Actividad oscilatoria neuronal asociada con la orientación de la atención hacia las representaciones mentales de la memoria operativa

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Madrid, 2015

Tesis doctoral dirigida por:
Dr. Luis Carretié
Dr. Pablo Campo

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“The true art of memory is the art of attention”

Samuel Johnson

Abstract

Selective attention mechanisms allow us to focus on information that is relevant to the current behavior and, equally important, ignore irrelevant information. Neural synchrony has been proposed to be a key mechanism underlying selective attention. Several models postulate that gamma and alpha band oscillations play a pivotal role in top-down processes such as selective attention, with antagonist roles. Whereas gamma synchronization is associated to processing of information; alpha synchronization has been associated with the functional inhibition of task-irrelevant regions. Recent studies have shown that, in the same way that attention can be selectively oriented to bias sensory processing in favor of relevant stimuli in perceptual tasks, it is also possible to retrospectively orient attention to internal representations held in working memory. However, these studies have not explored the associated oscillatory phenomena. In the present dissertation we explored the patterns of oscillatory activity associated to retrospectively orienting attention under the hypothesis that modulation of oscillatory activity is a general mechanism resulting from deployment of attention to the perceptual and mnemonic domains. MEG activity was recorded while participants performed a retro-cue change detection task. Participants benefited from retro-cues in terms of accuracy and reaction time. Lateralized gamma and alpha activity were found in occipital cortex. Gamma power was more pronounced in the ventral occipital cortex contralateral to the attended hemifield. While alpha was more strongly suppressed in the contralateral occipital cortex at the beginning of the delay period, it increased at the end of the retention in the ipsilateral occipital cortex. A subsequent behavioral experiment revealed that when participants cannot anticipate the probe location, the retro-cue is still beneficial, and thus, the benefit of retro-cue is not only due to anticipatory attentional mechanisms. An EEG experiment further found lateralized alpha activity in the absence of preparatory attention. These findings suggest that the oscillatory mechanisms underlying attentional orienting to representations held in working memory are similar to those engaged when attention is oriented in the perceptual space.

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List of abbreviations

ADAN: Anterior directing attention negativity

ANOVA: Analysis of variance

CBM: Coherence based model

CDA: Contralateral delayed activity

DLPFC: Dorsolateral prefrontal cortex

EDAN: Early directing attention negativity

EEG: Electroencephalography

EOG: Electrooculogram

ERP: Event related potentials

FEF: Frontal eye field

FFA: Fusiform face area

fMRI: Functional magnetic resonance

FoA: Focus of attention

FWE: Family wise error

IFG: Inferior frontal gyrus

IT: Inferior temporal

LDAP: Late directing attention positivity

LFP: Local field potential

lPFC: Lateral prefrontal cortex

MEG: Magnetoencephalography

MVPA: Multivariate pattern analysis

NIfTI: Neuroimaging Informatics Technology Initiative images

PET: Positron emission tomography

PPA: Parahippocampal place area

PPC: Posterior parietal cortex

RF: Receptive field

rTMS: repetitive Transcranial magnetic stimulation

RTs: Reaction times

SEF: Supplementary eye field

SPL: Superior parietal lobule

TF: Time-frequency

vlPFC: Ventrolateral prefrontal cortex

VWM: Visual working memory

WM: Working memory

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Glossary of terms

Presentation

Presentación

Presentation

The visual system has limited processing capacity, thus, 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, like the frontal and parietal cortex, exert a biasing signal towards the visual regions processing the relevant items. As a consequence, sensory regions show increased activity for the relevant vs the irrelevant items. Neural synchrony has been proposed 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. Whereas gamma synchronization represent a high excitability state of the underlying neural population, and thus associated to processing of information; alpha synchronization represent a state of low excitability and has been associated with the functional inhibition of task-irrelevant regions.

Restricted capacity is a shared feature of working memory (WM), in which only limited amount of information can be represented during a short interval. However, top-down mechanisms have been shown to operate during the maintenance interval to optimize WM performance. Contemporary neurophysiological models of WM posit that the maintenance of information is mediated by the same regions involved in its encoding. Additionally, recent theoretical conceptualizations, highlight the flexible nature of memory representations. Memory representations are maintained in different accessibility states and the allocation of attention can move them into a high prioritized state. To study the benefit of orienting attention to representations already held in WM, a spatial cue indicating which item is likely to be probed is given during the retention period. 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. In addition, both processes elicit a similar modulation of evoked visual activity. 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 among internal representation (i.e., WM), and when selecting items in the outside world. 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 largely unaddressed until now.

Given the importance of neural synchrony for neural computation, in the present dissertation we aimed to elucidate the neural oscillatory modulation associated with orienting attention to memory representations. Specifically, here we investigate whether attentional modulation of oscillatory neuronal responses in visual areas operates through a common mechanism in the orientation of attention to sensory inputs and to memory representations. We first conducted a Magnetoencephalography (MEG) experiment in which participants performed a retro-cue task. This experiment was recorded in the UPM MEG system. The system has two type of sensors which differently record the underlying magnetic signal: magnetometers and gradiometers. The analysis of the electrophysiological signal was undergone in two steps. First, magnetometer data was analyzed under the co-supervision of Dr. Gareth Barnes and Dr. Pablo Campo in the Wellcome Trust Center for Neuroimaging of the University Collage of London, during an eight months research stay. These data were then published in European Journal of Neuroscience (Poch, Campo, & Barnes, 2014). The second part involved the analysis of the gradiometer data, which was conducted in the Autonoma University of Madrid, under the co-supervision of Dr. Pablo Campo and Dr. Luis Carretié. The MEG experiment raised methodological issues that were then addressed conducting a behavioral and an Electroencephalography (EEG) experiments, which were conducted in the UAM.

The dissertation begins with a general introduction in which the present work is framed. I review the most relevant and influential literature about the neural basis of attention, the neural basis of WM, and gamma and alpha oscillations related to attention and memory. After the introduction, the objectives and hypothesis are formulated. In the following chapter, the main results derived from the three experiments are expounded. In chapter three, results are discussed in detail and is followed by the conclusions. The methods chapter is placed at the end in order to facilitate the reading of the work. A glossary of terms is provided at the end of the dissertation.

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Presentación

El sistema visual tiene una capacidad de procesamiento limitada, de esta forma, los estímulos que se presentan simultáneamente en el campo visual suprimen mutuamente su actividad evocada en la corteza visual. La competición entre estímulos puede resolverse mediante mecanismos top-down, tales como la atención selectiva, o mediante mecanismos bottom-up, tales como la saliencia del estímulo. La atención selectiva hacia estímulos relevantes se considera un proceso top-down en el cual áreas de procesamiento superiores como la corteza frontal y parietal ejercen un sesgo en las regiones visuales que procesan los estímulos relevantes. Como consecuencia dichas áreas sensoriales muestran un incremento de actividad para los ítems relevantes en comparación con los irrelevantes. Se ha propuesto la sincronización neuronal como un mecanismo clave para incrementar la representación neuronal de los inputs sensoriales atendidos. Diferentes modelos postulan que las oscilaciones en las bandas de frecuencia alpha y gamma desempeñan un papel fundamental en los procesos top-down con roles contrapuestos. Mientras que la sincronización en gamma representa un estado de alta excitabilidad de la población neuronal subyacente, y por tanto se asocia con el procesamiento de información; la sincronización en alpha representa un estado de baja excitabilidad y se ha asociado con la inhibición funcional de regiones irrelevantes para la tarea.

La capacidad limitada es una característica compartida por la memoria operativa en la cual sólo una cantidad restringida de información se puede representar durante un intervalo corto de tiempo. Sin embargo, se ha demostrado que los mecanismos top-down operan durante el periodo de mantenimiento para optimizar el rendimiento de la memoria operativa. Modelos neurofisiológicos contemporáneos de memoria operativa establecen que el mantenimiento de información se lleva a cabo en las mismas regiones involucradas en su codificación. Además, conceptualizaciones teóricas recientes subrayan la naturaleza flexible de las representaciones mnémicas. Dichas representaciones se mantienen en diferentes estados de accesibilidad y pueden situarse en un estado de alta prioridad mediante la dirección de la atención. Para estudiar los beneficios de la orientación de la atención hacia representaciones mantenidas en la memoria operativa, se proporciona una clave espacial que indica qué ítem se será evaluado tras el periodo de mantenimiento. Esto se conoce como el paradigma de retro-clave, ya que la clave se proporciona una vez que el conjunto de ítems ya se ha codificado. El uso de este paradigma ha demostrado que la orientación de la atención hacia las representaciones perceptivas, esto es, antes de la codificación, y la orientación de la atención hacia representaciones mnémicas, esto es después de la codificación, muestra un beneficio conductual similar. Más aún, ambos procesos elicitan una modulación de la actividad visual evocada. Estos resultados sugieren que un conjunto común de mecanismos de control atencional (top-down) se utilizan en ambos contextos cognitivos, esto es cuando se seleccionan ítems dentro de las representaciones internas (memoria operativa) y cuando se seleccionan ítems en el mundo exterior. Mientras existe una abundante literatura acerca de los patrones oscilatorios neuronales que subyacen a los procesos atencionales en el dominio perceptivo, la modulación de la actividad oscilatoria por el uso de retro-claves no ha sido contemplada hasta ahora.

Dada la importancia de la sincronización neuronal para la computación neuronal, en esta tesis se plantea determinar la modulación de las oscilaciones neuronales relacionada con la orientación de la atención hacia las representaciones mnémicas. Específicamente, se investiga si la modulación atencional de la respuesta oscilatoria neuronal en las áreas visuales opera de acuerdo a un mecanismo común en la orientación de la atención hacia los inputs sensoriales y las representaciones mnémicas. En primer lugar se llevó a cabo un experimento de Magnetoencefalografía (MEG) en el que los participantes realizaban una tarea de retro-clave. Este experimento fue registrado en el sistema MEG de la Universidad Politécnica de Madrid. El sistema consta de dos tipos de sensores que registran de forma diferente la señal electromagnética subyacente: magnetómetros y gradiómetros. El análisis de la señal electrofisiológica se llevó a cabo en dos fases. Primero, los datos de los magnetómetros se analizaron bajo la supervisión del Dr. Gareth Barnes y Dr. Pablo Campo en el Wellcome Trust Centre for Neuroimaging de la University College of London durante una estancia de ocho meses. Estos datos fueron publicados en la revista European Journal of Neuroscience (Poch, Campo, & Barnes, 2014). La segunda fase supuso el análisis de los datos obtenidos de los gradiómetros y se llevó a cabo en la Universidad Autónoma de Madrid (UAM) bajo la supervisión del Dr. Luis Carretié y del Dr. Pablo Campo. Los resultados del experimento de MEG desvelaron algunos aspectos metodológicos que fueron abordados mediante la realización de un experimento conductual y un experimento de electroencefalografía (EEG), ambos llevados a cabo en la UAM.

Este trabajo de tesis comienza con una introducción general en la cual se contextualiza el presente trabajo. En ella se revisa la literatura más relevante e influyente acerca de las bases neuronales de la atención, bases neuronales de la memoria operativa, y las oscilaciones en banda alpha y gamma asociadas a la atención y a la memoria operativa. En el siguiente capítulo, se exponen los resultados principales derivados de los tres experimentos realizados. El capítulo tres discute en detalle los resultados, y es seguido por las conclusiones. La sección de métodos se sitúa al final con la idea de facilitar la lectura del trabajo. Además se proporciona un glosario de términos al final de la tesis.

La tesis se desarrolló con la financiación para la formación de profesorado universitario del Ministerio de Educación (AP2009-4131) y la financiación para el desarrollo del proyecto de investigación otorgada por el Ministerio de Ciencia en Innovación al Dr. Pablo Campo (PSI2010-16742).

1 Introduction

Introduction

1.1 Neural correlates of visuospatial attention

Our visual environment is usually cluttered with multiple objects. However, only a limited amount of information can be processed by our visual system at each moment of time. Given limited processing capacity, simultaneous visual input compete for neural representation. The competition is resolved either by virtue of a stimulus physical salience (bottom-up attention) or according to internal behavioral goals (top-down attention) (figure 1). Attention directed to a specific position in space facilitates the processing of a single stimulus appearing at that location (Posner, 1980). For example, faint stimuli are detected better at the attended location (Bashinski & Bacharach, 1980) and their properties, like their orientation, can be better discriminated (Downing, 1988). But visual scenes usually contains multiple stimuli, so attention also selects behaviorally relevant stimuli among competing distracters (Duncan & Humphreys, 1989; Treisman & Gelade, 1980; Verghese, 2001).

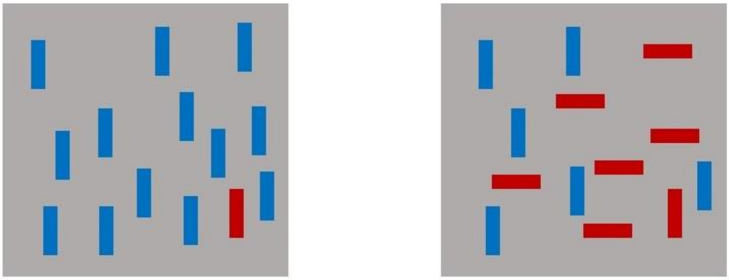

Figure 1. Multiple stimuli in the visual field compete for neural representation. This figures depicts two experimental conditions involving bottom-up or data-driven allocation of attention (left panel), and top-down controlled allocation of attention to expected targets (right panel).

Visual processing is believed to be organized into two distinct anatomical and functional pathways that originate in the striate cortex (V1). Lesional studies in monkeys showed dissociable deficits in spatial and object vision which yielded to characterized a 'ventral stream' for object vision and a 'dorsal stream' for spatial vision (Mishkin & Ungerleider, 1982). Anatomically, the dorsal stream projects into the parietal cortex, evolving through the occipitoparietal cortex to the posterior part of the inferior parietal cortex, extending to the dorsolateral prefrontal cortex. It is involved in visually guided action and captures the spatial relation between objects (Kravitz, Saleem, Baker, & Mishkin, 2011). The ventral stream projects into the temporal cortex evolving through the occipitotemporal cortex to the anterior part of the inferior temporal cortex (IT) extending into the ventrolateral prefrontal cortex (Kravitz, Saleem, Baker, Ungerleider, & Mishkin, 2013). It is crucial for forming specific representations of visual information and therefore for object recognition. The ventral pathway is a recurrent network retinotopically organized. V1, V2, V4, TEO, and TE are not a series of sequential projections, but instead a set of bidirectional projections. Early visual areas are linked to IT through multiple routes over which visual information is processed. While V1 and V2 processes simple features (e.g. edge orientation) and have very small receptive fields (RFs), V4 processes more complex stimuli (e.g. combination of shape and color) and have larger RFs, finishing in IT (TE and TEO) with selectivity for whole objects and larger RFs.

Additionally, prefrontal and parietal cortex recurrent (i.e. feedback) projections to ventral stream areas has been also described (Cavada & Goldman-Rakic, 1989; Ungerleider, Gaffan, & Pelak, 1989; Webster, Bachevalier, & Ungerleider). Recurrent projections both within the ventral stream and from areas beyond this processing pathway are believed to constitute the anatomical basis for top-down influences, such as attention, on object perception.

1.1.1 Effects of attention in visual processing

At a neural level, attention modulates activity along the ventral stream. In order to facilitate the selection of visual information relevant for ongoing behavioral goals, attention is used to bias perceptual processing of external visual information. Modulation of neural activity as a result of the allocation of attention has been observed in relatively early stages of visual processing and also at later stages where more complex features are processed. Attentional facilitation and selection may be accomplished by a combination of feedforward connections with and local inhibition with top-down feedback that originates from parietal and frontal areas to ventral visual cortex. Attentional facilitation produce an enhancement of perceptual representations as indexed by increased neural activity selective to the visual areas that code the attended stimuli. Neural enhancement is also found selective to the retinotopic position of the focus of spatial attention in the absence of visual stimulation. Single-unit recordings in monkeys have assessed the effects of attending to a single stimulus appearing alone in a neuron´s RF. During the task, monkeys are trained to maintain fixation at a central spot and to covertly orient attention (without eye movements) to a peripheral stimulus inside a neuron´s RF. The attended stimulus condition is then compared to the condition in which attention is directed outside the RF. Increased firing rates to the attended compared to the unattended stimulus have been found mainly in extrastriate regions although V1 has been also reported (Buffalo, Fries, Landman, Liang, & Desimone, 2010; Mehta, Ulbert, & Schroeder, 2000; Motter, 1993). However, increased firing rates with attention have been only found under certain tasks configurations. Task difficulty, number of stimuli in the visual field or stimuli contrast are variables that affect neural enhancement (Motter, 1993; Reynolds, Pasternak, & Desimone, 2000; Spitzer, Desimone, & Moran, 1988). For example, Reynolds et al. (2000), measured contrast sensitivity of V4 neurons, and found that the contrast threshold to elicit a neuron´s response was of 10 %, but when attention was directed inside the RF the threshold was reduced by 50%. However, attention did not have any effect at high contrasts. Firing rates are usually not augmented when attention is directed to a high contrast stimulus appearing alone at the neuron´s RF (Luck, Chelazzi, Hillyard, & Desimone, 1997; Moran & Desimone, 1985). In such case, neural synchronization may be a potential mechanism mediating attentional facilitation (for a review Womelsdorf & Fries, 2007). Attended stimulus elicit a stronger synchronization in the gamma-frequency range than do unattended stimuli in V4 (Fries, Reynolds, Rorie, & Desimone, 2001a), but not in V1 (Chalk et al., 2010). Neural synchronization enhancement has been observed in the local field potential (LFP) (Taylor, Mandon, Freiwald, & Kreiter, 2005), between the firing rates with the LFP (Fries et al., 2001), and among spike trains (Fries, Womelsdorf, Oostenveld, & Desimone, 2008). Furthermore, behavior can be partially predicted by the attentional modulation in gamma-band synchronization (Taylor et al., 2005; Womelsdorf, Fries, Mitra, & Desimone, 2006).

Neuroimaging and neurophysiology studies in humans have found similar activity enhancement to that found in monkeys. EEG studies have investigated the temporal dynamics of visuospatial attention. Orienting attention to a cued stimulus results in the enhancement of the P1 (80-130 ms) and N1 (140-200 ms) event related potentials

(ERP) components over occipital cortex, while it does not affect the earlier C1 component (50-90 ms) (for a review see Hillyard & Anllo-Vento, 1998). Positron emission tomography (PET) or functional magnetic resonance (fMRI) and EEG combined recordings have modelled the cortical sources of these visual components. In these experiments, participants are cued to attend one of the two visual hemifields and then discriminate a stimulus property. It is widely found that spatial attention modulates activity in contralateral ventral extrastriate regions, specifically the fusiform gyrus. These neural sources are believed to account for the P1 and N1 waveforms (Heinze et al., 1994; Mangun et al., 2001; Martínez et al., 1999). In contrast, the C1 component may arise from the striate cortex (Mangun et al., 2001; Martínez et al., 1999). Although ERP studies do not find an attentional modulation in the C1 component (believed to arise from V1), neuroimaging experiments have found attention-related changes in striate cortex (Martínez et al., 1999). Consistent with animal findings, in which V1 activates later in time than V4 (Buffalo et al., 2010; Mehta et al., 2000), it has been hypothesized that striate attentional effects result from feedback of enhanced visual signals originating from higher extrastriate areas.

Interestingly, there is evidence showing that in addition to stimulus evoked signals, prestimulus activity is increased relative to the attended location favoring the processing of stimulus that will appear at that location (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Fries et al., 2008; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Luck et al., 1997; Offen, Schluppeck, & Heeger, 2009). Single unit studies have found spontaneous firing rates increases in extrastriate areas when attention is directed inside the RFs in the cue-stimulus period (Luck et al., 1997). Accordingly, gamma band synchronization is enhanced as well with spatial attention, while low frequency power is decreased (Fries et al., 2001), mainly in the alpha range (Fries et al., 2008). In humans, alpha band decreases contralateral to the attended hemifield and increases over the ipsilateral attended hemifield have been related to the processing of the upcoming target stimulus (Capilla, Schoffelen, Paterson, Thut, & Gross, 2014; Thut, Nietzel, Brandt, & Pascual-Leone, 2006). Neuroimaging studies in humans have observed a prestimulus activity increase in extrastriate areas as well as in striate regions at the retinotopic corresponding location (Kastner & Ungerleider, 2000; Munneke, Heslenfeld, & Theeuwes, 2008). Electrophysiological experiments have identified a sequence of lateralized posterior ERP components modulated by preparatory attention. An early directing attention negativity (EDAN) ranging from 200 and 400 ms after cue onset has been related to the initiation of the shift of attention (Hopf & Mangun, 2000) although it has been also related to the processing of physical properties of the cue (Jongen, Smulders, & Van Der Heiden, 2007; Nobre, Sebestyen,

& Miniussi, 2000). A late attention positivity (LDAP) at around 500 ms might reflect the encoding of the to-be-attended positions as well as general processes involved in allocation of attention to these locations (Green & McDonald, 2006).

So far, I have described results of neuronal modulation when attention is directed to an isolated stimulus inside a neuron´s RF. However, everyday visual scenes contain multiple objects competing for neuronal representation and attention must select the relevant stimulus for behavior. The "Competition biased model" (CBM) (Desimone & Duncan, 1995)is based on the assumptions that given limited processing capacity, when multiple sensory stimuli are simultaneously presented, neuronal populations representing the sensory inputs automatically enter in competition; and that attention can bias this competition in favor of neurons that represent the attended stimulus. The following findings are in line with the CBM. When two stimuli are presented within a neuron´s RF they act in a mutually suppressive way. When a preferred stimulus is presented with a non-preferred stimulus within a RF, the response of the cell is suppressed to the preferred stimulus, and the resulting response is a weighted average of the response to both stimuli (Moran & Desimone, 1985; Reynolds, Chelazzi, & Desimone, 1999). Using fMRI, it was found that when multiple stimuli are presented simultaneously in a visual field, the visual evoked response is attenuated compared to when those stimuli are presented sequentially (Bles, Schwarzbach, De Weerd, Goebel, & Jansma, 2006; Kastner et al., 1998; Sabine Kastner & Ungerleider, 2001). The CBM predicts that suppressive interactions depends on the RF size, so larger effects are expected to occur in V4 and IT. Accordingly, differences in evoked activity between the simultaneous and sequential condition were found to be smallest in V1, increasing in further areas of the ventral stream. Larger stimulus separation resulted in reduced suppressive interactions in earlier visual areas while later ones remained unaffected (Bles et al., 2006; Sabine Kastner & Ungerleider, 2001). However, when attention is directed to one of the two objects, the competition is biased towards the attended stimulus, and the neuronal response is the same as if the attended stimulus was presented alone (Kastner et al., 1998; Luck et al., 1997; Moran & Desimone, n.d.; Reynolds et al., 1999). Filtering of irrelevant stimuli also seem to be scaled to RF. Similar to competition effects, an fMRI study found that the reduction of the suppression by the allocation of attention is maximal in V4 and TEO (Bles et al., 2006). These data support the idea that competition from distracters may be resolved by filtering out irrelevant information, which is accomplished by counteracting the sensory suppressive interactions induced by nearby distracters.

