selecting a memory item based on its color resulted in a modulation of posterior alpha activity, which appears as more desynchronization in the contralateral than in the ipsilateral hemisphere. Alpha lateralization is considered a robust correlate of external and internal shifts of spatial attention (Wolff et al. 2017). We propose that current findings, together with several lines of evidence we discuss below, support the idea that selection of a memory item based on a non-location feature would be accomplished by a spatial attentional mechanism.

Directing attention to a location in the internal space results in alpha lateralization, with more desynchronization for the contralateral than to the ipsilateral hemisphere. Alpha band desynchronization reflects a state of high cortical excitability, either associated to sensory, cognitive or motor processing (Pfurtscheller 1992; Haegens et al. 2011). Alpha desynchronization might respond to stimulation, but it can also be triggered by top-down processes. In the context of internal selective attention, a more prominent alpha desynchronization of the contralateral cortex is interpreted as a neural signature of top-down guidance of attention to the cued memory representation. Sensory recruitment models of WM propose that information maintenance is supported by the same neural mechanisms engaged during the encoding of sensory information (Serences et al. 2009; D'Esposito and Postle 2015; Eriksson et al. 2015). In this line, alpha desynchronization emerges from attention to regions processing the memory items (Poch et al. 2017). Complementarily, alpha synchronization over the ipsilateral hemisphere is considered to reflect a functional mechanism inhibiting irrelevant information (Jokisch and Jensen 2007; Händel et al. 2011; Bonnefond and Jensen 2013). In the current study, the color-feature retro-cue resulted in alpha lateralized activity in posterior electrodes, similar to the modulation that has been widely reported in spatial retro-cuing paradigms (Myers et al. 2015; Schneider et al. 2016; Poch et al. 2017). Based on empirical evidence that proposes that location is a special feature and it has an obligated encoding into WM (Poch et al. 2010; Kondo and Saiki 2012; Rajsic and Wilson 2014), object properties would have been retinotopically maintained and thus, orienting attention to an item based on non-location information would have resulted in spatial activity modulation.

Recently, a TMS study explored the neural underpinnings of feature and spatial based attentional selection in WM (Heuer et al. 2016). The authors reported that while TMS delivery to the supramarginal gyrus selectively improved performance for the spatial cue condition, lateral occipital cortex stimulation resulted in the selective facilitation for the feature condition. While these results posited different cortical mechanisms involved in both processes, they also

reported that visual facilitation was exclusive for the contralateral cortex for both conditions, which would imply a spatial mechanism in the feature condition. Likewise, an EEG experiment found lateralized ERP components (N2pc, Pd, ADAN) following a color retro-cue, associated to the allocation of spatial attention to the cued WM representations (Schneider et al. 2017). Nonetheless, Vicente-Grabovetsky showed that retinotopic maintenance depends on the demands of the task (Vicente-grabovetsky et al. 2014) . Thus, when a spatial strategy is discouraged by centrally presented probes, memory information is not retinotopically represented. They concluded that spatial coding might be representing prospective attention to probe items rather than maintenance per se. While this explanation cannot be dismissed, it contrasts with other findings in which lateralized activity is found with centrally presented probes (Kuo et al. 2012; Schneider et al. 2016, 2017). In our experiment, probes were presented in their original locations, so lateralized activity could be due to prospective attention to the probe location. However, to prospectively direct attention to the probe location, spatial information must be retrieved based on a retained stimulus attribute, so items should have been encoded including their locations. In a similar way, if the spatial strategy were imposed by the task, and lateralized activity arised from prospective attention to probe locations, it could be reasonable that lateralized activity would be sustained until probe presentation. In the perceptual domain, alpha activity modulation is found to be sustained until target presentation, biasing cerebral areas that are going to process the target. In our experiment, alpha lateralization was resolved before probe onset, thus, improbably reflecting anticipatory attention to the target. This indicates that transient alpha modulation is more likely to be due to attentional focusing on the relevant item. Related to this, it has been proposed that retro-cue benefit is based on the transient allocation of attention on the relevant information. Thus, focusing attention to an item would transform it into a more robust representational state and then attention would be no longer needed (Myers et al. 2017; Wolff et al. 2017).

Our results also contribute to clarify another important issue. Spatial retro-cue experiments commonly use a cue that could be considered exogenous. Central cues are not symmetrical, right cues have arrows in right central hemifield that does not have the left hemifield. Even centrally presented, they can induce large lateralized activity (Capilla et al. 2016). Accordingly, it could be considered that alpha lateralization found in internal spatial attentional studies could emerge from cue related activity. Furthermore, the cue itself is spatial in nature (an arrow indicating a specific location), so it cannot be ruled out that the lateralized alpha response reflects spatial attention to the region pointed at by the arrow. Unlike spatial or symbolic cues (Spitzer and Blankenburg 2011 ; Poch et al., 2014; Myers et al., 2015), the use of a memorized non-spatial attribute of the stimulus as the cue offers a strong proof that alpha lateralization is related to internal orienting of attention to memorized items. Thus, we demonstrate that alpha lateralization in retro-cue attentional guidance signals an endogenous attentional mechanism.

