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A dual mechanism underlying alpha lateralization in attentional orienting to mental representation

Claudia Poch[a,b], Luis Carretie[d], Pablo Campo[c,*]

[a] Instituto Pluridisciplinar, Universidad Complutense de Madrid, Spain
[b] Departamento de Psicología Básica I, Universidad Complutense de Madrid, Spain
[c] Departamento de Psicología Básica, Facultad de Psicología, Universidad Autónoma de Madrid, Calle Ivan Pavlov 6, 28049, Madrid, Spain
[d] Departamento de Psicología Biológica y de la Salud, Universidad Autónoma de Madrid, Spain

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ABSTRACT

Numerous electrophysiological findings support the notion that selective attention modulates alpha oscillatory activity. Specifically, alpha enhancement and suppression can be dissociated in time and space. It is now accepted that selective attention operates in either the perceptual or the representational environments. Lateralized alpha activity resulting from directing attention to mental representations, might arise from a transient alpha desynchronization, as recent proposals hypothesized. However, the contribution of enhancement vs suppression, as well as their neural correlates to the lateralized alpha modulation remain unstudied. To investigate these questions, we recorded magnetoencephalography while participants performed a retrospective cueing paradigm. Time-frequency analysis revealed a larger transient alpha desynchronization for the sensors contralateral to the relevant items which originated from the ventral lateral occipital cortex. Additionally, greater ipsilateral alpha enhancement in the medial occipital cortex occurred later and was maintained until probe presentation. Based on these differences we reasoned that the former would reflect the allocation of selective attention to relevant items, while the later might signal the inhibition of the irrelevant external hemifield instead of irrelevant WM items. Altogether, our results suggest that alpha lateralization does not arise from a unitary phenomenon. Dissociated anatomical and temporal alpha activity might be signaling different functional roles.

The visual system has limited processing capacity, so simultaneous stimuli present in the visual field mutually suppress their evoked activity in the visual cortex. Competition between stimuli can be resolved by top-down mechanisms, such as selective attention, or by bottom-up stimulus-driven mechanisms, such as saliency. Selective attention to the behavioral relevant stimuli is considered a top-down process, in which high-level processing areas in the prefrontal and posterior parietal cortices, exert a biasing signal towards the visual regions processing the relevant items (Miller & D'Esposito, 2005). As a consequence, sensory regions show increased activity for the relevant vs the irrelevant items (Armstrong, Fitzgerald, & Moore, 2006; Buffalo, Fries, Landman, Liang, & Desimone, 2010), making stimulus processing more accurate (Richter, Thompson, Bosman, & Fries, 2017). Neural synchrony seems to be a key mechanism to enhance neural representation of the attended sensory input. Several models postulate that gamma and alpha band oscillations play a pivotal role in top-down processes such as selective attention, with antagonist roles (Fries, Reynolds, Rorie, & Desimone, 2001; Fries, Womelsdorf, Oostenveld, & Desimone, 2008; Jensen & Mazaheri, 2010; Klimesch et al., 2007; Womelsdorf, Fries, Mitra, & Desimone, 2006). Whereas gamma synchronization represents a high excitability state of the underlying neural population (Fries et al., 2001), and is thus associated with processing of information; alpha synchronization represents a state of low excitability and has been associated with the functional inhibition of task-irrelevant regions (Jensen & Mazaheri, 2010). In this line, alpha modulation in visual areas represents an anticipatory visuospatial attention correlate. Some experiments have found an alpha power increase (or alpha synchronization) ipsilateral to the attended hemifield related to the suppression of unattended neural representations (Kelly, Lalor, Reilly, & Foxe, 2006; Rihs, Michel, & Thut, 2007;Worden, Foxe, Wang, & Simpson, 2000), whereas others have found an alpha power decrease (or desynchronization) contralateral to the attended hemifield (Kelly, Gomez-Ramirez, & Foxe, 2009; Sauseng et al., 2005; Yamagishi, Goda, Callan, Anderson, & Kawato, 2005) linked to enhancement of neural excitability in cortical areas processing the attended stimulus.

Like visuospatial attention, working memory (WM) has capacity

* Corresponding author.
E-mail address: pablo.campo@uam.es (P. Campo).

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restrictions, in which only limited amount of information can be represented during a short interval. Top-down mechanisms have been shown to operate during the maintenance interval to optimize WM performance (Griffin & Nobre, 2003; Lepsien & Nobre, 2007). Additionally, recent theoretical conceptualizations highlight the flexible nature of memory representations, which are maintained in different accessibility states and the allocation of attention can move them into a high prioritized state (Lewis-Peacock & Postle, 2012; LaRocque, Lewis-Peacock, Drysdale, Oberauer, & Postle, 2013; Zokaei, Manohar, Husain, & Feredoes, 2013, Zokaei, Ning, Manohar, Feredoes, & Husain, 2014; Heuer & Schubö, 2016a). An efficient experimental strategy to study the benefit of orienting attention to representations already held in WM is presenting a spatial cue during the retention period indicating which item is likely to be probed. This is widely known as the retro-cue paradigm, because the cue is provided after the memory set is encoded. The use of this paradigm has demonstrated that orienting attention to perceptual representation, this is, before encoding, and orienting attention to memory representation, this is, after encoding, exhibit a similar behavioral benefit (Griffin & Nobre, 2003; Myers, Walther, Wallis, Stokes, & Nobre, 2015). In addition, both processes elicit a similar modulation of evoked visual activity (Griffin & Nobre, 2003). These results suggest that a common set of attentional control (i.e. top-down) mechanisms can be used in both cognitive contexts, this is, when selecting items in the outside world, and when selecting items among internal representations (i.e., WM). While there is abundant research about the patterns of neural oscillatory activity underlying attentional processes in the perceptual domain, the modulation of oscillatory activity by the retro-cue has been much less studied.