1.1.2 Top-down control of attention

This far I have described the modulation of neural activity in the ventral stream when attention is directed to a stimulus, either in isolation or surrounded by competing stimuli. The described attentional effects in the ventral stream may be accomplished by feedback signals from later stages of processing, specifically, parietal and frontal areas, which are believed to be the sources of top-down signals. Cortical areas that have been systematically involved in attentional control are the Superior Parietal Lobe (SPL) , the intraparietal sulcus (IPS), the frontal eye field (FEF), the supplementary eye field (SEF), the prefrontal cortex (PFC) (Corbetta, Miezin, Shulman, & Petersen, 1993; Kastner et al., 1999) and the anterior cingulate cortex (Gitelman et al., 1999; a Nobre et al., 1997). Feedback anatomical connections of the frontal and parietal lobule with the ventral stream areas provides only indirect evidence about their role in the top-down attentional network. However, novel methodologies have offered direct evidence for frontal and parietal initiated top-down signals (B. T. Miller & D'Esposito, 2005). Neuroimaging studies have found that planned eye movements and covert orienting visuospatial attention share a common brain anatomical network (Beauchamp, Petit, Ellmore, Ingeholm, & Haxby, 2001; Corbetta et al., 1998; Nobre et al., 2000; Rizzolatti, Riggio, Dascola, & Umiltá, 1987). More recent studies have provided direct evidence of the involvement of oculomotor or gaze function´s anatomical structures in visuospatial attention. Specifically, there are several studies in which electrical microsimulation is applied to the FEF, showing that behavioural and physiological effects mimic voluntary attentional effects. Stimulating the FEF below the threshold to evoke a saccade, improves the monkey's sensitivity to detect changes in a stimulus located within the 'movement field', this is the region of space to which suprathreshold stimulation would have change monkey´s gaze (Moore & Fallah, 2001). Furthermore, FEF subthreshold stimulation causes attention-like effects in extrastriate cortex. Response of V4 neurons to a visual stimulus was enhanced when the FEF subthreshold stimulation overlapped the V4 neuron´s RF (Moore & Armstrong, 2003). FEF subthreshold stimulation has also been found to bias V4 neuronal activity towards the attended stimulus when two competing stimuli are presented within the neuron RF (Armstrong, Fitzgerald, & Moore, 2006). Further evidence for direct evidence of feedback from frontal cortex into extrastriate areas comes from a recent study (Gregoriou, Rossi, Ungerleider, & Desimone, 2014). In this experiment, the lateral PFC, including the FEF, was surgically removed in two macaques, leaving V4 without input from PFC in one hemisphere while the other remained intact. Attentional effects on V4 firing rates and gamma synchrony on the affected hemisphere were reduced, but not abolished, suggesting that the PFC is not the only source of top-down signals.

Communication between distant areas is thought to be facilitated by neuronal synchronization (Engel, Fries, & Singer, 2001; Engel, Kreiter, König, & Singer, 1991; Fries et al., 2008; Womelsdorf et al., 2007). Single unit activity recordings in monkeys have found that gamma coherence is enhanced between FEF and V4 with attention. Granger causality analysis of these data revealed that top-down influences from FEF to V4 predominated at the onset of spatially directed attention (Gregoriou, Gotts, Zhou, & Desimone, 2009a). Neural synchronization has also been found between lateral prefrontal cortex (lPFC), FEF and LIP, with attentional effects reflecting first in PFC (Buschman & Miller, 2007). The top-down influence of the parietal cortex on visual areas has been also investigated. In a study by Saalman et al., spike activity was measured in LIP and MT neurons, both exhibiting increased activity when attention was directed inside the RF. Enhanced coherence with attention was found in the gamma band between both areas. Critically, the onset of attentional effects was first seen in LIP, in accordance to its hypothesized role as a source of feedback to MT.

1.2 Neural correlates of visuospatial working memory

WM is a core cognitive process that underlies, and constrains, our ability to process information across cognitive domains. It underpins a range of behaviors as it make possible to coordinate processing when multiple goals are active and to guide behavior with information that is not present in the immediate environment. In the visual domain, WM enables us to form a representation of our surroundings, selectively preserving salient information over time (Baddeley, 2003; Sperling 1960) and across eye movements (Irwin, 1991), to guide efficient exploration of the environment (Soto, Humphreys, & Rotshtein, 2007).

Neural substrates of WM were first investigated in non-human primates. Pribram et al. (1964), based on lesional studies, were the first to suggest that the neural machinery supporting WM might include the PFC. Soon thereafter, recordings of single cell activity of dorsolateral PFC (DLPFC) of monkeys performing a delayed task, revealed sustained elevated firing rates of neurons in the cue target interval (Fuster & Alexander, 1971; Kubota & Niki, 1971). Moreover, it was shown that PFC neurons delayed activity was specific for determined locations of the visual field (Funahashi, Bruce, &

Goldman-Rakic, 1989; Niki & Watanabe, 1976) and for other stimulus properties, like luminance (Constantinidis, Franowicz, & Goldman-Rakic, 2001). Neuroimaging studies have also found sustained delay activity in the DLPC (Cohen et al., 1997; Courtney, Ungerleider, Keil, & Haxby, 1997). The finding of selective elevated firings rates to stimuli properties in the delay period and the fact that lesions of DLPFC impairs WM led to the formulation of an influential model of PFC cortex function in which it is believed to sustain a neural representation of sensory properties of the stimuli in WM (Goldman-Rakic, 1995), with different storages for each domain (Wilson, Scalaidhe, & Goldman-Rakic, 1993).

From an anatomical point of view, contrary to the prevailing view that PFC stores information, much recent work has provided mounting evidence in favor of sensory recruitment models of WM (Awh & Jonides, 2001; Jonides, Lacey, & Nee, 2015; Pasternak & Greenlee, 2005; Postle 2006). These models are based on the premise that the retention of information in WM is accomplished by the temporary enrollment of the same networks engage that process information during perception. Complementarily, the PFC, rather than storing information in WM itself, may be more important for biasing the salience of mnemonic representations, and allocating resources when the capacity limits of WM are taxed (Lara & Wallis, 2014). In visual object WM, sustained elevated firing rates have been observed during the delay period of IT neurons selective to the remembered object (Chelazzi, Duncan, Miller, & Desimone, 1998; Fuster & Jervey, 1981; Miller, Li, & Desimone, 1993). Similarly, neuroimaging studies have also identified sustained activity during maintenance of objects in IT (Courtney et al., 1997; Postle & Druzgal, 2003). Furthermore, several studies have reported category specific activity in the temporal lobe. Thus, fusiform face area (FFA) and parahippocampal place area (PPA), exhibit specific delayed activity for faces and for scenes respectively (Postle & Druzgal, 2003; Ranganath, DeGutis, & D’Esposito, 2004). In the spatial domain, an attention based rehearsal mechanism is hypothesized to support the maintenance of spatial information (Edward Awh & Jonides, 2001). On the one hand, the anatomical structures involved in spatial WM overlap with those found in the control of selective spatial attention. FEF and posterior parietal cortex (PPC) activations have been found in several neuroimaging studies (Corbetta, Kincade, & Shulman, 2002; Curtis, Rao, & D’Esposito, 2004; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002; Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000). On the other hand, the modulation of early visual areas by selective attention has also been demonstrated during the maintenance of locations in memory (Postle,Awh, Jonides, Smith, & D’Esposito, 2004). Contralateral sustained activity to the memorized location has been found in visual areas (Awh et al., 1999), as well as similar ERP modulations of the P1 and N1 components to those found in spatial selective attention (Awh, Anllo-Vento, & Hillyard, 2000). More compelling evidence supporting sensory recruitment models derives from neuroimaging and neurophysiology research applying multivariate pattern analysis (MVPA). While univariate analysis only takes into account activity in a single neuron or single voxel or electrode, multivariate methods consider activity distributed across neural population to identify a pattern associated with the encoded information (for a review see Sreenivasan, Curtis, & D'Esposito, 2014). Following this approach it has been possible to demonstrate that early visual areas, including V1, can retain specific features held in WM. For example, Harrison and Tong (2009) were able to predict which orientation from two gratings was being maintained in the delay period, from the pattern of activity from V1 to V4. Different stimulus properties of the remembered object have been also decoded from early visual areas, such as color (Serences, Ester, Vogel, & Awh, 2009), contrast (Xing, Ledgeway, McGraw, & Schluppeck, 2013) and motion (Riggall & Postle, 2012). Crucially, the sustained activation patterns were similar to those evoked by bottom-up stimulation, which suggest that early visual areas are recruited to maintain a "copy" of the perceived stimulus (Albers, Kok, Toni, Dijkerman, & De Lange, 2013; Serences et al., 2009). Similarly, consistent with research that posit a role of temporal cortex in WM (Ranganath et al., 2004), category specific information of faces or scenes have been decoded from the ventral occipitotemporal cortex (Han, Berg, Oh, Samaras, & Leung, 2013; Sreenivasan, Gratton, Vytlacil, & D'Esposito, 2014b). Moreover, the quality of sensory representations has been functionally related to WM performance (Emrich, Riggall, Larocque, & Postle, 2013; Ester, Anderson, Serences, & Awh, 2013). In one study the dispersion of the orientation selective patterns in early visual areas correlated with participant´s accuracy (Ester et al., 2013). In the other study the motion classification declined as a function of load and correlated with participant´s accuracy. Although these results provide strong evidence that sustained patterns of activity in early visual cortex may represent the neural correlate of VWM they do not provide a causal link between sensory representation and performance. This question has been addressed in a transcranial magnetic stimulation (TMS) study, in which the delivery of a pulse over the contralateral visual cortex during the maintenance of the target stimulus impaired memory performance (van de Ven, Jacobs, & Sack, 2012).

In recent years, the MVPA studies have questioned the relation between persistent delay activity and its role in memory storage. On one hand, sustained specific stimulus patterns in visual areas have been found in absence of above baseline persistent activity in those areas (Emrich et al., 2013; Harrison & Tong, 2009; Riggall & Postle, 2012;

Serences et al., 2009). On the other hand, it has not been possible to decode specific stimulus properties from sustained elevated activity in frontal and parietal areas (Lee, Kravitz, & Baker, 2013; Riggall & Postle, 2012). In Lee study, perceptual identity was decoded from ventral occipitotemporal cortex, while category identity was decoded in DLPF. The study of Rigall had a similar finding: while perceptual properties, like direction and motion, were decoded in extrastriate areas, frontal regions represented more abstract information of the type that was important for the trial, that is, motion or direction. In accordance to these findings, the PFC would be more involved in maintaining task rules, goals or category information as well as in attentional demands of the (Lara & Wallis, 2014; Lebedev, Messinger, Kralik, & Wise, 2004; Magen, Emmanouil, McMains, Kastner, & Treisman, 2009; Mitchell & Cusack, 2008), rather than in the storage of sensory information. This is in line with models that posit that the main role of PFC is to influence posterior areas representing information (Curtis, 2006; Petrides, 2000; Postle 2006; Ruchkin, Grafman, Cameron, & Berndt, 2003), enhancing memory representation, filtering distraction and controlling memory rehearsal.

1.2.1 Working memory capacity

Limited capacity is one of the main hallmarks of WM. The study of visual WM (VWM) has put forward that both the quantity and quality of the representations that are stored in WM are limited. Following the pioneering work of Luck and Vogel (1997), much effort has been devoted to elucidate the nature and the neural correlates of that limitation. Two types of model have been proposed to explain the nature of VWM constraints. The 'slots models' assume that capacity is fixed and limited to a determined number of objects, usually to 3 or 4 (Luck & Vogel, 2013). These models found support from imaging studies claiming to show plateaus in the activation function at a particular set size. These models are usually based on findings using the change-detection paradigm with discrete stimulus set. However, when memory is tested by recall instead of recognition, the precision of each item can be tested individually. Using this procedure, the 'resources models' have found that as the number of items remembered increases, the precision with which each one is remembered decreases (Bays & Husain, 2008). Such a limited resource account of WM representations is based on the principle that memory representations are noisy, and get noisier with increasing memory load (Bays & Husain, 2008; Carrasco, 2012; Palmer, 1990; Salmela, Lähde, & Saarinen, 2012; Wilken & Ma, 2004). This has led to formulate that VWM capacity is a single and flexible attentional resource that can

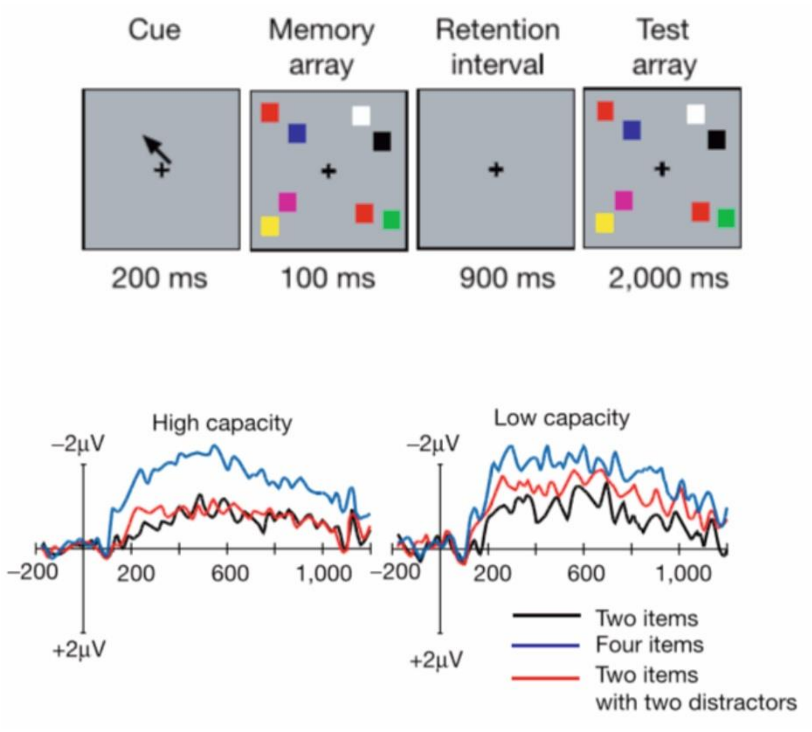

Figure 2. Contralateral delay activity. On the top: Color change-detection paradigm. Subjects are instructed to remember the colors of the items on the cued side and report whether a color has changed on that side in the test array. On the bottom: Grand averaged ERP difference waves (contralateral activity minus ipsilateral activity relative to the side of the array that was encoded into memory) averaged across posterior electrode sites. Time zero is the onset of the test array. Waveforms are differentially depicted for the high and low memory capacity groups (Vogel et al., 2005)

be distributed among the whole set size, reducing the precision for individual items as more items have to be maintained (Ma, Husain, & Bays, 2014). However, "hybrid models" propose that VWM is constrained by both the number of items and the precision with which they are retained. When small number of items have to be retained it is possible to allocate flexible resources between them (Alvarez & Cavanagh, 2008; Machizawa, Goh, & Driver, 2012; Zhang & Luck, 2008). Currently, there is general agreement that WM is a flexibly allocated resource of limited capacity (Brady, Konkle, & Alvarez, 2011). Neuroimaging studies searching for the neural basis of VWM capacity have identified PFC and PPC to correlate with load (Linden et al.,

2003; Todd & Marois, 2004; Xu & Chun, 2006), whereas EEG research have identified an ERP component that index item maintenance. This component known as Contralateral Delay Activity (CDA), also called the sustained posterior contralateral negativity (SPCN; Jolicoeur, Brisson, & Robitaille, 2008; Wiegand et al., 2014), increases gradually with the number of objects maintained in WM, reaching an asymptotic level when participants approach their individual WM capacity limit (typically three to four items) (Luck & Vogel, 2013) (figure 2). It appears as a sustained negative voltage deflection contralateral to the side of the pre-cued hemifield over posterior scalp sites (Anderson, Vogel, & Awh, 2011; Vogel & Machizawa, 2004). It has been localized to the ventral extrastriate and parietal cortex (Becke, Müller, Vellage, Schoenfeld, & Hopf, 2015).
This discovery accommodates well with slot models, however, not only the quantity of information may affect CDA amplitude. Quality of the representations also affects the CDA that was found to be higher for fine precision items than for the low precision ones when load was preserved constant (Machizawa et al., 2012).

However, as previously exposed, recent work has challenged one of the most pervasive findings in WM literature: the suprathreshold persistent activity as a neural correlate of WM storage (Sreenivasan, Curtis, et al., 2014). Applying MVPA, it was found that classification accuracy in sensory cortex decreases with WM load and that the precision of recall was correlated with decoding sensitivity (Emrich et al., 2013). This finding sums evidence to pure 'resources models' or 'hybrid models', demonstrating that as memory load increases less resources are available for individual items, resulting in less signal contained in the neuronal patterns representing that item. Crucially, it was only possible to decode memory representations from sensory cortex, which did not show elevated delay activity, and was not possible to decode memory representations from PPC which in turn did show elevated activity. In this context, load sensitivity signals in PPC and lateral PFC (lPFC) have been interpreted as reflecting attentional resources devoted to neural representations, and not as the maintenance of information per se (Ma et al., 2014).

1.2.2 Top-down modulation in working memory

Given the limited capacity of WM, neural coding of sensory representations should prioritize task-relevant over task-irrelevant information. This goal can be achieved by balancing the demands of top-down and bottom-up factors, which is accomplished by selective attention operating in different stages of WM. The top-down mechanisms associated with orienting attention during the preparatory phase, encoding and maintenance of a memory task resemble those described in experiments of selective attention in the perceptual domain and have been shown to modulate activity in sensory cortices and in top-down control exerting areas like the PFC and the PPC (Gazzaley & Nobre, 2012).

In this way, a cue given prior to the appearance of the memory array can improve performance in the same way as a cue given before the target in a perceptual task (Bollinger, Rubens, Zanto, & Gazzaley, 2010; Griffin & Nobre, 2003; Murray, 2008; Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005). As in the perceptual domain, selective attention to the to-be-remembered items modulates activity in the cue-stimulus period. An EEG study by Murray et al (2008) found that the ERP markers of spatial preparatory attention, EDAN and the anterior directing attention negativity (ADAN), correlated with WM performance; this is, participants with larger ERPs effects presented greater cue benefits. The probability of encoding only the relevant items was increased by selective attentional processes manifested in the modulation of ERPs markers of preparatory attention (Murray, 2008). Additionally, an fMRI study investigated the attentional network in the expectation period of complex stimuli. FFA activity was increased when the cue predicted that category faces compared to the neutral condition in which participants did not know whether faces or scenes were going to be presented. Top-down control from a frontoparietal attention network was further investigated using functional connectivity. The analysis showed that FFA activity following the presentation of the valid cued correlated with the degree of functional connectivity between FFA, various regions of PFC and IPS (Bollinger et al., 2010).

Visual activity is also modulated by selective attention during the encoding phase of VWM, as shown by an enhancement in areas representing the relevant stimulus for the task and suppression of activity of irrelevant stimulus (Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005). Experiments studying the temporal modulation of visual activity have revealed that the modulation of early components associated with selective attention, P1 and N1, correlates with WM performance (Rutman, Clapp, Chadick, & Gazzaley, 2009; Zanto & Gazzaley, 2009). Moreover, WM performance has been linked to the efficient filtering of irrelevant information. In one study, visual activity modulation was only seen during high performance trials and the absence of modulation in the low performance trials was explained as an improper allocation of attention to irrelevant stimuli (Zanto & Gazzaley, 2009). Complementarily, Vogel et al (2005), found that WM capacity was associated with selective attention. Using CDA as an index of items being maintained in WM, showed that while high capacity individuals processed only the relevant items, low capacity participants processed relevant and irrelevant ones, (figure 2. Vogel et al., 2005), thus indicating less effective distractor-filtering (see also McNab & Dolan, 2014).

Functional connectivity analysis of neuroimaging data have identified the inferior frontal junction (IFG), a region in the PFC, as a source of top-down control of selective attention to visual features (Zanto, Rubens, Bollinger, & Gazzaley, 2010). The casual role of PFC in generating visual modulation was tested in a subsequent study (Zanto, Rubens, Thangavel, & Gazzaley, 2011). PFC function was disrupted applying repetitive transcranial magnetic stimulation (rTMS) to the right IFJ during 10 min before the start of each block. The experimenters found that early visual modulation, P1, declined as it did WM performance. Crucially, as the P1 recovered with time, performance improved as well. Furthermore, accuracy could be predicted on the basis of the induced rTMS P1 modulation. These findings led the authors to conclude that top-down modulation of posterior early processing is causally related to WM performance.