In summary, we further elucidated detailed neural oscillatory correlates of directing attention within representations held in WM. We found that feature based orienting attention within WM resulted in lateralized alpha activity, which is considered to be a correlate of spatial attention. These findings suggest that item prioritization in WM based on the memory of one of its features (i.e. color) is accomplished via allocation of attention to the location of the relevant item. Moreover, we showed that alpha lateralization in retro-cueing is a neurophysiological marker of endogenous attention. Thus, our results extend previous findings and underscore the role of alpha oscillatory activity in modulating the excitability of posterior regions during attentional orientation within WM.

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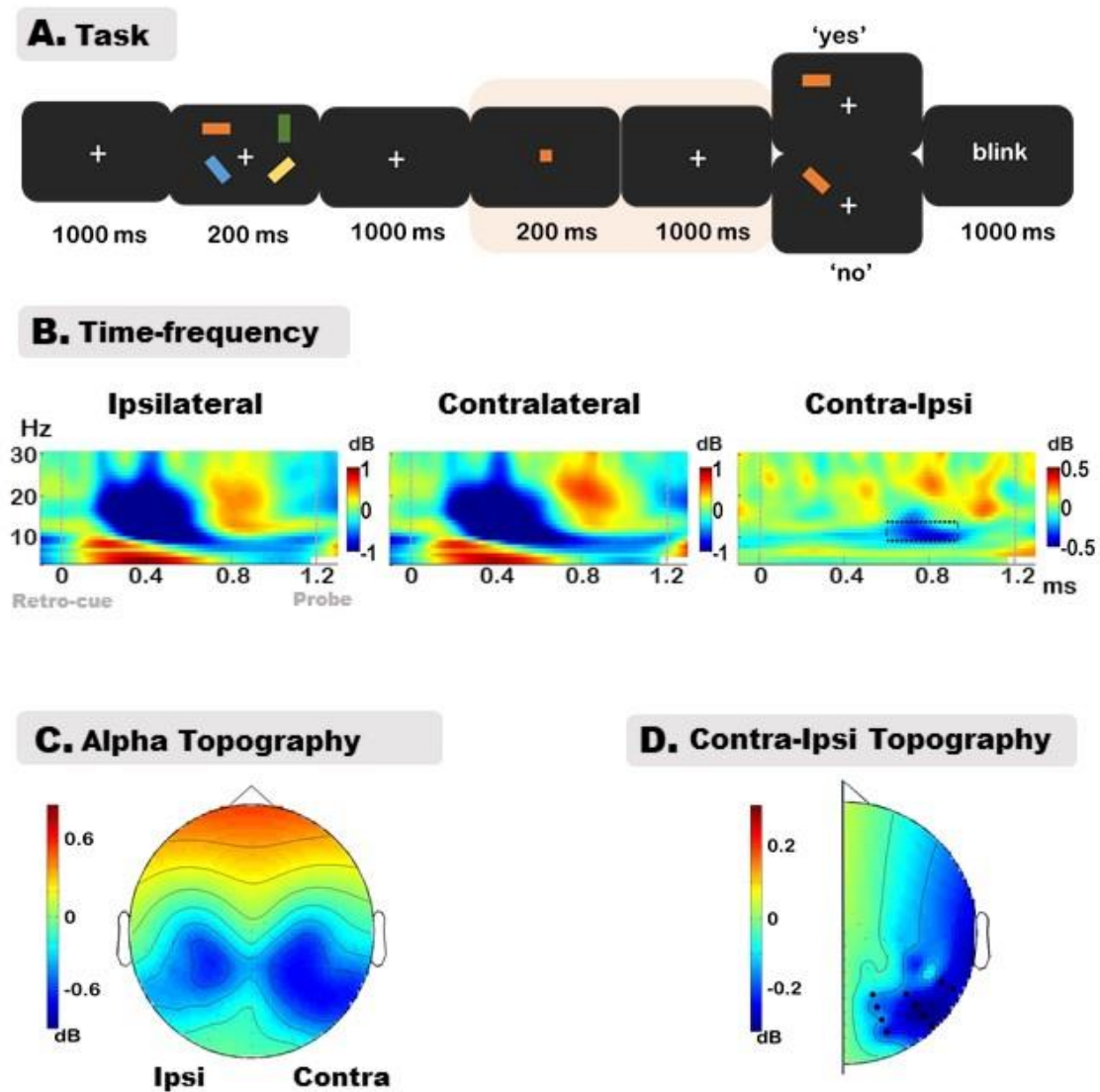
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Figure 1



A. Schematic representation of the feature retro-cue task. After 1000 ms fixation a set of different colored oriented rectangles was briefly displayed (200 ms) for encoding. 1000 ms after the offset of the memory array, participants were presented with a color cue (i.e. retro-cue). Cue was presented for 200 ms and was followed by another 1000ms of delay interval. Finally, participants were presented with a single rectangle in its original position for 1500 ms during which they were required to respond.

- B. Time-frequency representation after cue presentation of the group of electrodes conforming the significant cluster.
- C. Topographic representation of averaged alpha band (8-12 Hz) activity in the significant time-window (580-960 ms after retro-cue).
- D. Topographic representation of the contralateral minus ipsilateral hemisphere in the time window (580-960 ms). Bold circles denote the cluster of significant difference.