Similarly to orienting attention to the perceptual space, retro-cue experiments also find an alpha modulation related to orienting attention to memory representations (Nobre, Gitelman, Dias, & Mesulam, 2000; Kastner & Ungerleider, 2001; Poch, Campo, & Barnes, 2014; Wallis, Stokes, Cousijn, Woolrich, & Nobre, 2015; Mok, Myers, Wallis, & Nobre, 2016; Schneider, Mertes, & Wascher, 2016). However, contrary to the much studied phenomenon in perception, the characteristics of alpha modulations in WM are still under examination.

Visuospatial attention experiments have proven useful to disentangle the neural generators of alpha modulation in order to determine its functionality. A recent MEG study found two dissociated generators of alpha activity related to different attentional mechanisms (Capilla, Schoffelen, Paterson, Thut, & Gross, 2014). While alpha ipsilateral increases arised from the dorsal stream to support attentional shifts, contralateral alpha suppression in the ventral occipital cortex was related to feature processing. This dissociation would be of great relevance in WM as it could provide further understanding of sensory recruitment proposals which posit that maintenance of information is accomplished by sensory cortices (Postle, 2006; Serences, Ester, Vogel, & Awh, 2009).

Whether item prioritization needs sustained attention to encoded information or not is matter of debate. Some authors have argued that retro-cue guides attention to the relevant item, and that it stays under focal attention until probe presentation (Makovsik & Jiang, 2007; Matsukura, Luck, & Vecera, 2007; Makovski, Sussman, & Jiang, 2008; Pertzov, Bays, Joseph, & Husain, 2013). However, other authors have found that sustained attention is not needed for the benefit of the retro cue (Hollingworth & Maxcey-Richard, 2013; Rerko, Souza, & Oberauer, 2014). Convergently, electrophysiological experiments have found a transient alpha lateralization related to attentional orienting (Mok et al., 2016; Myers et al., 2015; Wallis et al., 2015). In this line, it has been proposed that transient alpha desynchronization is an index of access to memory representation and, once a representation is accessed, a change in the representational state takes place and alpha modulation is no longer needed (Wolff, Jochim, Akyürek, & Stokes, 2017).

Behavioural studies have found divergent results about the extent of the retro-cue benefit. Some authors reported that retrocue benefits are observed only for one single item (Makovsik & Jiang, 2007), while others have found that is possible to retrospectively orient attention to more than one (Heuer & Schubö, 2016b). Electrophysiological retro-cue studies have mainly explored the effects of retro-cueing one item (Griffin & Nobre, 2003; Myers, Stokes, & Nobre, 2017; Schneider et al., 2016). To our knowledge, the only electrophysiological work manipulating retro-cued load found that alpha power was modulated by relevant cued information (Manza, Hau, & Leung, 2014). However, this study used bilateral arrays, so it did not address alpha lateralization differences related to selecting varying amounts of items.

In the present study we use a retro-cue paradigm with three conditions, one-cue, two-cue, and neutral-cue. We explore the dynamics of alpha band activity related to the retro-cue and use source localization to address the issues previously exposed. We hypothesized that according to a current theory of item prioritization (Myers et al., 2017), alpha desynchronization would transiently emerge from areas coding sensory information. Furthermore, accordingly to this model, the two-cue condition would be expected to produce a more pronounced alpha lateralization respect to one-cue with greater disinhibition of the contralateral sensory cortex.

1. Methods

1.1. Participants

Seventeen adult subjects [mean age, 25.36 years; standard deviation (SD), 3.13 years; range, 22–32 years; nine females], without any history of neurological or psychiatric illness, volunteered for participation in the study, which was approved by the local ethical committee of the Center of Biomedical Technology (Madrid, Spain), 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).

1.2. Stimuli and tasks

The experimental task was adapted from a retro-cueing paradigm developed by Giffrin and Nobre (Griffin & Nobre, 2003; Lepsien & Nobre, 2006) and is illustrated in Fig. 1. 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 gray rectangles with different orientations (0°, 45°, 90 °,13°) displayed in four locations on a black background. Each rectangle size was of 7.62° of visual angle and their center was located at 7.62° eccentricity for the horizontal and vertical planes. 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 could be presented with either an informative spatial cue (i.e. retro-cue) or with a non-informative cue (i.e. neutral cue). The retro-cue consisted of one or two arrows originating from the fixation cross pointing to one or two of the four locations that had been occupied by a rectangle in the memory array, thus indicating the item or items that will be subsequently probed (validity 100%) (Lepsien, Griffin, Devlin, & Nobre, 2005; Matsukura et al., 2007). The neutral cue consisted of four arrows originating from the fixation cross pointing to each of the four locations, thus providing no information regarding the relevant item. Cues were presented for 200 ms, and were followed by another 1000-ms delay interval. Finally, participants were presented with a single rectangle in one location for 1500 ms, during which they were required to respond. The task was to indicate, by button press, whether the probe had the same orientation as the memory item. Following this response period, a blank screen was shown for 1800 ms before the onset of the next trial (Fig. 1). A total of 360 trials were presented, of which 120 had retro-cues indicating one location, 120 had retro-cues indicating two locations, and 120 had neutral cues. Cues pointing to one or two locations