Performance on a WM task significantly rests on the ability to bridge the temporal gap between the sample and the subsequent contingent response. As recent perspectives of VWM consider that PFC neurons do not encode nor maintain sensory information, a function attributed to PFC signals is to be a top-down attentional mechanism that helps prioritize processing to certain items in the visual field. Thus, recent neural models of short term retention of information hypothesize that the conscious maintenance of information is mediated by the top-down influence of the PFC over posterior cortices (Awh et al., 2000; Awh & Jonides, 2001; Postle 2006; Ruchkin et al., 2003). In this view, the short term memory storage is supported by the same structures in which information was initially processed and is sustained during the delay period by attentional control from PFC. In this line, recent theoretical formulations of WM (the *state-base* models), propose that short term retention of information is mediated by the allocation of attention to long-term memory representations (Cowan, 2001; Larocque, Lewis-Peacock, & Postle, 2014; McElree, 2001). Long-term memory and short-term memory are conceptualized as different states of the same representation. These models agree in that there is a representational state in which an item (or items) is highly prioritized by focused attention over other items maintained in WM. Thus, the item in the focus of attention (FoA) is accessed more accurately and faster than the other items in a different representational state. The critical point of state-based models is that they make a clear differentiation between retention of information, in any of the activated long term memory states, from attention to representations, which is capacity limited and can be only directed to a small subset of representations. From a neural perspective, it is hypothesized that univariate recording results, in which sustained delay activity is assumed to be the mechanism of short-term retention, might have confounded memory with attention, as the to-be remembered information is usually the most relevant one, and for that reason is probably maintained inside the FoA. Studies incorporating the use of MVPC demonstrated that not all items in short-term memory could be detected in the delay period activity. Only information about the item inside the FoA could be extracted from the delay activity (LaRocque, Lewis-Peacock, Drysdale, Oberauer, & Postle, 2013; Lewis-Peacock & Postle, 2012), demonstrating that information is maintained in different representational states and that delay neural activity only contains activity about the information in the FoA. More compelling evidence for different representational states comes from two TMS studies (Zokaei, Manohar, Husain, & Feredoes, 2013; Nahid Zokaei, Ning, Manohar, Feredoes, & Husain, 2014). In these experiments, TMS was applied to MT+ during the retention of two motion direction memory targets, in which only one was maintained in a privileged state. The results showed that only the prioritized item was negatively affected by TMS disruption.

Another crucial aspect of this WM conceptualization is that information can flexibly move in and out of the FoA, permitting behavior to adapt to dynamic changing goals. An experimental manipulation to move an item inside or outside the FoA is the use of a retro-cue. In this experimental paradigm participants first encode items into VWM, followed by a retention interval. During this delay, participants are cued (most often an arrow) to the spatial location of an item of the array of stimuli that was the upcoming test item, probed via change detection (Griffin & Nobre, 2003) (figure 3). Participants responded faster and more accurate to a target that was cued compared to neutral cues in which no spatial information was provided to the participants. This robust effect consistently reveals a performance benefit of 5-15 % in recognition probes using various stimuli. Of importance, the delay interval between stimulus offset and retro-cue onset is at least 900 ms, thus, long after the iconic image of these objects had faded (~500 ms; Sperling, 1960). The beneficial effect of the retro-cues could be could be explained by considering the reallocation of attentional resources within the memory space, resulting in the protection of the cued representation from memory-related degradation processes such as decay, or possible interferences by other representations; the so-called ‘protection hypothesis’ (Makovsik & Jiang, 2007; Matsukura, Luck, & Vecera, 2007; Pertzov, Bays, Joseph, & Husain, 2013). Alternatively, although not mutually exclusive, it has been proposed that by focusing attention on the cued representation, participants actively remove the non-cued irrelevant items from memory, since they are going to be tested, therefore presumably reducing the interitem interference and competition for resources; the so-called ‘removal hypothesis’ (Kuo, Stokes, & Nobre, 2012; Souza, Rerko, & Oberauer, 2014; Williams & Woodman, 2012; Woodman, Vogel, & Luck, 2012).

Experiments using this procedure obtain higher accuracy and reaction times (RTs) for the cued item and thus, demonstrate that is possible to allocate selective attention to representations held in WM (Astle, Scerif, Kuo, & Nobre, 2009; Berryhill, Richmond, Shay, & Olson, 2012; Griffin & Nobre, 2003; Lepsien & Nobre, 2007; Lepsien, Thornton, & Nobre, 2011; Makovsik & Jiang, 2007; Matsukura et al., 2007; Pertzov et al., 2013; Sligte, Scholte, & Lamme, 2008). The allocation of selective attention to the contents of WM trigger top-down processes similar to those described for the perceptual domain. In the pioneer study by Griffin and Nobre (2003), orienting attention to mental representations was compared to orienting attention to spatial locations in the perceptual domain (figure 3).

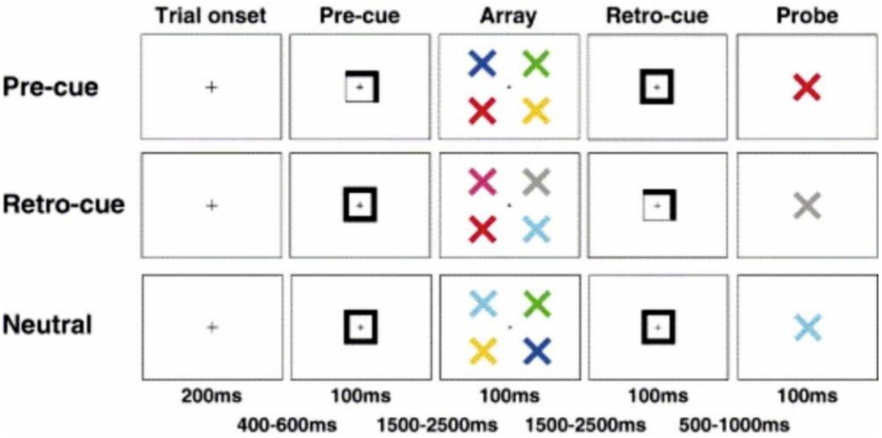

Figure 3. Retro-cue paradigm. This figure shows the experimental conditions of the Retro-cueing paradigm used in the study by Griffin and Nobre (2003). Participants were shown a memory array of four colored crosses (100 ms) and after a delay of 2,000–3,500 ms responded according to whether a central probe stimulus had been present in the array (50% probability). All trials contained a pre-cue (100 ms), a retro-cue (100 ms), and a neutral cue (100 ms). In pre-cue trials, the spatially informative orienting cue (80% validity) was presented before the stimulus array. In retro-cue trials, the spatially informative orienting cue (80% validity) was presented after the stimulus array. In neutral trials, there was no spatially informative orienting cue.

At a behavioral level, the pre-cue and retro-cue tasks presented similar levels of performance. Comparison of electroencephalographic activity elicited by pre-cues and retro-cues revealed similar modulatory activity as well as some differences. Orienting attention in advance (pre-cue) and after the memory array (retro-cue) resulted in an early contralateral deflection in occipital electrodes, which has been previously associated with the initial stages of attentional orientation (Nobre et al., 2000). An additional common neural signature to both processes is a late positive deflection over frontal sites. However, retro-cues selectively modulated neural activity over frontal electrodes between 120 and 200 ms, an activity that has not been usually reported in attention to external stimuli studies. Complementary to the analysis of the cue related activity, another experiment compared the delay period activity elicited by pre-cues and retro-cues (Eimer & Kiss, 2010). In this study, a cue, either before or after stimuli encoding, indicated the relevant hemifield for the task. As in previous WM studies a sustained posterior contralateral negativity (CDA) to the maintained hemifield was found in the pre-cue condition. Importantly, the CDA was also modulated after the presentation of the retro-cue. Additionally, WM experiments typically show that CDA increases with set size (Vogel & Machizawa, 2004; Vogel et al., 2005). Consistent with the hypothesis that retro-cues trigger top-down mechanisms that modulate delay period neural activity, a reduction in the magnitude of the CDA was found after the retro-cue, reflecting a reduction in memory load (Kuo et al., 2012). Further support to the flexible allocation of attentional resources to internal representations in a retinotopically specific manner comes from an fMRI experiment (Munneke, Belopolsky, & Theeuwes, 2012). In this study, BOLD magnitude in early visual areas (V1-V3) reflected the location being maintained in the FoA. When attention was switched away from a relevant item, activity coding for that location decreased whereas activity coding for the new relevant item increased. Similar to spatial-based attention retro-cue studies, modulatory activity in posterior regions has been also studied in relation to internal attention to objects maintained in WM (Lepsien & Nobre, 2007; Lepsien et al., 2011). Specifically, retro-cues presented during the delay period directed attention selectively to either a scene or a face being held in WM. The fMRI results showed a modulation in areas coding for specific objects. When attention was directed toward the representation of a face an activity increased was seen in FG, while orienting toward the representation of a scene increased activity in the PHG (Lepsien & Nobre, 2007). In a later experiment, the ratio of relevant/irrelevant objects was manipulated to further investigate load dependent changes after the cue (Lepsien et al., 2011). Regions in the PFC and the PPC showed a modulation of activity dependent of the number of items selected after the cue. Specifically, another study showed a reduction of load related activity in the right anterior IPS (Trapp & Lepsien, 2012), which could reflect changes in attentional demands (Magen et al., 2009).

Neuroimaging studies have also been interested on the neural structures coordinating spatial attention to internal representations. When pre-cue and retro-cue conditions were compared, an overlapping fronto-parietal network, previously identified in external attention experiments, was found for both conditions (Nobre et al., 2004). However, right prefrontal activity was selectively enhanced in the retro-cue condition. The differential contribution of this structure in external vs internal shifts of spatial attention was investigated in a TMS experiment (Tanoue, Jones, Peterson, & Berryhill, 2013). Setting a transient virtual lesion at the prefrontal site resulted in a more accentuated impairment of performance in the retro-cue task compared to the pre-cue task, demonstrating greater enrollment of PFC in internal shifts of attention vs external shifts. Several hypothesis were proposed to explain this divergence. It is possible that these prefrontal regions are involved in orienting attention in a mnemonic context. An alternative is that it might be involved in the selection of the relevant item among distractors. This last hypothesis could be related to a TMS-fMRI experiment that found that DLPF-TMS administration during the maintenance period enhances posterior neural activity associated with the relevant items being maintained in WM only when distractors irrupted during the delay (Feredoes, Heinen, Weiskopf, Ruff, & Driver, 2011). Taken together, PFC activity associated to retro-cued oriented attention might be related to the neural enhancement of the prioritized item.

1.3 Alpha and gamma oscillations related to visuospatial attention and visual working memory

Brain operations, such as memory and attention, arise from the activity of groups of interconnected neurons in a localized volume of cortical tissue forming assemblies and networks. Excitatory and inhibitory cell activity can lead the neural network to oscillate at a certain frequency. Crucially, a mesoscopic variable that is relatively easy to record are the oscillations of LFP and the EEG, which reflects coordinated transmembrane currents summed across nearby neurons. Despite the fact that any transmembrane current, irrespective of its origin, contributes to the LFP (this is extracellular voltage deflection), it is believed that it primarily reflects the weighted sum of transmembrane currents of a large group of neurons arising from synchronized postsynaptic potentials. The synchronous oscillations of an ensemble of neurons recorded by the LFP revealed a tight correlation to the rhythmic firing pattern of the involved neurons (Gray & Singer, 1989; Lakatos et al., 2005), hence, reflecting cyclical changes of excitability in cortical ensembles. Therefore, neural synchronization affects efficacy of neurons' spike output, this is, the efficient summation of postsynaptic potentials, but also the sensitivity to neural input (Salinas 2001). Because oscillatory activity reflects shifts between depolarized and hyperpolarized states in the local neural ensemble, the momentary phase at which an input arrives will determine whether it is attenuated or amplified (Tiesinga, Fellous, Salinas, José, & Sejnowski). If both, output and input, are in the same excitability peak, they are in an optimal temporal window to communicate, what it has been called 'communication through coherence' and implies phase-locking between the oscillatory neuronal groups (Bosman et al., 2012; Fries, 2005; Womelsdorf et al., 2007).

1.3.1 Gamma band oscillations

As previously pointed out, the temporal coordination of activity in a source population has been suggested to determine corticocortical signaling efficacy. Temporally coordinated input can facilitate the transmission and integration of information within neurons. Postsynaptic potentials only summate effectively in the postsynaptic neuron when they arrive with a difference in the millisecond range. Inputs arriving at the same time would trigger rapid depolarizations which are more effective in eliciting action potentials. A mechanism proposed to achieve such temporal coincidence is the synchronization of the presynaptic neurons in the gamma-band (Fries, Schröder, Roelfsema, Singer, & Engel, 2002; Womelsdorf et al., 2006). Gamma synchronization would lead the presynaptic neurons to concentrate their spikes in between 12 ms and 6 ms (half a cycle of 40-80 Hz), which would establish an optimal time window to the effective summation of the postsynaptic potentials. Therefore, gamma-band synchronization has been proposed to have an important role in neural communication. Gamma oscillations are believed to result from the synchronous activity of fast-spiking inhibitory interneurons. The gamma synchrony is then established by the narrow window for effective excitation imposed by the rhythmic inhibition (Cardin et al., 2009). One of the first demonstrations to link oscillatory gamma synchronization to cognitive function relates to the "binding problem". The binding problem refers to how the brain accomplish the transient association of different cortical regions processing different features to form a coherent percept. A time-based coding model was proposed to overcome the binding problem (von der Malsburg, 1995). The model proposed that distributed neurons representing different object attributes are bound together by the synchronization of their action potential to form a functional neural assembly. Specifically, evidence from animal experiments showed that neurons representing specific features synchronized their responses to the oscillatory gamma cycle (Eckhorn et al., 1988; Gray & Singer, 1989). The role of gamma activity in feature binding has been also investigated in humans, extending its role to object representation (Catherine Tallon-Baudry & Bertrand, 1999). Induced gamma enhancement was found when subjects viewed coherent stimulus in comparison to incoherent stimulus (Keil, Müller, Ray, Gruber, & Elbert, 1999; Moratti, Méndez-Bértolo, Del-Pozo, & Strange, 2014; Müller et al., 1996; Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1996). Thus, when two stimuli share the same physical properties, gamma activity is only strengthen in the condition where subjects perceive a coherent objet. These studies provided experimental evidence that gamma synchrony could provide the mechanism for binding different neuronal groups into a coherent assembly.

Beyond simple perceptual tasks involving bottom-up processes, gamma band synchronization has been related to top-down modulation of sensory processing, being specifically involved in selective attention and WM. It has been proposed that gain control by gamma synchronization might underlie selective attention (Fries et al., 2001; Fries et al., 2008; Womelsdorf et al., 2006). As previously explained, gamma synchronization of the presynaptic neurons make greater impact on their postsynaptic target, which increases the effective synaptic gain (Salinas & Sejnowski, 2001). Thus, it has been hypothesized that, even when attention does not lead to changes in firing rates, for example with high contrast stimulus, enhanced gamma synchronization of presynaptic neurons might lead to prominent changes in firing-rates in downstream areas. Indeed, several animal studies have found gamma enhancement selective to the attended stimulus (Bichot, Rossi, & Desimone, 2005; Fries et al., 2001; Fries et al., 2008; Taylor et al., 2005; Womelsdorf et al., 2006). Specifically, recordings from area V4 revealed that neurons with RFs overlapping with the attended stimulus synchronize their spikes more strongly with the LFP gamma oscillation in comparison to neurons activated by distracters (Engel et al., 2001). Moreover, RTs to a change detection stimulus were shorter when neurons representing the attended stimuli had a strong synchronization with the gamma LFP (Womelsdorf et al., 2006). In addition to spike-LFP synchronization, gamma power recorded in the LFP also reflects the spatial focus of attention (Fries et al., 2001; Taylor et al., 2005). However, these measures only provide indirect evidence about the spike output form the recorded visual area. In a following work, direct assessment of neural output was studied. Spike to spike coherence revealed enhanced gamma band synchronization of spike trains to the attended stimulus (Fries et al., 2008). Enhancement of synaptic gain of the attended stimulus might not be only mediated by synchronization of neural output, but also by the selective synchronization with its postsynaptic target neurons (Fries 2005). To test this hypothesis, Bosman et al. (2012) recorded LFP in monkey's area V1 and V4. Two stimuli activated distinct sites of V1 but both activated the same place in V4. When both stimuli were presented, only the attended one enhanced gamma synchronization between V1 and V4. Gamma phase coherence has also been found between more distant parts of the cortex. Specifically, coherence between FEF and V4 was also reported to be modulated with spatial attention (Gregoriou et al., 2009a). These findings provide compelling evidence to the CTC model that postulates that effective connectivity is mediated by phase synchronization of input and target groups of neurons.

Attention dependent modulation of gamma band synchronization has been also reported in the human literature. In a series of studies, gamma power modulation with spatial attention was demonstrated with M/EEG recordings (Bauer et al., 2012; Gruber, Müller, Keil, & Elbert, 1999; Müller, Gruber, & Keil, 2000; Siegel, Donner, Oostenveld, Fries, & Engel, 2008; Sokolov et al., 1999). Attending to a lateralized stimulus resulted in a contralateral gamma increased over occipital electrodes, relative to the ipsilateral activity elicited by the unattended stimulus. As in the animal study by Wolmelsdorf et al. (2006), the strength of gamma activity over the occipital cortex during a change detection task, predicted RTs to report the change (Hoogenboom, Schoffelen, Oostenveld, & Fries, 2010). Large-scale gamma phase synchronization is also found to be modulated by spatial attention (Doesburg, Roggeveen, Kitajo, & Ward, 2008; Siegel et al., 2008). Increased phase coherence in the gamma band was found between visual areas processing the attended stimulus and the top-down control areas PPC and FEF (Siegel et al., 2008).

Besides mediating the formation of a coherent representation of an object built from the sensory input by bottom-up processes (feature binding) or representation enhancement by the allocation of top-down resources, gamma activity has also been related to maintenance of object representations in WM. (Jokisch & Jensen, 2007; Pesaran, Pezaris, Sahani, Mitra, & Andersen, 2002; Tallon-Baudry, Bertrand, Peronnet, & Pernier, 1998). Following the hypothesis that internal representations are maintained in the sensory cortices where they were encoded, maintenance of object representations would depend on the synchronous activity of the neuronal ensemble representing that object. Indeed, gamma enhancement over temporo-occipital electrodes was seen when participants had to maintain abstract shapes (Tallon-Baudry et al., 1998), or over dorsal electrodes when the orientation of a stimulus had to be retained (Jokisch & Jensen, 2007). Intracranial recordings from epileptic patients have also revealed a gamma modulation with WM load (Howard et al., 2003). An influential model of WM postulates a pivotal role of gamma oscillations in maintaining multiple items in WM (Lisman & Idart, 1995). In this model, each item is codified by a neural assembly synchronized in the gamma range. Then, each item represented by a gamma cycle is bound to a consecutive theta phase, thus allowing a defined order. The factors that contribute to this mechanism might imply that power changes in high-oscillations would be affected by the fluctuations of membrane potentials of the low-frequency oscillations. Supporting human evidence for this model comes from an iEEG study that found cross frequency coupling of gamma amplitude to the theta phase modulation with WM load in the human hippocampus (Axmacher et al., 2010). However, another human study that found theta phase locked gamma amplitude in the occipital cortex during the retention period did not find a load dependent modulation (Sauseng et al., 2009). Subsequent analysis demonstrated that memory load modulated theta-gamma phase coupling, which might provide high temporal precision for representing non-interfering multiple items in WM. It has been proposed that similar to the role of theta coordinating sequential representation, alpha oscillations might have a similar role in coordinating spatial neural representations by a release of inhibition in each alpha cycle (Bonnefond & Jensen, 2015; Jensen, Gips, Bergmann, & Bonnefond, 2014).

1.3.2 Alpha band oscillations

Although initially proposed to underlie an idling or resting state (Pfurtscheller, Stancák, & Neuper, 1996), converging electrophysiological evidence points toward a functional role of alpha oscillations in active inhibition (Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007) or in neural processing (Palva & Palva, 2007). Alpha oscillations, as other frequency oscillations, reflect cyclical changes of neural excitability. Accordingly, it has been assumed that high alpha amplitude (synchronized alpha) reflects a state of inhibition, while low alpha amplitude (desynchronized alpha) reflects a high excitable state (Klimesch et al., 2007). In fact, it has been demonstrated that during periods of low alpha, neuronal firing rate is increased, whereas in periods of high alpha, firing is prevented in a phasic manner, which implies that spikes are more likely to happen at the trough than at the peak of the cycle and therefore neuronal firing is phase synchronized to the alpha cycle (S. Haegens, Nacher, Luna, Romo, & Jensen, 2011). Moreover, gamma power, which is associated to neural processing, has been shown to be anti-correlated to alpha power (Fries et al., 2008; Haegens, Osipova, Oostenveld, & Jensen, 2010; Jokisch & Jensen, 2007; Spaak, Bonnefond, Maier, Leopold, & Jensen, 2012). When alpha power is low enough, gamma can synchronize during the whole cycle of alpha. Nevertheless, when alpha power increases, gamma bursts can only occur at phases of low inhibition (i.e. the trough) (Bonnefond & Jensen, 2015; Osipova, Hermes, & Jensen, 2008; Voytek et al., 2010) (figure 4).

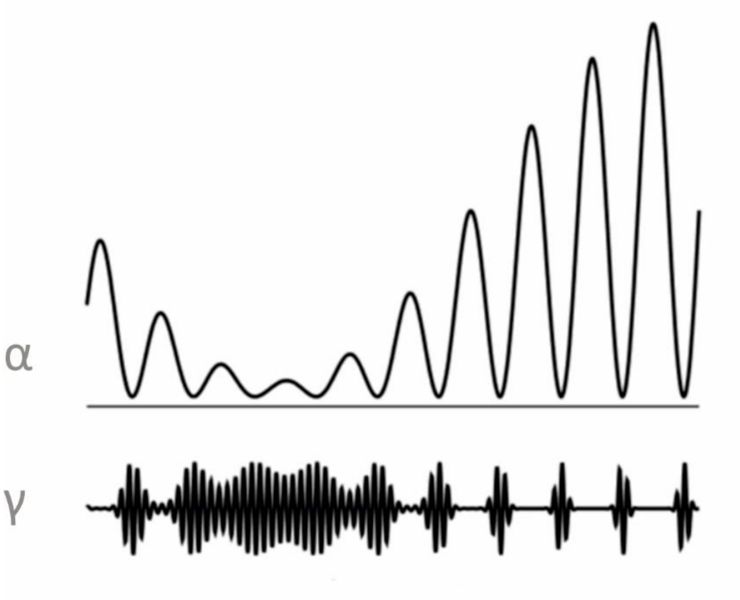

Figure 4. Modulation of gamma amplitude through the phase of alpha oscillations. Gamma bursts can synchronize continuously when alpha amplitude is low. However, strong alpha will break the duty cycle of gamma oscillations, and gamma bursts will only occur near the peak of excitability (i.e. trough)

The functional inhibitory role of alpha in neural processing has been expounded in two influential models of alpha oscillatory activity in cognitive neuroscience: the inhibitory-timing hypothesis (Klimesch et al., 2007; Klimesch, 2012) and the gating by inhibition hypothesis (Jensen & Mazaheri, 2010; Mazaheri & Jensen, 2010).There is now extensive experimental evidence supporting the inhibitory nature of alpha activity. One of the first evidences describing alpha-band oscillations as a mechanism mediating selective suppression of distracting information comes from an intersensory attention experiment (Foxe, Simpson, & Ahlfors, 1998). In the study, participants were cued to attend either the visual or auditory part of a stimulus. The cue-stimulus period was characterized by larger parieto-occipital alpha when participants were cued to attend the auditory modality than when they had to attend the visual modality. The authors interpreted the alpha enhancement as a mechanism by which visual space could be selective inhibited when task irrelevant, and proposed that this alpha-gating mechanism should occur in cortices that are likely to process distractors. This prediction was further tested in a visuo-spatial cueing study (Worden, Foxe, Wang, & Simpson, 2000), which propitiated a large amount of studies replicating and extending the results. In Worden's experiment, participants were instructed with a centrally presented arrow cue to attend to one of the four quadrants of the visual field. Participants were requested to make a judgment about the stimulus appearing only in the attended location, and to ignore the stimulus in the non-cued locations. Compellingly, they found that covert shifts of attention induced focal increases of alpha power contralateral to the ignored hemifield in the prestimulus period. Additionally, alpha increases were also topographic organized respect to the upper or lower quadrant. This finding has been replicated in other studies (Kelly, Lalor, Reilly, & Foxe, 2006; Rihs, Michel, & Thut, 2007). However, other experiments have found that covert shifts of attention induced the inverse mechanism, which implies a contralateral desynchronization of alpha to the attended hemifield, (Kelly, Gomez-Ramirez, & Foxe, 2009; Sauseng et al., 2005b; Thut et al., 2006; Yamagishi, Goda, Callan, Anderson, & Kawato, 2005). Alpha desynchronization to the contralateral attended hemifield has been interpreted as a release of inhibition leading to increased cortical excitation. In fact, it has been shown that performance in a perception task is inversely related to the prestimulus alpha amplitude. Thus, correct performance was preceded by low prestimulus alpha power (Hanslmayr et al., 2005, 2007). Both mechanisms, synchronization and desynchronization of alpha during covert shifts of attention, have been shown to coexist in other studies (Capilla et al., 2014; Doesburg, Green, McDonald, & Ward, 2009; Rihs, Michel, & Thut, 2009). The degree of alpha-band amplitude lateralization in anticipation to a stimulus has been shown to predict performance (Capilla et al., 2014; Gould, Rushworth, & Nobre, 2011a; Haegens, Händel, & Jensen, 2011; Kelly et al., 2009; Thut et al., 2006). Mainly, performance was shown to be inversely related to the amplitude of contralateral alpha desynchronization. Alpha band lateralization has been also found in the delay period of WM tasks, using Vogel´s paradigm (Grimault et al., 2009; Sauseng et al., 2009). In neither study contralateral alpha desynchronization was load modulated. Nevertheless, Sauseng et al found that ipsilateral synchronization was related to the number of items that had to be ignored. Another WM study had similar findings, demonstrating that alpha power in anticipation of a distracter can be predictor of performance (see also Bonnefond & Jensen, 2012). These findings add evidence to the proposed role of alpha in functional inhibition. Furthermore, they found that entrainment of alpha frequency in ipsilateral sites, by application of 10 Hz rTMS, increased memory capacity, whereas application to the contralateral hemisphere decreased memory capacity (Sauseng et al., 2009). This is consistent with the discovery that alpha entrainment impairs perception in the contralateral stimulated hemifield, but improves detection in the ipsilateral (Romei, Gross, & Thut, 2010).

A fundamental piece of evidence supporting the functional role of alpha in inhibiting irrelevant information has been brought about by WM experiments. It has been shown that alpha activity increases as a function of memory load during the short term retention of information (Busch & Herrmann, 2003; Jensen, Gelfand, Kounios, & Lisman, 2002; Scheeringa et al., 2009; Tuladhar et al., 2007). The data were explained in terms of disengagement of posterior areas by alpha oscillations to reduced interfering visual stimuli. Nevertheless, other investigators defended that alpha power during the short-term retention of information reflects the active maintenance of information (Palva & Palva, 2007). In favor of the inhibition hypothesis are the results of a face retention task, in which alpha load modulation was localized to the parieto-occipital sulcus, but not in the temporal lobe involved in the maintenance and processing of faces (Tuladhar et al., 2007). Similar results were found when participants had to maintain either the identity or the orientation of a face. Larger alpha was found around the parieto-occipital sulcus during the retention of the identity in comparison to the retention of orientation (Jokisch & Jensen, 2007). Therefore, in both studies alpha increases were localized to areas not relevant for the maintenance of the visual information, discarding the hypothesis that posterior alpha is related to the maintenance of relevant information.

Alpha oscillations in sensory cortices are considered to be modulated by top-down control signals from the fronto-parietal network. It has been proposed that alpha oscillations might coordinate long-range interactions between cortical areas mediating top-down interactions (von Stein, Chiang, & König, 2000). This is in line with studies revealing the laminar specificity of neural oscillations (Buffalo, Fries, Landman, Buschman, & Desimone, 2011; Spaak et al., 2012). A consequence of such specificity is that alpha and gamma band coherence will be established with different cortical areas. Thus, gamma activity, from superficial layers, is most probable to influence downstream areas, whereas alpha synchrony, from deeper layers, would affect upstream and subcortical areas. However, as previously reviewed, gamma coherence has been also reported mediating top-down interactions (Doesburg et al., 2008; Gregoriou, Gotts, Zhou, & Desimone, 2009b; Siegel et al., 2008).

Alpha coherence between prefrontal and visual areas have been shown during top-down processing in selective attention and during WM retention (Sauseng et al., 2005a;

Sauseng et al., 2009; Zanto et al., 2010). Prefrontal alpha increase was coupled to posterior decreased in a WM task (Sauseng et al., 2005a). Similarly, using an attentional cueing task, alpha coherence was larger between prefrontal and the contralateral to the attended stimulus cortex (Sauseng et al., 2005a). A similar pattern was observed between the parietal and visual cortex (Doesburg et al., 2009). The causal relation of the prefrontal-parieto network in modulating visual alpha activity has been studied by interfering the top-down controlling areas by TMS. When the right FEF or right IPS was virtually lesioned, anticipated alpha desynchronization in visual cortex was disrupted as well as performance (Capotosto, Babiloni, Romani, & Corbetta, 2009; Marshall, O'Shea, Jensen, & Bergmann, 2015; Sauseng, Feldheim, Freunberger, & Hummel, 2011). Additionally, disruption of the right IFG resulted in a decreased alpha coherence between this region and visual cortex (Zanto et al., 2011).

2 Objectives & Hypothesis

Objectives and hypotheses

As we have outlined above, deployment of selective attention and its neural correlates in the human brain have been studied extensively with the use of cueing paradigms in which the location of targets is pre-cued. More recently, a series of studies have demonstrated that, using a retro-cueing paradigm, it is possible to voluntarily orient attention to specific aspects of internal representations held in WM in a similar fashion to orienting attention to perceptual stimuli. However, there are several issues, both behaviorally and neuronally, that remain still unresolved. The main objective of the current work is to shed light on them, and contribute to further understanding the interaction between selective attention and WM. This work was conducted under a theoretical framework influenced by the 'sensory recruitment' and 'state-based' models of WM, and by cognitive neuroscience data showing that while gamma activity is assumed to reflect functional processing, alpha oscillations are thought to reflect functional inhibition in order to suppress the processing of distracting information.

Our first objective was to investigate whether attention can select more than one item during VWM maintenance. If temporary representation of stimuli takes place in the same regions that are engaged to perceive information, then, as in perception, it should be feasible to select more than one item already held in VWM, as long as the number of the attended items does not exceed VWM capacity. To this aim, we conducted a retro-cue paradigm experiment with three conditions: neutral cue, spatial cue load 1 and spatial cue load 2. Our first hypothesis was that it will be possible to orient attention to more than one item. Therefore there will be a retro-cue benefit for the condition of load two and condition of load one.

Our second objective was to determine whether the patterns of neural oscillatory activity associated with orienting attention to mental representations held in WM are similar to those observed during attentional orienting to external perceptual representations, thus indicating a common neurophysiological mechanism. We consider that a common set of attentional control mechanisms can be used in both cognitive contexts, this is, when selecting items among internal representation (i.e., WM), and when selecting items in the outside world. To this aim, we recorded MEG activity while participants performed a retro-cue task. Our second hypothesis was that orienting attention within WM representations will modulate oscillatory activity in alpha and gamma bands. More specifically, neural activity in alpha band will exhibit a desynchronization in contralateral posterior cortex, reflecting the recruitment of attentional resources devoted to the memory representations. There will be also an enhancement of alpha activity over the ipsilateral posterior cortex, reflecting an active functional inhibition of task irrelevant areas. There will be an enhancement of gamma band activity in contralateral posterior cortex, signaling the processing of the attended stimulus.

Our third objective was to explore whether the benefit of the retro-cues could be observed even when the anticipatory effect of the cue is neutralized. We hypothesized that when the anticipatory effect of the retro-cues is neutralized, we still will observe the retro-cue benefit.

Our four objective was to investigate whether the lateralized oscillatory response is not uniquely reflecting attentional mechanisms related to the anticipation of the location of the probe. To this aim, we recorded EEG activity while participants performed a retro-cue task in which the cue did not predict the location of the probe. The hypothesis was that there will be an alpha and gamma posterior lateralized activity respect to the cued item.

3 Results

Results

3.1 Benefit of orienting attention to working memory representations

Participants performed a change detection task inside the MEG, in which a spatial retro-cue or a neutral cue was presented during the maintenance period (Lepsien & Nobre, 2006). Typically, participants first encoded items into VWM, followed by a retention interval. During this interval, in the spatial retro-cue condition, one or two elements from one hemifield (right or left) were indicated to be relevant for subsequent retrieval. This condition was compared with trials in which a non-informative cue (the so-called neutral cue) was presented (figure 5).

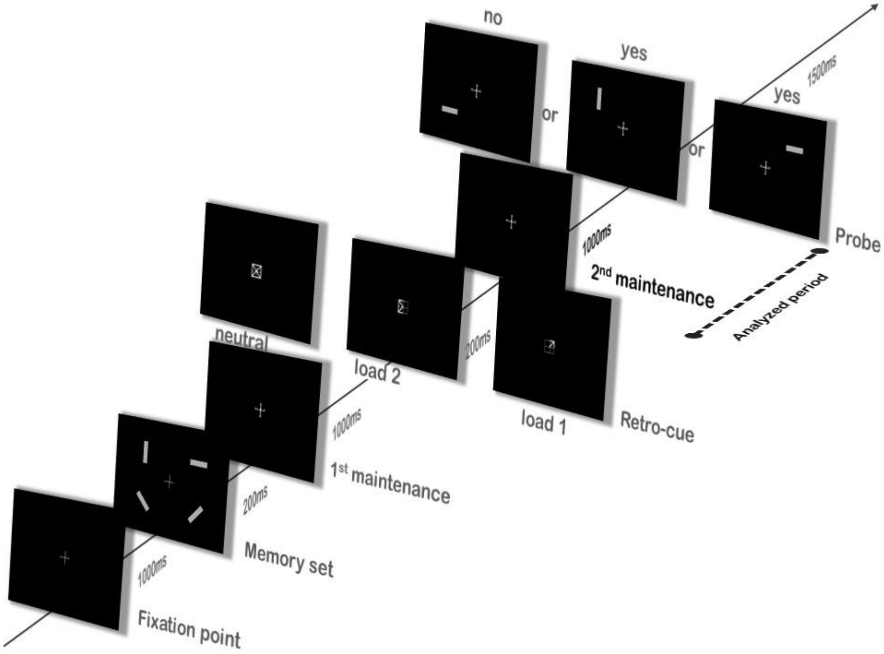

Figure 5. Experimental MEG paradigm. Depiction of the flow and timing of events for each condition of the MEG experiment. At the beginning of a trial, participants saw a white central fixation cross for 1000 ms. A set of items was then briefly displayed (200 ms) for study, consisting of four grey rectangles with different orientations

> displayed in four locations on a black background. 1000 ms after the offset of the memory array, participants could be presented with either an informative spatial cue (i.e. retro-cue) or with no cueing information (i.e. neutral cue). A retro-cue consisted of one or two arrows originating from the fixation cross pointing to one (load 1) or two (load 2) of the four locations that had been occupied by a rectangle in the memory array, thus indicating where a relevant item or items were present (validity 100%). 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 1000ms of delay interval. Finally, participants were presented with a single rectangle in one location for 1500 ms during which they were required to respond.

Analysis of the behavioral data revealed that there was a significant benefit in the use of the spatial retro-cue compared to when no spatial information about the upcoming target was presented. This benefit was observed both in accuracy and reaction time.

A repeated measures analysis of variance (ANOVA) with the factor Condition (one-element, two-element, neutral) for detection rate revealed a main effect of Condition ($F_{2,32} = 23.99$, $P < 0.001$). Planned comparisons showed that participants were more accurate in the one-element condition (mean = 0.89, SD = 0.16) than in the two-element condition (mean = 0.78, SD = 0.16) ($t_{16} = 5.05$, $P < 0.001$) and than in the neutral condition (mean = 0.72; SD = 0.15) ($t_{16} = 6.8$, $p < 0.001$). We also observed a trend for a better performance in the two-element condition than in the neutral condition ($t_{16} = 2.09$, $p = 0.053$) (figure 6a).

RTs also showed a main effect of stimulus condition ($F_{2,32} = 234.83$, $P < 0.001$), revealing that participants' reaction time significantly increased with increasing number of to-be-attended items. Participants were slower in the neutral condition (mean = 509.89 ms, SD = 58.45 ms) than in both the one-element (mean = 386.05 ms, SD = 51 ms) ($t_{16} = 17.07$, $P < 0.001$), and the two-element conditions (mean = 484.43 ms, SD = 58.85 ms) ($t_{16} = 17.14$, $P < 0.001$). Participants were also slower in the two-element condition than in the one-element condition ($t_{16} = 5.23$, $P < 0.001$) (figure 6b).

Analysis of cue direction revealed an advantage for right hemifield cues compared to the left hemifield cues. Accuracy and RTs were significantly affected by cueing direction ($F_{1,16} = 8,792$, $p<0.005$; $F_{1,16} = 19.87$, $p<0.001$; respectively). Individuals presented higher accuracy for right targets (mean = 0.86, SD = 0.13) compared to left targets (mean = 0.81, SD = 0.16); as well as faster RTs for right cued items (mean = 422.07 ms, SD = 54.83) than for left cued items (mean = 448.41 ms, SD = 55.44).

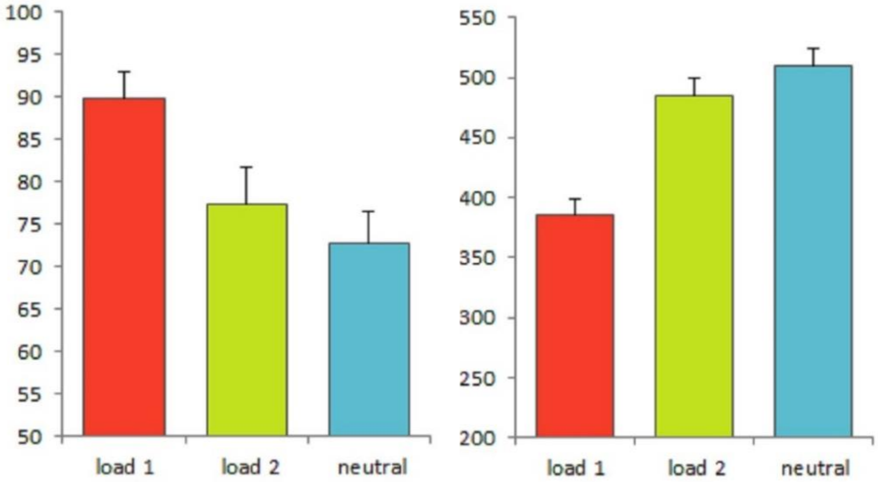

Figure 6. Behavioral results of the MEG experiment. Results of the retro-cue task in the MEG experiment as a function of cue type. Left panel, mean detection rate; right panel; mean RTs. Errors bars represent the standard error of the mean (s.e.m.).

3.2 Alpha and gamma band lateralized activity in the occipital cortex

Previous studies have shown that orienting attention to a region of space in the perceptual domain modulates oscillatory activity (Bichot, Rossi, & Desimone, 2005; Fries et al., 2001; Fries et al., 2008; Taylor et al., 2005; Womelsdorf et al., 2006; Capilla et al., 2014; Doesburg et al., 2009; Kelly et al., 2009; Rihs et al., 2009; Sauseng et al., 2005b; Thut et al., 2006; Yamagishi et al., 2005). Mainly, two frequency bands, alpha and gamma, have been associated with spatial selective attention. Alpha band synchronization and desynchronization are seen in ipsilateral and contralateral sensory cortex respectively, while the opposite pattern is found for the gamma band.

To test whether orienting spatial attention to the contents of WM would elicit a similar oscillatory modulation than in the perceptual domain, neural activity was recorded with MEG while participants performed the task described in results section 1.

Time-courses obtained from magnetometers sensors were time-frequency (TF) transformed. As the topography arising from this type of sensors is difficult to interpret, as it represents the exit and entry points of the magnetic field in and out the head, lateralization effects were assessed on the activity projected onto the cortical surface. Signal in the source space was inverted separately for the alpha (8–14 Hz) and gamma bands (50– 80 Hz), in the time windows obtained as being significantly modulated in the orienting conditions (one-element and two-element) respect to baseline.

TF datasets were transformed into Neuroimaging Informatics Technology Initiative images (NIfTI format). Specifically, the 4D [space (x, y), time, frequency] datasets were converted into a 3D data (channel space x time). In this case, power was averaged in the alpha (8–14 Hz) and gamma bands (50– 80 Hz) to obtain scalp–time images. TF statistical analysis was performed on baseline normalized data. Using this analysis, we tested for averaged effects of condition (i.e. effects that were significant across all experimental conditions relative to the pre-stimulus baseline). Importantly, this contrast was orthogonal to the main effects of interest, and was used only to define a TF window of interest.

To illustrate the oscillatory components present during orientation, averaged frequency responses were computed for each sensor, with the use of all trials, collapsing one-element and two element trials for each participant for frequencies from 8 to 14 Hz. We found a significant [$p < 0.05$, familywise error (FWE) corrected over sensors and time] sustained increase in alpha power after retro-cue presentation (i.e. 200–1200 ms) over posterior sensors (figure 7). We also evaluated whether neural activity in the gamma frequency band showed an attentional orienting effect. A significant gamma power increase ($P < 0.05$, FWE -corrected at the cluster level over sensors and time) occurred during the retro-cue delay period over posterior sensors (figure 7b). The interval where this activity was significant was between 250 and 660 ms after the retro-cue presentation.

Although we did not explicitly formulate a hypothesis about the involvement of frontal regions in this work, a significant alpha activity increased was found over frontal sensors.

Having established a significant modulation of neural activity in the alpha and gamma bands at the level of MEG sensors, we were interested in determining if the underlying generative sources were differently lateralized respect to cue direction. Hence, oscillatory activity was reconstructed on the basis of the time-windows where significant modulation of neural activity was found in the sensor analysis (see above). An ipsilateral increase in alpha activity was found for the right cued condition in the right occipital cortex ($p < 0.05$, whole-brain FWE corrected) as compared with the left condition. Likewise, an increase in the left occipital cortex was observed for the left cued condition ($p < 0.05$, whole-brain FWE -corrected) compared with the right condition (figure 8). A contralateral increase in gamma power was observed in the right occipital cortex when participants were cued to orient attention to items in the left hemifield ($P < 0.05$, FWE -corrected). Similarly, gamma activity was increased in the left occipital cortex when participants were cued to orient attention to items in the right hemifield ($P < 0.05$, FWE -corrected) (figure 8). On the basis of our prior hypotheses of contralateral gamma power increases at ipsilateral alpha enhancement sites, we tested within a priori-defined 20-mm radius volumes centered at $x = 32$, $y = 76$, and $z = 14$ in the right hemisphere, and at $x = 22$, $y = 84$, and $z = 2$ in the left hemisphere. We did try this analysis without the use of a region of interest, but found no FWE-corrected significant effect at the wholebrain level.

We did not find a load-dependent modulation of oscillatory activity in either the alpha or gamma frequency bands.

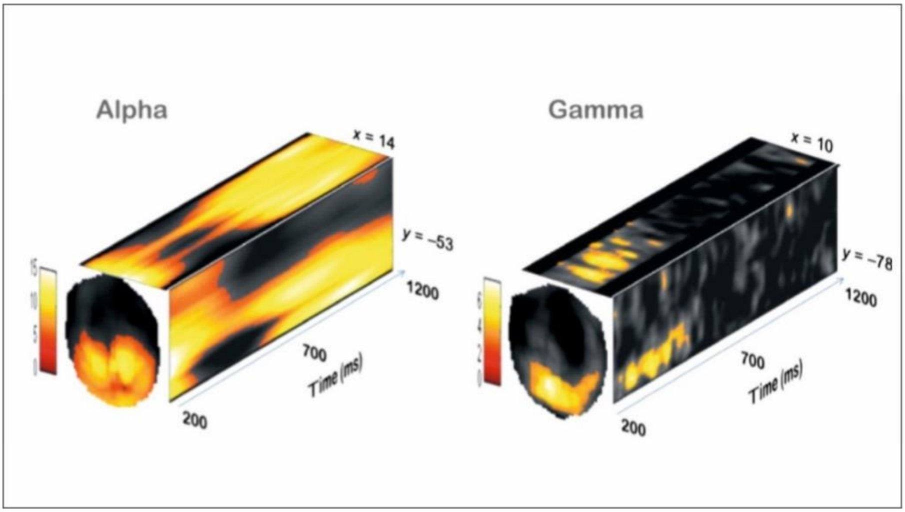

Figure 7. Magnetometer sensor results. T-Statistic sensor-level maps of significant activity in experimental conditions relative to baseline (between 500 and 0 ms before stimulus onset) in the alpha ($P < 0.05$, FWE-corrected) and gamma ($P < 0.05$, FWE-corrected at the cluster level) frequency bands as a function of time. The front faces of the cubes show the distribution over the sensors of significant alpha (left) and gamma (right) band power changes at time bins of 700 and 550 ms, respectively. The top and side faces of these cubes show the projection of the maxima within these individual t-statistic maps onto the outer cube surface over time.

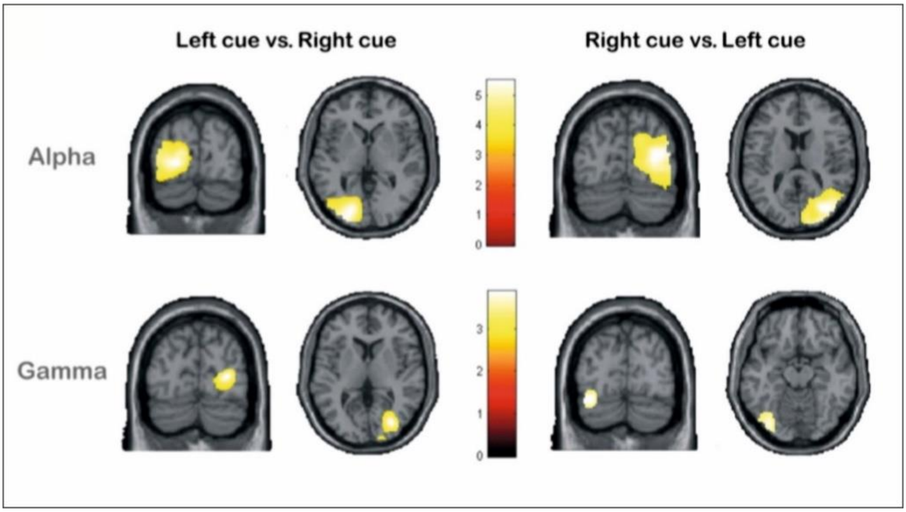

Figure 8. Source localization magnetometer results. Localization of significant cortical sources for alpha and gamma resulting from comparison of the left retro-cue condition with the right retro-cue condition (left column), and comparison of the right retro-cue condition with the left retro-cue condition (right column). For display purposes, only the t-value images are thresholded at $P < 0.001$ and $P < 0.005$, uncorrected, for alpha and gamma bands, respectively. The color scales indicate t-values.

3.3 Prefrontal alpha activity associated to retrospective orienting attention

To further investigate the effect of orienting attention to mental representations, alpha source images were tested for average effects of condition, this is, alpha increments present across all experimental conditions relative to the neutral condition. This contrast revealed more alpha power in the IFG [34 44 -8] for the orienting condition in comparison to the neutral condition ($p < 0.05$ FWE-corrected) (figure 9).

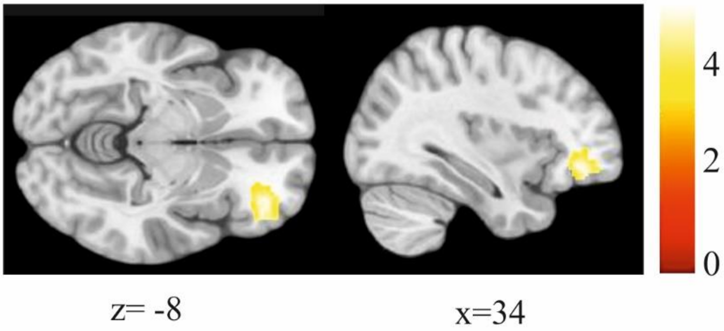

Figure 9. PFC alpha activity. Localisation of significant cortical source resulting from comparison of the retro-cue condition with the neutral condition, this is activity across the four retro-cue conditions that is greater than in the neutral condition. For display purposes, t-value image is thresholded at P < 0.001. The color scales indicate t-values.

3.4 Temporal dynamics of posterior alpha activity

The previous analysis showed that the oscillatory modulatory signal is affected by cueing side. However, there are two issues that need more attention, these are, the time-course of the oscillatory modulation and the sign of the lateralization. It is not clear from previous studies whether there is an increase in alpha activity ipsilateral to the cued side, a reduction in the contralateral activity, or both.

Here, we computed TF representation in gradiometer planar sensors. Unlike magnetometer sensors, planar gradiometer can proportionate the location of the maximum just above the corresponding source, so lateralization effects are easy to interpret from the topography. TF analysis showed alpha and gamma modulation in posterior sensors (figure 10). Time-course of alpha activity showed an initial desynchronization followed by a synchronization sustained until target presentation (figure 11). As depicted in figure 10, alpha desynchronization was accompanied by gamma synchronization. Crucially, this oscillatory modulation seems to be lateralized

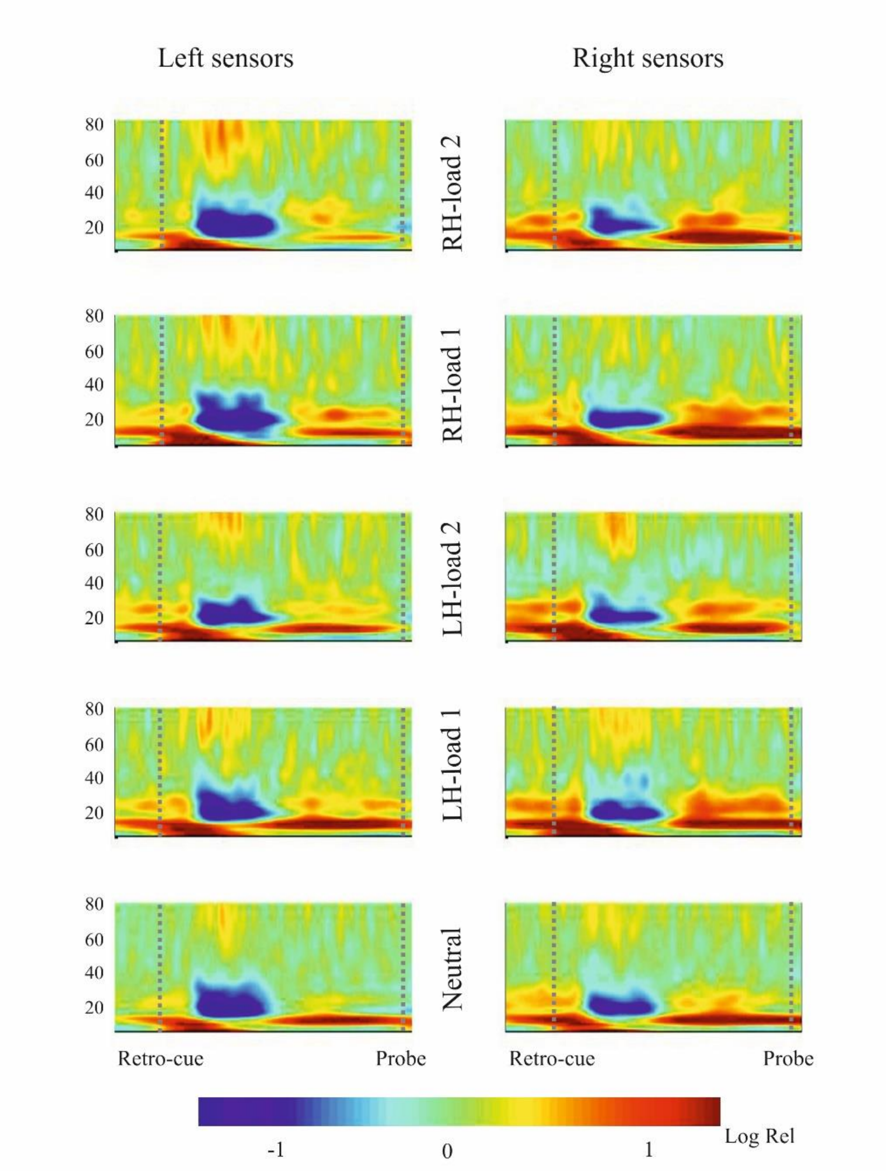

Figure 10. TF representation of gradiometer sensors data during the maintenance period after retro-cue. The y-axis represents frequencies from 4 Hz to 80 Hz. The x-axis represents the time period from the retro-cue to the probe. Power changes are depicted as the log relative change with respect to baseline. Left column representation are the averaged TF representations of left posterior sensors. Right column are the averaged TF representations of right posterior sensors.

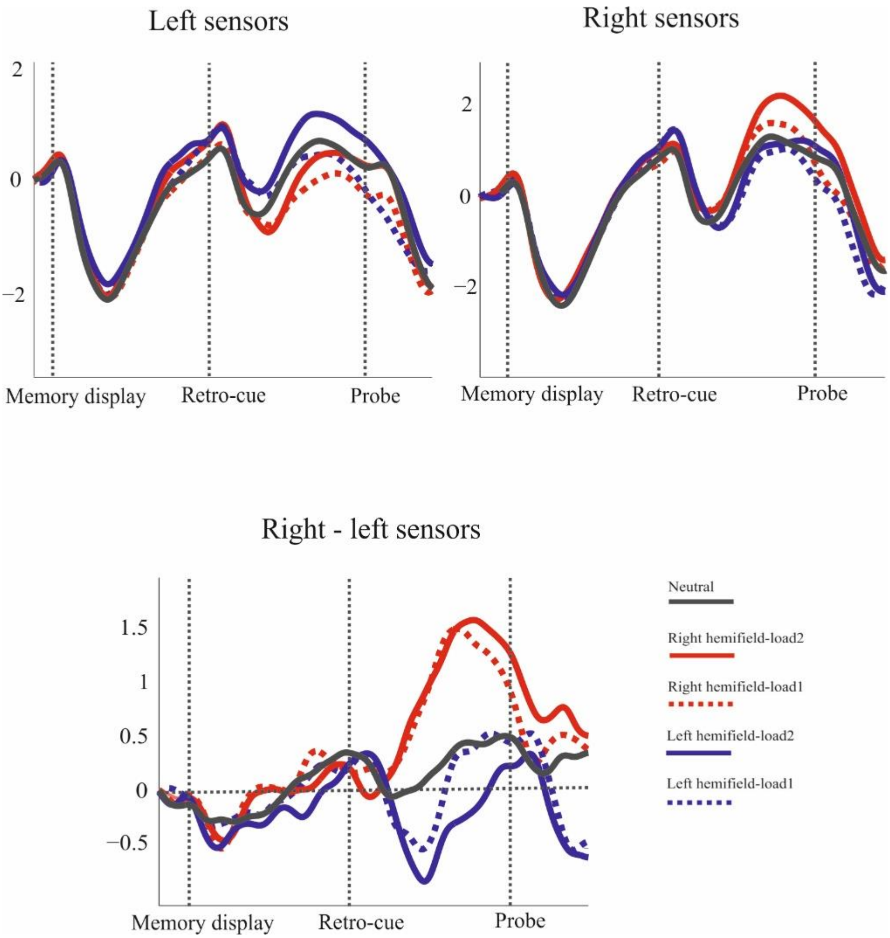

Figure 11. Time courses of alpha activity. Waveforms were averaged across left posterior sensors (left plot) and right posterior sensors (right plot). Alpha power is expressed as the log relative change respect to baseline. The plot below represent the subtraction between right and left sensors alpha time courses for each condition. Above zero values indicate more alpha power for right sensors, and below zero values indicate more alpha power over the left sensors.

with respect to the cued side. Time-courses of the differences between ipsilateral and contralateral sensors are shown for each condition in figure 11.

Alpha topographies are depicted for right, left and neutral condition at 300 ms intervals, starting from 250 ms after the cue onset (figure 12). An initial desynchronization is seen in posterior lateral sensors followed by a synchronization in posterior central sensors.

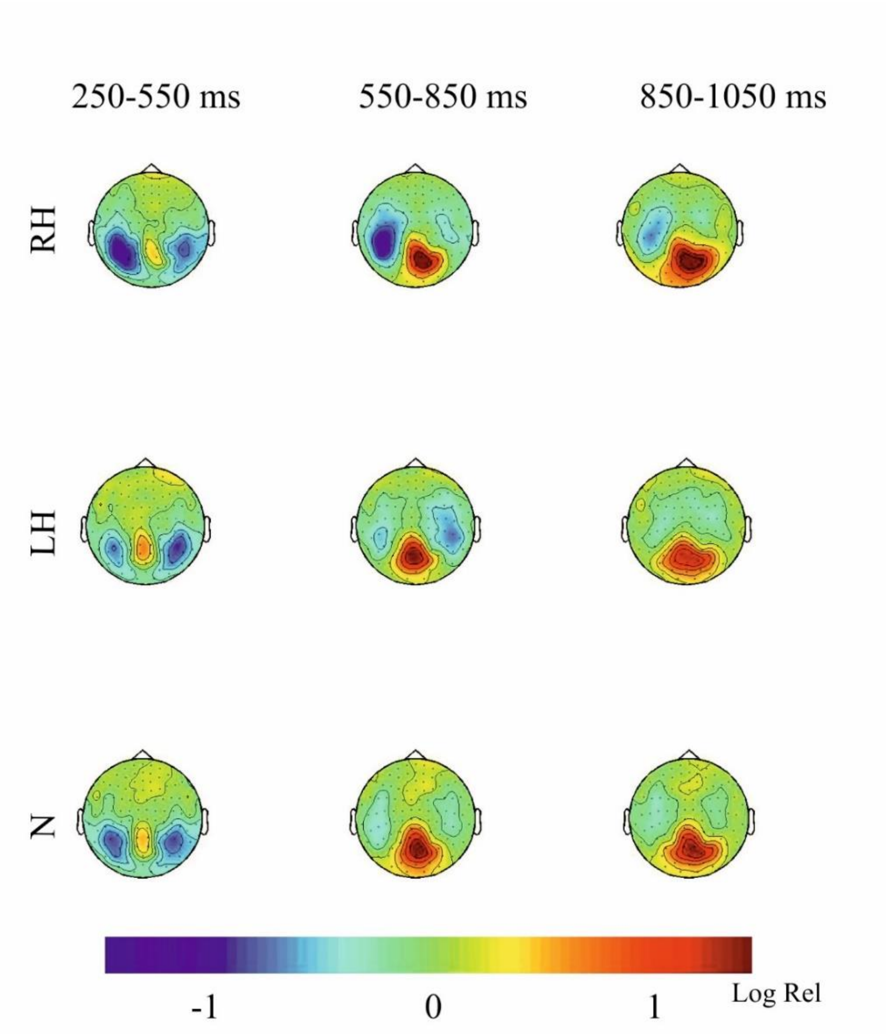

Figure 12. Topography representations of alpha band activity. Power was averaged across the three time windows of interest. Alpha power is expressed as the log relative change respect to baseline. First row depicts alpha topography for the right hemifield condition averaged for the one and two load conditions. Second row shows left hemifield topographies averaged across the one and two load conditions. The last row depicts topographies for the neutral condition.

To test for significance, an ANOVA was computed for each of the three time windows averaging the group of sensors showing modulation in each case. For the first window, analysis revealed a significant decrement in contralateral sensors compared to ipsilateral sensors ($F_{1,16} = 10.56$, $p<0.01$), as well as an hemifield effect ($F_{1,16} = 6.34$, $p<0.05$), with decreased alpha activity in the right cue condition compared to the left. The second time segment showed a significant increase in the ipsilateral compared to the contralateral sensors ($F_{1,16} = 39.52$, $p<0.001$), and a load effect, with greater power for the two-element condition compared to the one-element condition ($F_{1,16} = 16,8$, $p<0.005$). In the last analyzed period a significant interaction (sensor x cue direction) was found ($F_{1,16} = 11.58$, $p<0.005$). An increment in ipsilateral sensors compared to contralateral was only significant for the right cue condition ($p<0.001$). A sensor by load interaction was also found ($F_{1,16} = 14,33$, $p<0.005$), with significant greater alpha power in the two element condition compared to the one-element in the right-cue condition ($p<0.005$). Crucially, no lateralization was found for the neutral condition in any of the time windows ($p>0.05$).

Topographical analysis revealed a significant alpha lateralization in the first two analyzed windows that corresponded to an initial desynchronization followed by a resynchronization. However, after this period alpha resynchronization did only show a lateralization effect for the right cue condition. Topographies suggested different generating sources for the alpha decrement and increment. Therefore, alpha activity was source reconstructed for the time segments showing a contralateral decrement and an ipsilateral resynchronization. Figure 13 illustrates alpha activity suppression located to the ventral lateral occipital cortex for left- and right-cue conditions ($p<0.05$, FWE corrected). The minimum peak for either condition was located in the cortex contralateral to the cued hemifield (right condition [-36 -78 -6]); left condition [42 -84 -4]). An ANOVA revealed a significant hemisphere effect ($F_{1,16} = 19.01$, $p<0.001$), and a load effect ($F_{1,16} = 8.25$, $p<0.05$). Figure 13 shows ipsilateral alpha activity increase in the second time window located in the occipital cortex ($p<0.05$, FWE corrected). Maximal activity for both right- and left-cue conditions occurred in the visual cortex ipsilateral to the cued hemifield (right condition [20 -92 14]); left condition [-16 –92 4]). Statistical analysis revealed that alpha activity was significantly higher in the hemisphere ipsilateral to the cue compared to the contralateral hemisphere ($F_{1,16} =13.78$), $p<0.005$).

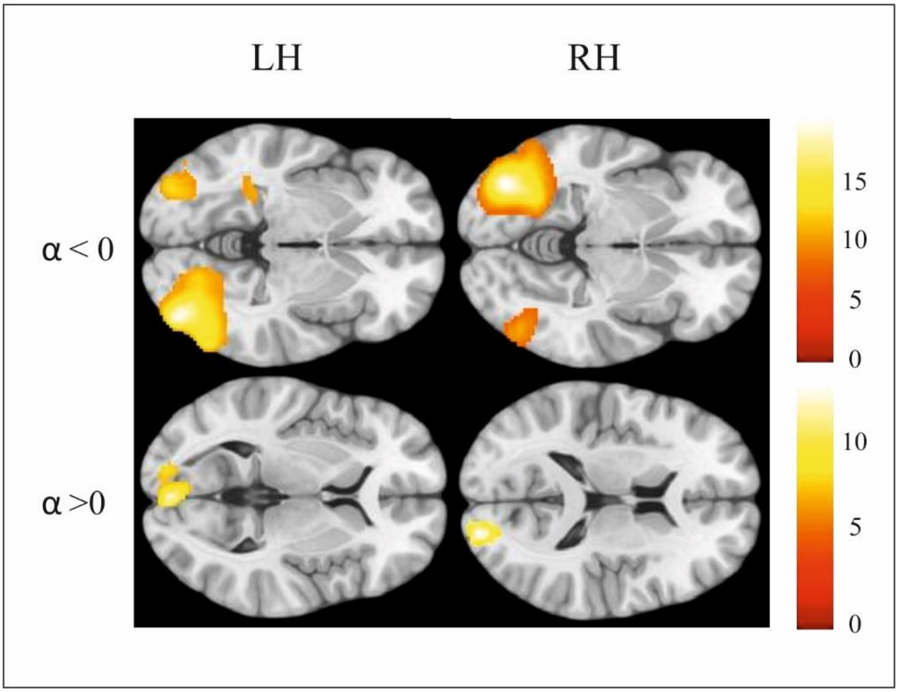

Figure 13. Localization of significant cortical sources of gradiometer data for alpha band activity. Left part images represent activity for the left hemifield condition resulted from collapsing the one and two load conditions. Right part images, illustrate significant activity for the right hemifield, resulted from collapsing the one and two load conditions. The top row depicts alpha activity that is decreased respect to baseline during the time window 250-550 ms. The bottom row shows alpha activity that is increased respect to baseline in the time period 550-850 ms. Statistical images are thresholded at $p<0.05$ (FWE corrected).

An additional analysis was conducted in the sensor data. Given that the visual presentation of the cue induces an alpha desynchronization in visual regions, it constitutes a confound to interpret alpha decrements and increments related to the attentional orienting. To cancel out the alpha desynchronization induced by the visual cue, difference waveforms were computed for the ipsilateral and contralateral sensors (figure 14) subtracting the neutral condition alpha time course. Visual inspection of the waveforms revealed a decrement in contralateral sensors compared to the neutral condition and an increase in ipsilateral sensors. Contralateral decrease was significant for the time period 410-800 ms ($p<0.05$), with a peak at 520 ms. Ipsilateral sensors showed a significant increase for the time period 900-1200 ms ($p<0.05$), peaking at 1050 ms.

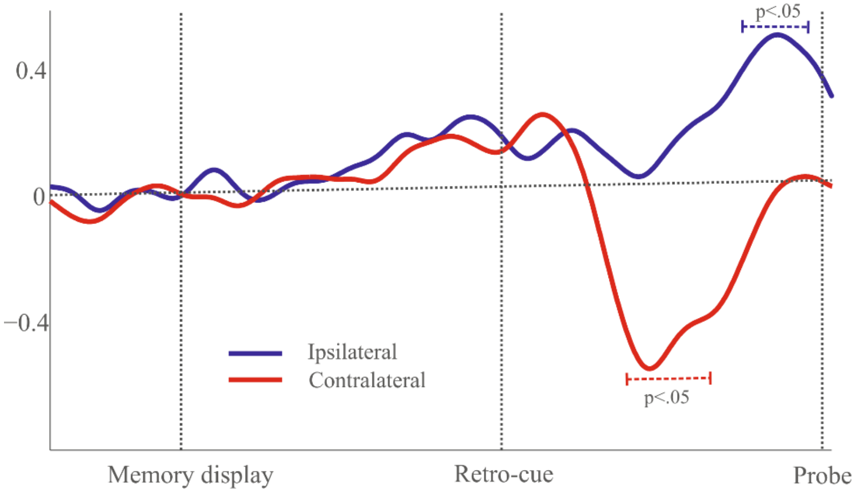

Figure 14. Alpha difference waveforms. The waveforms resulted from the subtraction of the neutral condition alpha time course to the averaged time course of load two right and left conditions. The figure illustrates significant ($p<0.05$ uncorrected) increment of alpha power over the ipsilateral hemisphere respect to the neutral condition. Contralateral sensors exhibit a significant decrement respect to the neutral condition.

3.5 Benefit of the retro-cue in the absence of anticipatory attention to the probe.

The previous experiment revealed that orienting attention to the contents of WM improved participants' performance. However, the experimental paradigm did not allow us to determine whether the benefit of the spatial cue was due to the allocation of attention to the contents of WM or from anticipatory attention to the probe. Accordingly, we designed a behavioral experiment with the aim of elucidating whether the performance benefit would occur in the absence of anticipatory attention to the target. Participants performed two blocks of a change detection task. Similarly to the

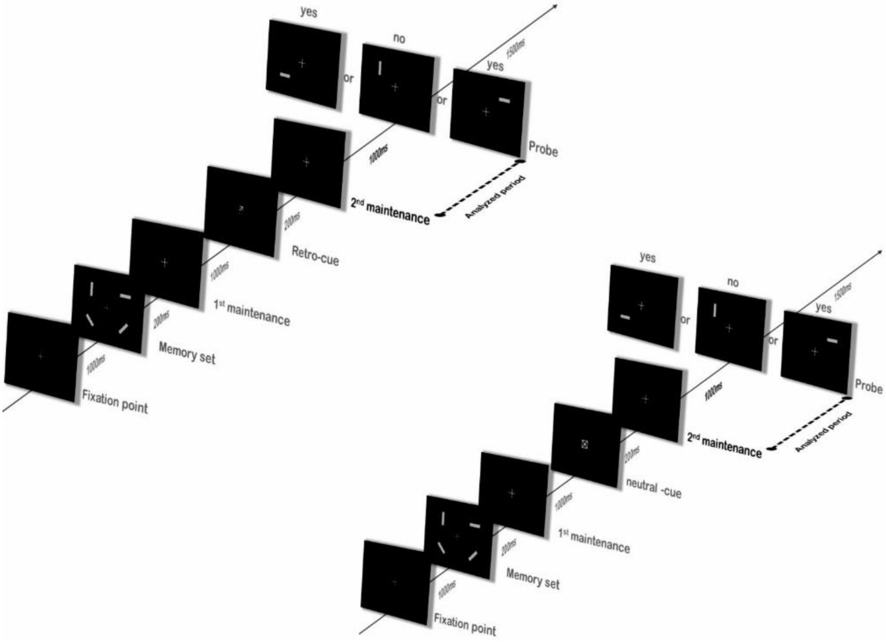

Figure 15. Behavioral study experimental paradigm. Depiction of the flow and timing of events for each condition of the behavioral experiment. In this case only the 'retro-cue load 1' condition and the 'neutral cue' condition were administered. Accordingly, the retro-cue consisted of one arrow originating from the fixation cross pointing to one of the four locations that had been occupied by a rectangle in the memory array.

previous experiment, in the spatial cueing condition one element was indicated to be the one that was going to be subsequently probed. However, differentially, in the recognition phase, this item could be presented randomly in the screen. This is, the cue predicted which item was going to be probed, but not the location at which it was going to be presented. By doing so, anticipatory effects were suppressed. As in the previous experiment, in the neutral condition a non-informative cue was presented. Hence, a random item in the same location as in encoding was tested for recognition in each trial (figure 15).

Analysis of performance revealed that in the absence of anticipatory attention to the target, individuals could use the spatial cue to orient attention to the relevant item being maintained, and improve recognition rate (mean = 0.8, SD = 0.12) compare to when

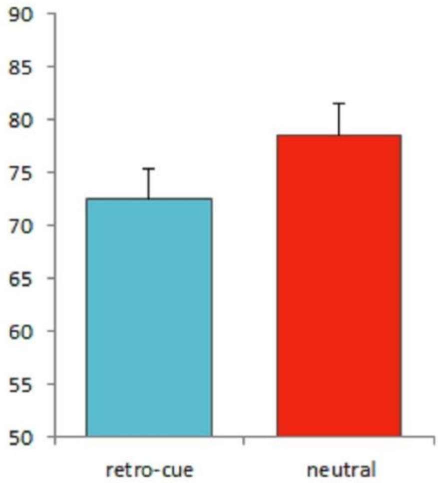

Figure 16. Behavioral study results. Mean percentage correct of the retro-cue task in the behavioral experiment as a function of cue type. Errors bars represent the standard error of the mean (s.e.m.).

no information about the tested item was provided (mean = 0.76, SD = 0.13), (t_{19}=2.14, $p<0.05$) (figure 16).

3.6 Alpha band lateralized activity in the absence of anticipatory attention to the probe

As described above, orienting attention to the contents of WM improved performance. This behavioral benefit was accompanied by a lateralization of alpha and gamma activity related to the cued hemifield. A subsequent behavioral experiment revealed that the cue benefit was not restricted to the anticipation of the probe. In this experiment, we tested whether alpha and gamma modulation was associated to orienting attention to WM representations in the absence of predictive cueing of the probe. EEG was recorded while participants performed a change detection task, in which a spatial cue was presented during the maintenance period. This cue referred to the random item of the array that would be tested at recognition. Crucially, the cue did not allow participants to anticipate at which location of the screen the item would be presented, as it could appear in any location of the screen (see figure 15).

Similarly to the MEG experiment, there was an advantage for right-cued items (mean = 0.93, SD = 0.06) versus left-cued items (mean= 0.89, SD = 0.09) in accuracy ($F_{1,19}$ = 6.52, $p < 0.05$). However, this asymmetry was not observed in RTs (mean left RT = 368.3 ms, SD = 8.91; mean right RT = 368.45 ms, SD = 7.07).

TF analysis of the time-series data revealed that orienting attention was associated with an alpha band (8-14Hz) modulation (figure 17). However, and unlike the MEG experiment, gamma band activity did not present an orienting modulation. Alpha modulation consisted in an initial desynchronization followed by a synchronization. When ipsilateral and contralateral electrodes are depicted separately, alpha time courses seem to present different magnitudes.

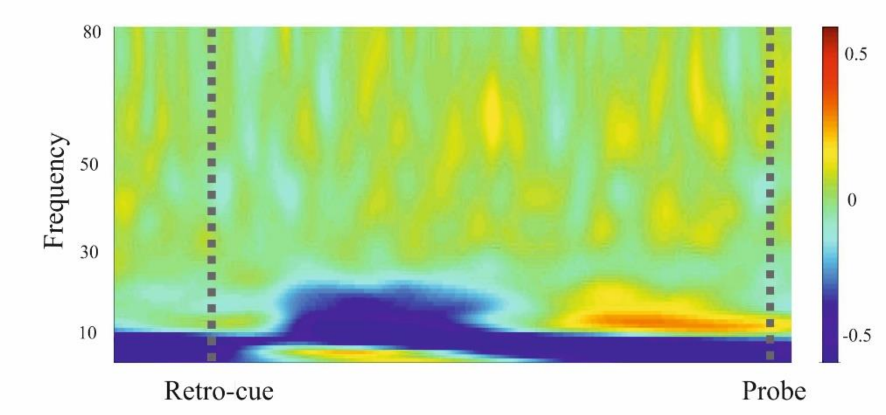

Figure 17. TF representation of the posterior electrode data during the maintenance period after retro-cue. Right and left condition and left and right posterior electrodes are averaged. Power changes are depicted as the log-relative change with respect to baseline.

Figure 18 depicts the topographic distribution of alpha power averaged over 300 ms windows for each cue condition (left and right). To test the hypothesis that alpha activity is lateralized with respect to cued side, a 2x2x3 repeated-measures ANOVA was conducted. Channels included in the analysis were O1, PO3 and P07 over the left hemisphere and O2, PO2 and PO8 over the right hemisphere. Statistical analysis revealed that alpha band activity was differently modulated over the ipsilateral and contralateral hemispheres ($F_{1,19} = 6.051$, $p < 0.05$), and over the three time windows ($F_{2,38} = 9.24$, $p < 0.05$). Alpha power was almost significantly differentially modulated by cue direction over the ipsilateral and contralateral hemispheres as a function of time (three way interaction hemisphere by hemifield by time, $F_{2,38} = 3.22$, $p = 0.051$). As it is noted in figure 19, alpha lateralization had a different time pattern in the two conditions. Power lateralization is firstly observed for the left condition, and then for the right condition. Alpha lateralization was significant for the first time window for the left condition ($p<0.05$), while it was significant for the second time window in the right cue condition ($p<0.05$).

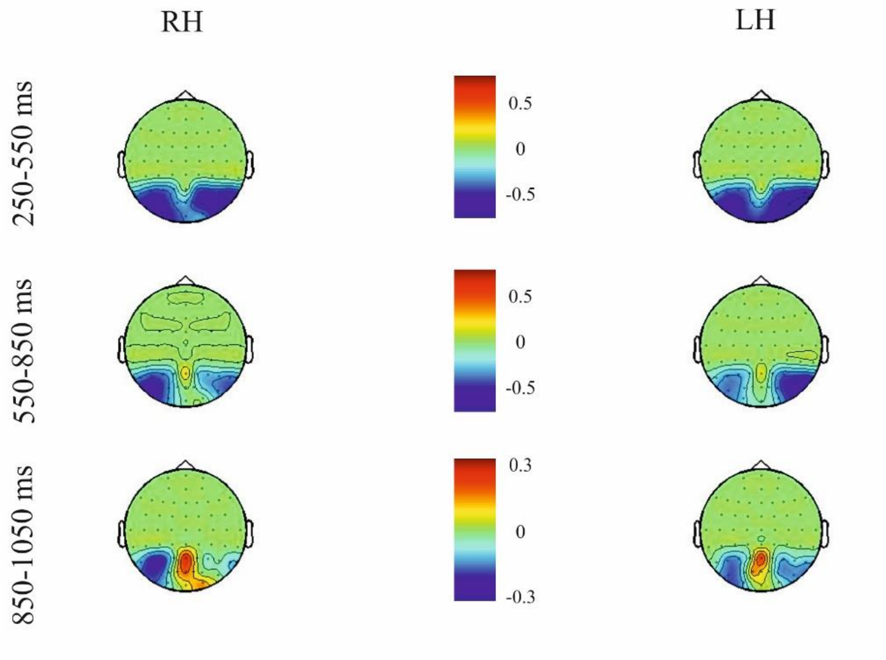

Figure 18. Topography representations of alpha band activity. Power was averaged across the three time windows of interest. Left column depicts alpha topography for the right hemifield condition. Right column shows left hemifield topographies. Topographies only include a group of posterior electrodes (O1, O2, PO7, PO8, P04 and PO3). Alpha power is expressed as the log relative change respect to baseline.

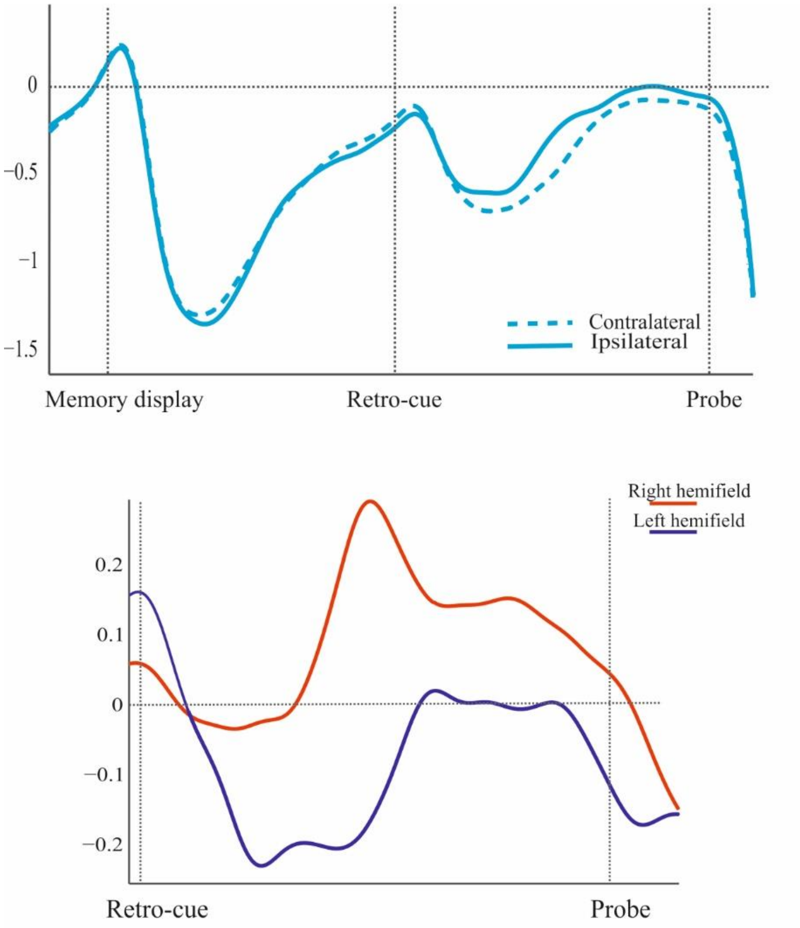

Figure 19. Time courses of alpha activity. The left graph shows time courses for ipsilateral and contralateral electrodes collapsed over right and left condition. Alpha power is expressed as the log relative change respect to baseline. The right graph shows difference waveforms of alpha time courses. Difference waveforms resulted from the subtraction of right electrode (O1, PO4, and PO8) minus left electrodes (O2, PO3, and PO7). Above zero values indicate more alpha power for right electrodes, and below zero values indicate more alpha power over the left electrodes.

4 Discussion

Discussion

Orienting attention to a memory representation has been shown to improve WM performance in the same way as orienting attention to a perceptual stimuli can enhance its detection and discriminability. Attentional top-down modulation of oscillatory sensory components has been widely studied in the perceptual domain. However, oscillatory response related to retrospectively orienting attention has not been study until now. The main goal of the present dissertation was to elucidate the oscillatory neural mechanisms associated to orienting attention to memory representations under the hypothesis that shared top-down modulations underlie attention to both sensory and memory representations. To this aim, we conducted an MEG and EEG experiments while participants performed a retro-cue task in which a location of the memory array was cued for later retrieval. MEG data were separately analyzed for magnetometers and gradiometers. Magnetometer analysis revealed alpha and gamma cue lateralized activity in the occipital cortex, and an additional prefrontal source in the alpha band related to attentional orienting. The time course of the alpha band obtained from the planar gradiometers was then analyzed revealing a contralateral alpha decrement followed by an ipsilateral alpha enhancement. A subsequent EEG experiment revealed that, in the absence of preparatory attention to the probe, alpha band activity was lateralized respect to the cue location. Behaviorally, analysis of performance of the MEG retro-cue task revealed a cue benefit both in detection rates and RTs for load 1, and a strong trend for load 2. Additionally, a behavioral experiment tested the performance benefit of the retro-cue when it was not predictive of the location of the probe. The results revealed that attention to a memory item improves performance, and thus, the retro-cue benefit is not only caused by anticipatory assigning resources to the location probe. Bellow, these result are discussed in further detail.

4.1 Retro-cue benefit in visual working memory

Recent cognitive research has shown that selective attention not only determines which subset of visual input is encoded in VWM, but that retrospectively cuing attention to representations maintained in WM can enhance VWM performance, the so-called retro benefit. After the pioneering studies by Landman (2003) and (Griffin & Nobre, 2003) Griffin and Nobre (2003), several experiments have confirmed that attention-directing cues can influence the selection of items from VWM. Although it can be influenced by certain variables (i.e. the validity of the retro-cues; (Gunseli, van Moorselaar, Meeter, & Olivers, 2015), in general, participants respond faster and more accurate to a target that is validly cued compared to neutral cues in which no spatial information is provided. This robust effect consistently reveals a performance benefit of 5-15 % in recognition probes using various stimuli. In the current work, we observed similar percentages of improved WM performance for cued stimulus locations during the maintenance period. Interestingly, it should be noted that this occurred even when the retro-cue was not predictive of the location where the target item was going to be probed (behavioral experiment). This pattern has implications for explanations of the cognitive mechanisms underlying the retro-cue benefit. It indicates that once attention has been directed to the cued representation, the items that were uncued are degraded or actively removed, since they did not lead to any interference to target item probed in matched locations (Makovski, Sussman, & Jiang, 2008). Thus, these results support the removal hypothesis (Kuo et al., 2012; Rerko, Souza, & Oberauer, 2014; Williams & Woodman, 2012). From the perspective of the *state-base* models (Cowan, 2001; McElree, 2001; Oberauer, 2002), and more specifically from the three-memory layer account by Oberauer, the retro-cue would serve to distinguish relevant from irrelevant task information, so that the latter can be removed from the capacity-limited part of WM (i.e., the region of direct access). Removing irrelevant information from the region of direct access should reduce interference for the cued object, and, additionally, free capacity (Rerko et al., 2014). From the perspective of the *resource-models* (Bays & Husain, 2008), this would be reflected in a reassignment of WM's capacity, that could be shifted to the cued item, thus receiving an extra amount of resources (Souza et al., 2014). Therefore, the retro-cue benefit could be accomplished by a combination of these cognitive operations, this is, strengthening the cued representation and removing the irrelevant non-cued WM representations. The neural mechanisms supporting this combination of processes could be accounted for by the results observed in the current dissertation (see below).

Switching attention within WM representations is not automatic, and therefore consumes resources (Janczyk & Berryhill, 2014). Derived from this, one critical question is whether attention can select more than a single item during VWM maintenance. Contrary to a previous study showing that orienting attention to a subset of items maintained in WM is observed only when attention focuses on a single memory item (Makovsik & Jiang, 2007), we found a trend for an improved performance when attention was directed to two cued items during WM maintenance as compared to when no items were cued. Similarly, in a series of experiments employing a cue set size of 3 (i.e. not exceeding the typical VWM of three to four items), (Matsukura & Vecera, 2015) reported that attention can select multiple items represented in VWM. As it is well known that attention can select at least two noncontiguous locations at the same time during sensory processing (Alvarez, Gill, & Cavanagh, 2012; Anderson, Ester, Serences, & Awh, 2013; Awh & Pashler, 2000), these results provide compelling evidence that attention operates in a similar manner across perceptual and WM representations.

Hemifield asymmetries were repeatedly found in the behavioral analysis, with an advantage for the right visual field targets. Visual attention experiments usually report behavioral performance differences across the visual field, associated to hemispheric asymmetries. For instance, attentional bias to the left visual field has been associated with greater white matter volume in the right hemisphere (Thiebaut de Schotten et al., 2011) or with more lateralized activity for left targets (Thut 2006), supporting right-hemisphere dominance theories of visual attention (Mesulam,1981). However, VWM experiments have reported right visual field bias under high resources demands (Sheremata, Bettencourt, & Somers, 2010; Sheremata & Shomstein, 2014). Such asymmetry has been associated to a dual representation of the right hemisphere. It was shown that while the left hemisphere represents the contralateral memory items, the right hemisphere represent both hemifields, and thus, right presented items would benefit from representation in both hemispheres (Sheremata & Shomstein, 2014). However, given the design of the paradigm is not possible to dissociate whether the right visual field biased emerged before or after the retro-cue, therefore visual field asymmetry could be related either to asymmetries in memory maintenance or to attentional orienting processes.

In summary, current results indicate that representations maintained in WM are in constant flux, and that similar to the way attention can be shifted from one location to another during visual processing, attention can be shifted to different representations within WM. Orienting attention within WM would allow us to focus on task-relevant information without getting distracted by irrelevant memory content. Removing the irrelevant non-cued WM representations enable the reassignment of WM's capacity. This benefit can be observed when more than a single item are cued during VWM maintenance.

4.2 Attentional dependent oscillatory activity

4.2.1 Modulation of visual processing

Extensive cognitive research has shown that attentional orienting can selectively bias information processing towards specific attributes within a visual scene. Physiologically, it is widely accepted that attention modulates neuronal responses in posterior sensory areas. Nevertheless, few studies have investigated the neural substrates of attentional selection of information already maintained in VWM. The neurophysiological results we have described demonstrate that spatial shifts of attention within WM representations induce a modulation of oscillatory activity in ventral occipital regions. Similarly, attentional dependent modulation of visual activity during VWM maintenance has been previously reported. Specifically, in an EEG experiment, it was shown that the spatial retro-cue modulated the contralateral visual N1 component in a similar way as did a pre-cue (Griffin & Nobre, 2003). This early negativity over posterior sites has been previously observed in studies of spatial orienting to the external space (Hopf & Mangun, 2000; Nobre et al., 2000). Additionally, an fMRI experiment also exhibited a retinotopic modulation of early visual areas associated to shifts of spatial attention to internal representations (Munneke et al., 2012). Together, these findings revealed that visual areas involved in shifts of attention to the external world, are also involved in shifts of attention within memorized representations. In addition to the visual modulation associated to visuospatial attention, the use of retro-cues has also been related to the modulation of posterior slow components associated to the short-term retention of information. When a cue given prior to the encoding stimulus indicates the relevant hemifield, a posterior sustained negativity is seen contralateral to the cued hemifield, and its amplitude is modulated by memory load. In a similar way, after a retro-cue, the magnitude of the CDA was reduced, reflecting a reduction of memory load (Kuo et al., 2012). The CDA has been accounted for by a modulation of alpha oscillatory brain activity. It has been proposed that ERPs with slow time courses are produced by induced asymmetrical amplitude modulations of alpha band oscillations (Mazaheri & Jensen, 2008). If the amplitude of an oscillation is symmetrical around zero, this implies that when averaged across trials the induced oscillatory component would be averaged out, and no slow field would be generated. In contrast, if the oscillatory signal is asymmetric, and for instance the peaks are more strongly modulated than the troughs, averaging across trials would lead to the generation of slow ERPs. Asymmetric modulation of alpha oscillatory activity has been reported (Stam, Pijn, Suffczynski, & Lopes da Silva, 1999), and has been demonstrated to generate evoke responses (Mazaheri & Jensen, 2008). Moreover, it was demonstrated that the slow component associated to the retention of items in WM, the CDA, could be explained by a modulation of alpha activity (van Dijk, van der Werf, Mazaheri, Medendorp, & Jensen, 2010). In van Dijk's experiment, lateralized alpha and ERFs emerged in the retention period of a WM task in which participants were cued to maintain the item presented in one hemifield. Lateralization effects in alpha activity and ERFs yielded the same posterior topography and were correlated across subjects. This study also showed an alpha increase ipsilateral to the attended hemifield, in accordance with an inhibitory role of alpha oscillatory activity (Jensen & Mazaheri, 2010; Klimesch et al., 2007). Taken together, the authors interpreted that the CDA does not reflect memory maintenance per se, but rather reflects the allocation of attentional resources to memory representations. However, although this study did not manipulate the memory load, another study by Sauseng et al. (2009), showed that alpha load lateralization during the WM delay was explained by the modulation of ipsilateral alpha that was dependent on the number of irrelevant items. This could be consistent with the role of alpha in explaining the load effects of the CDA, and the hypothesis of attentional resources instead of maintenance per se. In the magnetometer data presented here, no load effects were found for the alpha band, which is in agreement with Sauseng´s results. Unlike Sauseng´s task, ours only manipulated the number of relevant items, but did not manipulate the number of distracters. If the load modulation of alpha lateralization is produced by a modulation of ipsilateral alpha to the number of distracters, it is reasonable not to find it, here being that the number of distracters was maintained constant across load 1 and 2.

4.2.2 Lateralized posterior alpha oscillatory activity.

The modulation of oscillatory activity found in the analysis of magnetometer data supports the hypothesis that the allocation of attention to mnemonic representations and the allocation of attention to external space induce similar oscillatory modulations in posterior sensory regions. Lateralized effects of posterior alpha power have been repeatedly associated to spatial shifts of attention to external stimuli. Alpha modulation has been shown in the absence of external stimulation in the period following a spatial cue prior the appearance of the target stimuli. Visuospatial attention experiments report different alpha related spatial-biasing mechanisms. Some experiments have found an alpha power increase ipsilateral to the attended hemifield related to the suppression of unattended neural representations (Kelly et al., 2006; Rihs et al., 2007; Worden et al., 2000), whereas others have found an alpha contralateral power decrease to the attended hemifield (Kelly et al., 2009; Sauseng et al., 2005b; Yamagishi et al., 2005) linked to enhancement of neural excitability in cortical areas processing the attended stimulus. These mechanisms are not mutually exclusive, as both have been elicited together under the same experimental manipulations (Capilla et al., 2014; Doesburg et al., 2009; Rihs et al., 2009). The analysis performed on the magnetometer data did not allow us to adjudicate between these possibilities. To overtake this limitation, planar gradiometer data were analyzed in the sensor space. The time-course of alpha band activity elicited by the retro-cue corresponded with the time-course typically obtained in relation to the presentation of a stimulus (figure 12). Usually, a visual stimulus elicits an alpha band desynchronization that starts 200 ms after stimulus onset and peaks, depending on the task, around 350-650 ms after stimulus onset. This is followed by a resynchronization with a peak between 900-2000 ms (Klimesch et al., 2007). Here, alpha desynchronization was seen over posterior lateral sensors, starting around 150 ms post-cue, reaching it maximum at around 550 ms. Alpha desynchronization was more pronounced for the contralateral sensors compared to the ipsilateral sensors. In this respect, two aspects should be highlighted: first, it has been proposed that alpha band suppression reflects active information processing; second, cortical excitability results in a desynchronized EEG. Accordingly, alpha desynchronization has been interpreted as an electrophysiological correlate of cortical activation associated to sensory, cognitive or motor processing (Pfurtscheller et al., 1996). Desynchronized alpha means that the underlying neurons conforming the neural assembly are working in a desynchronized or independent way, which might imply maximum of information capacity in terms of information theory (Thatcher, McAlaster, Lester, Horst, & Cantor, 1983). Alpha desynchronization has been found in response to a variety of tasks, and has been associated to cognitive performance and intelligence. Furthermore, it has been proposed that alpha desynchronization might not respond only to bottom-up processes, but rather, it can be also triggered by top-down processes. Specifically, it has been shown that the allocation of attention to the stimulus inside the RF results in the suppression of the alpha activity in the recorded neuron (Fries et al., 2001; Fries et al., 2008). In the same way, directing attention to a stimulus in one hemifield results in alpha suppression in the contralateral hemisphere (Siegel et al., 2008; Zumer, Scheeringa, Schoffelen, Norris, & Jensen, 2014). This alpha reduction has been discovered to be already present in response to the cue before target presentation (Fries et al., 2001; Fries et al., 2008). A large body of human literature has reported desynchronization of alpha oscillations associated to covert shifts of spatial attention before target presentation (Capilla et al., 2014; Doesburg et al., 2009; Kelly et al., 2009; Rihs et al., 2009; Sauseng et al., 2005b; Thut et al., 2006; Yamagishi et al., 2005). Alpha desynchronization in contralateral posterior sensors to the attended hemifield has been reported under different experimental manipulations. It has been hypothesized that alpha desynchronization reflects changes in baseline excitability in areas involved in the processing of the upcoming stimulus. Such facilitatory function has been observed in a trial by trial basis. It has been shown that the level of prestimulus alpha correlated with later performance. Thus, lower prestimulus alpha in the contralateral hemisphere was predictive of good performance (Capilla et al., 2014; Kelly et al., 2009; Thut et al., 2006). Furthermore, studies localizing the origin of alpha suppression have found that it arises from visual areas coding for the upcoming stimulus attributes. Specifically, in Capilla et al. study (2014), in which participants were requested to discriminate a lateralized digit, alpha desynchronization emerged from ventro-lateral extrastriate visual cortex. In another study, in which the task was to judge the orientation of a bar, alpha suppression was localized in the calcarine sulcus (Yamagishi et al., 2005). These results are compatible with the hypothesis that baseline shifts of activity might reflect top-down signals that biases the upcoming sensory information. However, an alternative possibility is that baseline shifts do not arise from a memory template that include the stimulus properties of the upcoming target, and instead reflect the location of the expected target (Luck et al., 1997; McMains, Fehd, Emmanouil, & Kastner, 2007). In Mcmains et al.'s (2007) experiment, baseline shifts were found in visual representations of the attended location regardless of being an effective or ineffective stimuli. Similar results were found in Luck et al, in which equal increase in baseline activity in neurons in the extrastriate cortex was found for the effective and the ineffective stimulus. Therefore, these results could also could account for the different localizations found among the visual cortex.

Alpha desynchronization has been also observed in posterior areas during the delay of WM tasks (Gevins, Smith, McEvoy, & Yu, 1997; Sauseng et al., 2009; Sauseng et al., 2005a). Sensory recruitment models of WM postulate that the retention of information in WM is accomplished by the enrollment of the same networks engaged in perception (J Jonides et al., 1993; Pasternak & Greenlee, 2005; Postle 2006). Active maintenance of visuospatial information would be mediated by covert shifts of attention (Edward Awh & Jonides, 2001). In this way, allocation of attentional resources to the memory representations held in sensory cortices would result in an alpha suppression in the areas representing memory items. The neural generators of alpha desynchronization found in the current work are in agreement with this hypothesis. The cortical region exhibiting alpha desynchronization was the ventro-lateral occipital cortex. It is, then, very plausible that this region was involved in the processing of the stimulus. Therefore alpha suppression in this area might be interpreted as arising from attentional resources devoted to the memory representations. Remarkably, alpha desynchronization in the ventro-lateral occipital cortex was larger for load 2 compared to load 1. It has been proposed that an enhanced alpha desynchronization could be caused by the involvement of more cell assemblies in information processing (Pfurtscheller & Lopes Da Silva, 1999). Therefore, greater desynchronization for load 2 compared 1 could be the result of the enrollment of a larger neural network involved in the allocation of attention to two items compared to one. It has been shown that alpha activity is inversely related to the attentional demands of the task (Ray & Cole, 1985). During visuospatial WM, alpha activity has been shown to be modulated by tasks demands. In a visuospatial WM experiment, Sauseng et al. (2005) presented two conditions. In the retention condition participants had to maintain visuospatial information during a short interval. In the manipulation condition, participants had to additionally manipulate the visuospatial material before retention. During the delay, alpha activity was reduced in the occipital cortex. The study demonstrated that alpha desynchronization was larger during the first period of the delay period in the manipulation condition than during the retention condition. In another visuospatial WM experiment, task difficulty was manipulated, finding larger occipito-parietal decrease in the difficult task (Gevins et al., 1997). Hence, these studies showed that the amount of allocation of attention to mental representation induced different levels of alpha suppression. Here, allocation of attention to two items was likely to recruit more attentional resources, and accordingly results in a larger alpha suppression.

After the alpha suppression elicited by the retro cue, alpha resynchronized and was sustained until probe presentation. The time window that comprised the resynchronization and synchronization peak presented a lateralized cue effect. Alpha enhancement emerged from the ipsilateral occipital cortex. It has been proposed that alpha synchronization relates to the active functional inhibition of task irrelevant areas (Jensen & Mazaheri, 2010; Klimesch et al., 2007). In visuospatial attention tasks and VWM tasks it has been shown to reflect the inhibition of the unattended hemifield (Kelly et al., 2006; Worden et al., 2000). Furthermore, the retinotopic scalp distribution of ipsilateral alpha increase was dependent of the ignored locations, suggesting an active inhibitory mechanism (Rihs et al., 2007; Worden et al., 2000). Crucially, a causal relationship between alpha oscillations and the inhibition of task-irrelevant information was shown in a study by Sauseng et al., (2009) where rTMS at alpha frequencies (10 Hz) was applied over the task-irrelevant hemisphere and was associated with an improvement in WM capacity. A study localizing the neural source accounting for alpha increase has encountered a divergent result. Capilla et al. (2014) identified the parieto-occipital junction, and interpreted the alpha synchronization as a top-down signal involved in inhibiting the unattended location. However, alpha

increase occurred early on time reflecting transient shifts of attention, while synchronization in our study occurred later reflecting a more sustained process.
Alpha lateralization was only sustained until target presentation in the right condition. Although it has not been explored, this bias could be the responsible for the behavioral advantage for the right cued hemifield. Such asymmetry has been previously reported in a visuospatial attentional experiment, in which there was a performance advantage for the left hemifield, and lateralization effects were only evident for the left cue condition (Thut et al., 2006).

However, the interpretation of lateralized alpha desynchronization and synchronization must be carefully conducted. The externally induced alpha desynchronization imposed by the visual cue is superimposed to changes in alpha driven by endogenous attention. This raises two questions regarding the interpretation of the results. First, whether alpha desynchronization resulted from shifts of internal attention. Second, whether early lateralized effects resulted from physical differences of the cue and not from top-down processes. These questions were handled by comparing the spatial cuing condition to the neutral condition. Hence, the time-course of alpha activity in the neutral condition was subtracted from the orienting condition, resulting in two difference waveforms: the ipsilateral and the contralateral waveforms. Inspection of the waveforms revealed both a contralateral decreased peaking at 550 ms post-cue, and an ipsilateral synchronization peaking at 1050 ms post-cue presentation. This result argue in favor of the interpretation of a dual biasing mechanism. An initial shift of attention originates an alpha desynchronization in the contralateral hemisphere, while ipsilateral sensors tend to synchronize heavier later on time. This is in consonance with a study showing that alpha decreases occurred early and reflected shifts of attention, while alpha synchronization occurred later to sustain attention (Rihs et al., 2009). It can be arguable that the alpha desynchronization lateralized effect might be related to bottom-up processes related to the physical properties of the cue rather than reflecting the voluntary allocation of attention to memory representations. Although we cannot rule out this possibility, comparison of alpha time course of the neutral condition with the spatial condition makes it improbable. Physical properties of the neutral cue and load 2 spatial condition were equivalent for one hemifield. Thus, if alpha desynchronization was related to the physical attributes of the cue, alpha desynchronization would be expected to be similar in the contralateral hemisphere for both conditions. Furthermore, contralateral alpha desynchronization was larger and peaked later for the spatial cue than for the neutral cue, arguing in favor of a top-down modulatory mechanism. The methodological problem exposed here has been elegantly addressed by a study presenting auditory cues instead of visual cues, thus controlling for the confounding effect of stimuli induced alpha desynchronization (Thut et al., 2006). This study showed that posterior lateralized alpha band desynchronization emerged from covert shifts of attention.

4.2.3 Lateralized posterior gamma oscillatory activity

Magnetometer analysis revealed gamma synchronization in posterior sensors following the presentation of the retro-cue. Directing attention to one hemifield resulted in a contralateral gamma increased. The time course of gamma enhancement lasted from 200 to 600 ms after presentation of the retro-cue. Moreover, the source reconstruction revealed that gamma lateralization was circumscribed to the ventral-occipital cortex. Activated neural groups engage in gamma synchronization in many brain regions including the visual cortex (Fries, Nikolić, & Singer, 2007). Gamma synchronization has been related to sensory processing and the formation of coherent representations (Bertrand & Tallon-Baudry, 2000; Gray & Singer, 1989; Keil et al., 1999; Moratti et al., 2014; Catherine Tallon-Baudry & Bertrand, 1999), as well as to attentional selection and WM maintenance (Bauer et al., 2012; Fries et al., 2001; Gruber et al., 1999; Tallon-Baudry et al., 1998; Taylor et al., 2005).

Directing spatial attention towards a stimulus presented in isolation results in a better discriminability. Crucially, attention can select the relevant stimulus presented among distractors. In both cases, directing attention to a stimulus results in an increase in firing rates of the neurons processing the attended stimulus. In addition to the rate coding mechanism, attentional modulation may be also accomplished by synchronization of the spikes of the neural population. When two stimulus are competing for neural representation and attention is directed to one of them, higher-level visual areas respond as if only the attended one was presented in isolation (J H Reynolds et al., 1999; Reynolds & Chelazzi, 2004). This is a central concept in the biased competition model that supposes that neurons in lower visual areas, driven by ignored and attended stimuli, provide competitive input to higher-level target visual areas. The model states that the competition is biased by visuospatial attention to the relevant target that enhances the input neural gain for the lower-level neurons (Reynolds et al., 1999). A proposed mechanism mediating the input gain modulation is gamma band synchronization of the lower-level neurons. Precise synchronization of neural firing to the gamma cycle would allow the post-synaptic potentials to be focused in a short-time window with more probabilities to trigger activity in the target neuron, thus enhancing their postsynaptic impact. In this way, gamma synchronization of neurons in earlier stages would enable exclusive communication with later processing target neuronal group (Fries et al., 2001; Fries et al., 2008; Fries, 2005). Attentional modulation of gamma band synchronization has been observed in a variety of animal and human experiments. During stimulus presentation, gamma oscillatory enhancement in visual areas has been reported for the attended stimulus in the LFP as well as in the macroscopic EEG recording (Bauer et al., 2012; Fries et al., 2001; Fries et al., 2008; Siegel et al., 2008; Taylor et al., 2005; Womelsdorf et al., 2006). Gamma band synchronization has even seen in the absence of external stimulation with spatial attention in the prestimulus period (Fries et al., 2008). This is in accordance with Luck (1997) study in which increased firing rates were found in response to attention of the location of the neuron RF, even in the absence of stimulus. Human neuroimaging studies have also described attentional shifts of attention in the absence of external stimulation resulting in a baseline increased in a retinotopic manner (Kastner et al., 1999; Munneke et al., 2008). Despite gamma activity has not been reported in the absence of stimulation with spatial attention in the human literature, WM studies have informed gamma enhancement during the delay period (Jokisch & Jensen, 2007; Tallon-Baudry et al., 1998). It has been argued that gamma synchronization reflects sustained neural firing of WM representations. Gamma band synchronization in visual areas representing information during WM delay is likely to exert a stronger drive to higher level-processing areas (Jokisch & Jensen, 2007). In contrast, in our experiment, gamma activity was not sustained during the entire retention period; thus, instead of reflecting the sustained neural firing of WM representations, it might indicate the deployment of attention to the representation by means of the retro-cue and the subsequent selection of the task-relevant item related to a location-specific stage of processing. These two processes are considered to be mechanistically subserved by gamma band synchronization (Fries, 2009). Recently, it has been suggested that WM maintenance of information might not relay in above baseline activity. MVPA studies have found sustained specific stimulus patterns in visual areas in absence of above baseline persistent activity in those areas (Emrich et al., 2013; Harrison & Tong, 2009; Riggall & Postle, 2012; Serences et al., 2009). Additionally, it has been demonstrated that persistent delay activity reflects the focus of attention rather than the storage of information (LaRocque et al., 2013; Lewis-Peacock & Postle, 2012). Initial explanations of the retro-cue effect rested on the assumption that sustained attention was needed in order to keep the cued item in a prioritized state (Makovski & Jiang, 2007; Makovski et al., 2008; Matsukura et al., 2007; Pertzov et al., 2013). Recently, this assumption has been called into question. Shifting attention away from the cued item, has been probed not to decrease the retro-cue benefit (Hollingworth & Maxcey-Richard, 2013; Rerko et al., 2014). Thus, this studies concluded that sustained attention is not a requisite to maintain the cued representation in a state of heightened accessibility.

It is noticeable from the topography depicted in figure 11, that the significant increase in gamma power is coincident in time and space with no enhancement in alpha power. In fact, gamma power increased in the time period where gradiometer analysis revealed an alpha desynchronization. Alpha and gamma power have been shown to be anti-correlated (Haegens et al., 2010; Jokisch & Jensen, 2007; Siegel et al., 2008; Spaak et al., 2012; Kornblith, Buschman, & Miller, 2015). Monkey, as well as and human neurophysiological studies have shown that attention toward a stimulus increases higher-frequency band power and decreases lower-frequency power (Fries et al., 2008; Gregoriou et al., 2009a, 2014; Siegel et al., 2008; Siegel, Engel, & Donner, 2011). Both gamma synchronization and alpha band desynchronization have been related to neural processing. It has been argued that the desynchronization of alpha band rhythms might be a prerequisite for the development of gamma bursts (Pfurtscheller & Lopes Da Silva, 1999).

Taken together, visual gamma and alpha modulatory activity might be a consequence of the same top-down biasing mechanism, by which neural representations are selectively enhanced.

4.2.4 Lateralized posterior alpha oscillatory activity in absence of preparatory attention to the probe

The results presented so far seem to support the initial hypothesis that common top-down mechanisms modulate oscillatory activity towards an expected percept and towards representations held in WM. However, an alternative option is that modulation of oscillatory activity is not related to the allocation of attention to mnemonic representations. It is well established that during the expectation of a target, baseline activity in the visual cortex increases in the specific regions that represent the cued item (Kastner et al., 1999; Luck et al., 1997; McMains et al., 2007; Zumer et al., 2014). Similarly, alpha power is suppressed in the visual regions coding for the upcoming target (Capilla et al., 2014; Yamagishi et al., 2005). Interestingly, maintenance of visual information has been also related to the top-down modulation of visual activity in the same regions involved in the encoding of that information. In addition, top-down modulation of alpha activity has also been associated to WM maintenance (Sauseng et al., 2009; Sauseng et al., 2005a). As indicated elsewhere (Stokes, 2011), typical tasks used in the study of preparatory attention and VWM share a similar structure. One could argue that the activity following the cue, in the attentional task, or the to-be remembered stimuli in the memory task, could be reflecting the activity related to the maintenance of the mnemonic representation (or cue) or related to the expectation of the target (or probe). Transferring this reasoning to the results presented here, it is arguable that visual oscillatory modulation was elicited by the expectation to the probe, rather than to the allocation of spatial attention to the mnemonic representations. To test this alternative hypothesis, EEG activity was recorded while participants performed a retro-cue task. In this task, as usual, the cue informed the item to be remember, but differentially, the location of the probe was not predicted by the cue. Analysis of the occipital electrodes revealed an alpha lateralization. Similar to the MEG data, the retro-cue elicited an alpha desynchronization followed by a resynchronization. Crucially, despite not being predictable of probe location, statistical results revealed that alpha activity was lateralized respect to the hemifield that was retrospectively cued. During the first window, alpha activity was more strongly suppressed in the contralateral hemisphere for the left condition while it was more strongly resynchronize for the ipsilateral electrodes for the right condition. It has been shown that the degree of lateralized alpha activity declines when cue predictability decreases (Gould, Rushworth, & Nobre, 2011b), being nearly suppressed when the cue has not predictable value at all (50%) (Haegens et al., 2011). Therefore, current results support that retro-cued lateralized alpha activity is related to the shift of spatial attention to the cued memory item. Additionally, lateralized visual activity elicited by the retro-cue has been previously reported to central probes (Griffin & Nobre, 2003; Kuo et al., 2012)

It is worthily to note that alpha band synchronization was lower in the EEG than in the MEG. It could be questionable that differences in the predictability of the location of the probe in both tasks could be responsible for the divergence. Unpredictability of the probe would make alpha power to stay lower in order to perform better (Hanslmayr et al., 2007). However, when inspecting the alpha time-course of the task, it becomes apparent that baseline activity (prior stimuli presentation) was much larger in the EEG than in the MEG. Additionally, the relation to the pre-cue period is similar in both tasks. Altogether, the most reasonable explanation for the difference in alpha power could be attributable to differences in baseline activity.

A surprising finding is that alpha desynchronization was not accompanied by gamma power enhancement. Nevertheless, gamma band oscillations exhibit lower signal to noise ratio than oscillations in the alpha band (Nunez, Wingeier, & Silberstein, 2001). In fact, the TF representation of the time series data does not present induced gamma activity by the probe (not illustrated here), which in the MEG elicited a very large gamma induced activity. Therefore, the null finding of gamma power modulation could to be related to the recording technique, and not to differences in the task. Nonetheless, further studies are warranted to clarify this issue.

The present findings argue in favor of general mechanisms of top-down visual modulation. Thus, modulation of cortical excitability in the visual cortex might support a variety of high-level visual functions as preparatory attention, VWM or mental imaginary.

4.2.5 Prefrontal alpha activity associated to orienting attention to working memory representations.

In addition to the modulation of visual oscillatory activity, right IFC exhibited greater alpha power for the spatial retro-cue than for the neutral cue condition. Frontal involvement in retro-cued tasks has been previously reported. Physiological experiments comparing the effects of pre-cues and retro-cues have found similar visual modulation, but different frontal enrolment. Specifically, retro-cues elicited greater evoked activity in frontal electrodes (Griffin & Nobre, 2003). Additionally, fMRI data have revealed that retro-cues and pre-cues engage a similar network comprising occipital, parietal and frontal areas, but retro-cues show additional activations in several prefrontal regions (Nobre et al., 2004). Furthermore, functionally disrupting the right frontal cortex has been shown to impair the retro-cue trials more strongly than the pre-cue trials (Tanoue et al., 2013). One possibility is that these prefrontal regions might be involved in orienting attention to internal representations in a mnemonic context. Alternatively, PFC could be involved in the selection of the cued item surrounded by distractors (Lepsien & Nobre, 2006). A series of studies have demonstrated the involvement of the right IFG in the processing of relevant features in the presence of distraction (Zanto et al., 2010, 2011). Thus, ventrolateral PFC has been associated with the inhibition of distraction (Dolcos 2007). Additionally, it has been shown that PFC activity during the delay period is related to the maintenance of relevant items to overcome the disruption of distracting items (Feredoes et al., 2011). Thus, PFC activity has been interpreted as a top-down signal that bias sensory cortices to protect or prioritized representations against distracting information.

Although alpha synchronization in sensory regions might reflect cortical inhibition, alpha enhancement in the frontal cortex might be linked to attentional demands (Kornblith et al., 2015). It has been shown that ongoing alpha oscillations in different cortical regions play a different functional role (Mo, Schroeder, & Ding, 2011). In the context of our task, frontal alpha enhancement has been related to the manipulation of internal representations (Manza, Hau, & Leung, 2014; Sauseng et al., 2005a). Furthermore, alpha increase over PFC has been proved to enable a functional coupling with posterior regions (Sauseng et al., 2005a). Here, we interpret alpha synchronization over PFC as a top-down signal involved in the posterior neural enhancement of the prioritized item.

5 Conclusion

Conclusión

Conclusions

Directing attention to WM representations reduce WM load. Directing attention to one item has a clear benefit in performance, whereas directing to two items has a modest benefit reflected by a statistical trend.

Retrospective orienting attention to memory representations induce a similar oscillatory pattern to the previously associated to orienting attention in the perceptual domain. Contralateral occipital alpha desynchronization and contralateral occipital gamma synchronization reflect the selection of memory items, while ipsilateral alpha is associated with inhibiting distracting items.

The benefit of the retro-cues is not only related to the preparatory effect to the probe. When the location of the probe cannot be anticipated there is still a benefit in the use of the retro-cue. Furthermore, there is no interference with the probe item location, thus, supporting the removal of irrelevant items hypothesis.

In the absence of anticipation of the probe, posterior alpha band oscillations are lateralized respect to the cue. This indicates that alpha activity is related to the orientation of attention to WM representations, arguing in favor of general mechanisms of top-down modulation supporting attention to the perceptual domain and in the memory domain.

Conclusiones

La dirección de la atención hacia las representaciones mantenidas en la memoria operativa reduce la carga de memoria. Dirigir la atención sobre un ítem tiene un claro beneficio en la ejecución mientras que dirigirla sobre dos ítems conlleva un beneficio más moderado reflejado en una tendencia estadística.

Orientar la atención retrospectivamente hacia las representaciones mnémicas induce un patrón oscilatorio neuronal similar al descrito previamente asociado a la orientación de la atención en el dominio perceptivo. La desincronización de alpha y la sincronización de gamma en el córtex occipital contralateral refleja la selección de los ítems, mientras que la sincronización del alpha ipsilateral se asociada con la inhibición de los distractores.

El beneficio de la retro-clave no sólo está relacionado con el efecto de preparación hacia la prueba de memoria. Cuando la localización de la prueba no puede ser anticipada sigue existiendo un beneficio en el uso de la retro-clave. Además, el hecho de que la localización de la prueba no genere interferencia apoya la hipótesis que postula que la retro-clave elimina los ítems irrelevantes de la memoria operativa.

En ausencia de anticipación de la prueba de memoria, la actividad oscilatoria alpha está lateralizada respecto a la clave. Esto indica que la actividad oscilatoria en la banda de frecuencia alpha está relacionada con la orientación de la atención a las representaciones mantenidas en la memoria operativa, lo que apoya la idea de que mecanismos generales top-down median la orientación de la atención en los dominios perceptual y mnémico.

6 Methods

Methods

6.1 MEG experiment

6.1.1 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, 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).

6.1.2 Stimuli and tasks

The experimental task was adapted from a retro-cueing paradigm developed by Giffrin and Nobre (Giffrin & Nobre, 2003; see also Lepsien & Nobre, 2006). 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 displayed in four locations on a black background. 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 et al., 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 was present or absent in the to-be-remembered array. Following this response period, a blank screen was shown for 1800 ms before the onset of the next trial (figure 5). 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 were used in order to determine whether attention can be reoriented within WM to more than one item, such as in the perceptual space (Awh & Pashler, 2000; Makovski & Jiang, 2007; Matsukura & Vecera, 2015). The experiment lasted for ~40 min, and was performed in one single session during MEG scanning.

6.1.3 Behavioral analysis

Analysis of performance was assessed in detection rate and RTs. Detection rate was calculated as the hit minus false alarm rate. Only RTs of correct responses were included in the analysis. In order to investigate the benefit of directing attention to memory representations, an ANOVA was conducted for detection rate and another for RTs with three levels: one-element, two-element, neutral.

Differential effects of cue side were investigated on detection rates and RTs by a 2x2 ANOVA with factors cue side (left vs right) and load (one-element vs two-element).

6.1.4 Data acquisition and analysis

MEG recordings and preprocessing

MEG data were obtained with a whole-head 306-channel Vectorview system (Elekta-Neuromag, Helsinki, Finland), consisting of 102 magnetometers and 204 orthogonal planar gradiometers. Electro-oculographic (EOG) data were recorded supra- and infraorbitally (vertical EOG) as well as from the left *vs* right orbital rim (horizontal EOG). The signal was recorded continuously at a sampling rate of 600 Hz with an online bandpass filter from 0.1 to 200 Hz. The head position relative to the sensor array was measured at the beginning of the session with four head position indicator coils. Prior to the recording session, the anatomical landmarks (nasion and auricular) and extra points of the head shape were obtained with a 3D digitiser (Fastrak Polhemus, Colchester, VA, USA). Visually detectable bad channels were removed prior to signal preprocessing. External noise was removed with the signal space separation method implemented with MAX filter software (Taulu et al., 2004). Further analyses were performed with SPM8 (http://www.fil.ion.ucl.ac.uk/spm/). Data were first downsampled to 300 Hz and filtered with a high cutoff of 150 Hz. We then epoched data from 500 ms before memory array presentation to the presentation of the probe, for each trial, for each condition, for each participant. Trials were visually inspected, and rejected when they contained sensor or muscular artefacts, and/or eye blinks.

6.1.4.1 Magnetometer analysis

Time–frequency (TF) analysis

The TF decomposition was performed with a continuous Morlet wavelet transform (Mallat, 1998), from 4 to 80 Hz in 1-Hz steps, with a relation f0/rf, where rf = 1/(2prt) set to 7. Each epoch was averaged and then baseline-corrected using the average power in the 500 ms preceding the onset of the memory array (i.e., 1700 ms before cue onset) $\{P\mathit{corrected}\,(t, f) = [P\,(t, f)\ \ P\mathit{baseline}\,(f)]/P\mathit{baseline}\,(f)\}$, to obtain the induced activity in each condition. The time window of 1000 ms after retro-cue presentation was selected for analysis. TF datasets were transformed into NIfTI images. Specifically, the 4D [space (x, y), time, frequency] datasets were converted into a 3D data (channel x space x time). In this case, power was averaged in the alpha (8–14 Hz) and gamma (50– 80 Hz) bands to obtain scalp–time images. A second-level 2 by 2 ANOVA with the factors hemifield (left vs. right) and load (one element vs. two elements) was performed.

Source analysis

The linearly constrained minimum variance scalar beamformer spatial filter algorithm (Sekihara, Nagarajan, Poeppel, & Marantz, 2004), as implemented in SPM8, was used to generate maps of source activity in a 10-mm grid, with the use of a single-shell forward model fit to the inner skull surface of the inverse normalised SPM template (Nolte, 2003). Coregistration to Montreal Neurological Institute (MNI) space was carried out with the three anatomical landmarks and the extra digitalised points. The time-windows for covariance computation (and hence source inversion) windows were chosen on the basis of the sensor-level TF analysis results. For alpha band activity (8–14 Hz), a covariance window of 1000 ms after the presentation of the retro-cue was used. For gamma band activity (50–80 Hz), a window of 400 ms after the presentation of the retro-cue was used. Summary statistics images were calculated by subtracting the neutral condition image from the active conditions, generating four volumetric images for each participant. A second-level 2 by 2 ANOVA with the factors hemifield (left vs. right) and load (one element vs. two elements) was performed.

Statistics

For both source and sensor-level analysis, we corrected for multiple comparisons by using Gaussian random field theory (Kiebel & Friston, 2004a, 2004b; Worsley et al., 1996), as implemented in SPM8. At the sensor level, we produced maps of band-limited power (alpha or gamma) over time and space (at each sensor), and computed either peak-level or cluster-level significance. At the source level, we collapsed the data over time to produce volumetric images of power change (for the alpha and gamma bands), which, over space, were corrected at either the peak or the cluster level. In the case of cluster-level tests, we used a cluster-defining threshold of $p < 0.001$ (uncorrected). At the source level, we were able to bring to bear our prior hypotheses of contralateral visual cortex gamma power change, and therefore used a 2.5-cm sphere centered at the peak of ipsilateral alpha enhancement as our a priori region of interest.

6.1.4.2 Planar gradiometer analysis

Time–frequency analysis

TF representations of the data were performed convoluting trial data with Morlet wavelets (7 cycles width), for the interval 4 to 80 Hz in 1 Hz steps. TF representations were computed independently for vertical and horizontal planar gradiometers, and then averaged independently for each condition. Averaged data from the 102 pairs of channels were combined over both directions, by means of the Pythagoras rule, to obtain a single number positive-valued. Finally, averaged data were log-relative rescaled using the average power of the 200 ms preceding the onset of the memory array (i.e., 1500 ms before cue onset), to obtain TF power estimates for each subject and each condition at 102 locations.

Alpha activity (8-14 Hz) was averaged separately for each sensor, condition and participant. Channels included in the statistical analysis were chosen based on the alpha grand mean topographic distribution showing maximal cue related modulation. Different channels for the three time windows showing different modulations, desynchronization (250-550 ms after cue presentation), resynchronization (550-850 ms after cue presentation) and sustained alpha (850-1150 ms after cue presentation), were averaged for the right and the left hemisphere separately. Alpha lateralization was analyzed using a repeated-measure ANOVA (2x2x2), with the within subjects factors hemisphere (contralateral vs ipsilateral), cue side (left vs right), and load (one element vs. two elements) in each of the time-windows. Bonferroni correction was used for post-hoc comparisons.

Difference waveforms for ipsilateral and contralateral sensors were computed for the two element condition by subtracting the neutral alpha time course. A total of 5 right hemisphere and 5 left hemisphere sensors were averaged for computing the waveforms. Left and right conditions were collapsed in one condition. A one sample t-test for each time point was conducted for the ipsilateral and contralateral sensors.

Source analysis

The linearly constrained minimum variance scalar beamformer spatial filter algorithm (Sekihara et al., 2004), as implemented in SPM8, was used to generate maps of source activity in a 10-mm grid, with the use of a single-shell forward model fit to the inner skull surface of the inverse normalised SPM template (Nolte, 2003). Coregistration to MNI space was carried out with the three anatomical landmarks and the extra digitalised points. Source inversion was performed for two different time intervals using a 10% regularization. To explore the sources relative to alpha desynchronization, the time covariance window was 600 ms corresponding to 300ms-0ms before memory array presentation and 250-550 ms after cue onset. Alpha increase was explored using also a 600 ms time covariance window corresponding to 300 ms baseline and the 550-850 ms interval after cue presentation. Summary statistics images were calculated by subtracting the baseline period (300 ms before memory array presentation) image from the active time period, generating four volumetric images for each participant. The images were then smoothed using a Gaussian kernel at 10 mm FWHM and subjected to a group random effects analysis. Average effect of condition (this is, greater or lower activation than baseline), was performed independently for the right- and left-hemifield conditions for each time interval by means of Student t-test. Significant parametric maps were thresholded at $p < 0.05$ FWE for the whole brain volume. In the first time interval we were seeking for lateralization effects in alpha desynchronization. To test this hypothesis, the minimum peak value within the contralateral significant cluster and its mirrored value for each condition and subject were submitted to a 2x2x2 ANOVA with Hemisphere (ipsilateral vs contralateral), Hemifield (left vs. right), and Load (one element vs. two elements) as main factors. For the second interval, a lateralization effect was expected for alpha synchronization. To test the hypothesis, the maximum peak value within the ipsilateral significant cluster and its mirrored value for each condition and subject were submitted to a 2x2x2

ANOVA with Hemisphere (ipsilateral vs contralateral), Hemifield (left vs. right), and Load (one element vs. two elements) as main factors.

6.2 Behavioural experiment

6.2.1 Participants

Twenty adult subjects [mean age 30 years; SD = 6.35; eight males], 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).

6.2.2 Stimuli and tasks

Participants performed a retro-cueing task with two conditions separated in two blocks. The two conditions, the spatial retro-cue and the neutral condition had the same structure. At the start of each trial, participants first saw a 1000-ms white central fixation cross. This was followed by a sample memory set, consisting of four gray rectangles with different orientations displayed in four locations on a black background. 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. In the spatial retro cue condition after a 1000-ms delay interval, participants were presented with an informative spatial cue (i.e. retro-cue). The retro-cue consisted of one or arrow originating from the fixation cross pointing to one of the four locations that had been occupied by a rectangle in the memory array, thus indicating which item from the memory array was to be probed later (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 in one random location of the screen for 1500 ms, during which they were required to respond. The task was to indicate, by button press, whether the probe was identical to the cued item of the to-be-remembered array, regardless of the place of presentation. Following this response period, a blank screen was shown for 1800 ms before the onset of the next trial (figure 15). In the neutral condition the cue was not informative and participants had to make a judgment about a one of the four elements presented in the memory array. A total of 20 trials were presented for each condition.

6.2.3 Behavioral analysis

Accuracy was calculated as the rate of correct responses. To test for differences between conditions a paired t-test was conducted. RTs were not acquired due to a technical problem.

6.3 EEG experiment

6.3.1 Participants

Twenty adult subjects [mean age 30 years; SD = 6.35; eight males], 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).

6.3.2 Stimuli and tasks

The experimental task is the spatial retro-cue condition used in the behavioral experiment. At the start of each trial, participants first saw a 1000-ms white central fixation cross. This was followed by a sample memory set, consisting of four gray rectangles with different orientations displayed in four locations on a black background. 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 an informative spatial cue (i.e. retro-cue). The retro-cue consisted of one arrow originating from the fixation cross pointing to one of the four locations that had been occupied by a rectangle in the memory array, thus indicating which object from the memory array was to be probed later (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 in one random location of the screen for 1500 ms, during which they were required to respond. The task was to indicate, by button press, whether the probe was the same orientation of the cued item of the to-be-remembered array, regardless of the place of presentation. Following this response period, a blank screen was shown for 1800 ms before the onset of the next trial (figure 17). A total of 360 trials were presented. The experiment lasted for ~40 min, and was performed in one single EEG session.

6.3.3 Behavioral analysis

Accuracy was calculated as the rate of correct responses. Only RTs of correct responses were included in the analysis. To test for differences between right- and left-cue condition a 2x2 ANOVA was conducted for accuracy and reaction time with two main factors, Cue side with two levels (right vs left) and Quadrant with two levels (up vs lower).

6.3.4 Data acquisition and analysis

EEG recordings and preprocessing

EEG data were recorded with an electrode cap (ElectroCap International) in an electrically shielded room. 60 electrodes were homogeneously distributed among the scalp and referenced to the nose-tip. Horizontal and vertical EOG were also recorded. The signal was acquired continuously at a sampling rate of 420 Hz with an online band-pass filter from 0.1 to 140 Hz.

Analyses were performed with SPM8 (http://www.fil.ion.ucl.ac.uk/spm/) and in-house Matlab scripts for preprocessing. Data were first band-pass filtered with a low cut-off of 0.3 Hz and a high cut-off of 150 Hz, and then epoched to obtain 1400-ms data segments corresponding to 200 ms of baseline and 1200 ms after the retro-cue. Epoched data were analyzed during this period for each trial for each participant. Trials were visually inspected, and rejected when they contained electrode or muscular artefacts, and/or eye blinks. Similar to the MEG experiment, the attended top-left and attended bottom-left trials were collapsed to form an attended-left condition. Similarly, attended top-right and attend bottom-right were collapsed to form an attended-right condition.

Time–frequency (TF) analysis

The TF decomposition was performed with a continuous Morlet wavelet transform (Mallat, 1998), from 4 to 80 Hz in 1-Hz steps, with a relation f0/rf, where rf = 1/(2prt) set to 7. Each epoch was averaged and then log-relative transformed {P*corrected* (t, f) = [P(t, f) P*baseline* (f)]/P*baseline* (f)}, to obtain the induced activity.

Statistics

For statistical analysis six posterior electrodes showing maximal cue related modulation (O1, O2, PO7, PO8, P04 and PO3) were included. Alpha band power was averaged (8-14 Hz) separately for left and right electrodes. Three time segments (corresponding to desynchronization (250-550 ms post-cue), resynchronization (550-850 ms post-cue) and sustained power (850-1150 ms post-cue)), were averaged and tested for electrode hemisphere (left and right), hemifield cue (left and right) and time differences, in a 2x2x3 repeated-measures ANOVA. Bonferroni correction was used for post-hoc comparisons.

Glossary of terms

Glossary of terms

Assembly: A group of strongly interconnected active neurons.

Beamformer: Source reconstruction technique for M/EEG data based on the linear combination of sensor outputs. For source reconstruction, first, a source space is defined by a volumetric grid of target locations. For each target location, an optimum spatial filter is constructed formed by a set of beamformer weights. The spatial filter is then applied to the M/EEG data, by multiplying the sensor signal with its associated beamformer weight, to obtain the output of the beamformer for each target location.

BOLD: Blood Oxygenation Level Dependent signal is the standard technique to generate images in fMRI. It measures regional differences in cerebral blood flow to delineate regional activity. It relies on the principle that oxygenated blood and non-oxygenated blood has distinct neuromagnetic properties. When a specific region is activated by a task, an increase in blood flow increases which provide an increase in oxygenated blood. It is this increase in in local tissue oxygenation which is imaged.

Change detection task: first introduced by Phillips (1974) and popularized by Luck and Vogel (1997). A set of items is briefly displayed for study, followed by a retention interval. Finally, a test display is presented, and the participant must make a recognition judgment. In the *single-probed recognition* version of the task, one target is presented at a studied location. This target is either the studied item or a novel item. In the *whole-display recognition* version, a full set of items are presented at test. Either this set is the same as the original studied set, or, alternatively, one item is novel.

Covert attention: Peripheral deployment of attention to a location that is accomplished without directing eye movements toward it.

Delayed task: It refers to Delayed matching-to-sample task. It is a typical working memory paradigm in which information about a single test item has to be maintained for several seconds. Afterwards, subjects have to indicate whether a probe item matches the test item.

Downstream area: Higher processing region that receives projections from other areas.

Electroencephalography (EEG): It is a non-invasive technique used to record electrical activity of the brain by placing multiple electrodes on the scalp. EEG signal arises principally from the sum of the extracellular currents produced by the postsynaptic potentials of a large number of pyramidal neurons. These currents are distorted as they pass different brain tissues with different conductance. Due to the signal distortion, localization of its origin is not very precise.

Event related potentials: Electrical potentials generated in the brain in response to an event or stimulus. Electrical potentials that are time-locked to an event among multiple trials are averaged to extract the voltage fluctuations common to each trial that is much smaller in amplitude than the EEG noise. An ERP waveform is constituted by timed sequences of component waves, the so called ERP components that can be defined by their polarity (positive or negative voltage), timing, scalp distribution and sensitivity to task manipulation.

Familywise error (FWE): The probability of erroneously rejecting the null hypothesis (type I error) when testing when performing multiple hypothesis testing.

Feedback connections: denotes the effect/modulation on an earlier step in a processing pathway produced by a higher step. Feedback connections are defined as coming from deep or superficial layers, and terminating outside layer 4.

fMRI: It is a non-invasive neuroimaging technique that allows the mapping of human brain function. It has very good spatial resolution but very poor temporal resolution. fMRI images are based on the BOLD signal.

Functional connectivity: Measure of interdependence between different time-series in spatially distinct brain regions. In contrast to effective connectivity that measures casual relationships, functional connectivity only make statements about the observed correlations.

Granger causality analysis: Statistical method for determining directed functional ("causal") interactions from time-series data. In general terms, for two simultaneously measured time series, the first time series is said to have a causal influence on the second time series, if the variance of the prediction error for the second time series is reduced by including past measurements from the first time series in the linear regression model.

Hemifield: One of the two halves of the visual field, usually split vertically into left and right hemifield. This partition arise from the branching of the optic nerve at the optic chiasm. Visual information travels in separate pathways for each half of the visual field. Inputs in the right hemifield hit the left half of the retina and are then combined at the optic chiasm to travel to the left lateral geniculate nucleus of the thalamus and then to the striate cortex. The reverse happens for stimuli entering the left hemifield.

Induced oscillatory activity: Oscillatory activity whose latency jitters from trial to trial, so its temporal relation to the event is fairly loose. In contrast to the evoked response or ERPs, the oscillatory induced activity is canceled out when multiple trials are averaged, therefore time-varying spectral analysis of single trials must be used.

LFP: Extracellular voltage fluctuations surrounding the electrode tip which mainly originates from postsynaptic potentials.

Magnetoencephalography: It is a non-invasive technique that records the magnetic field associated to the intracellular currents produced by postsynaptic potentials in the apical dendrites of the pyramidal neurons. Unlike EEG that is sensitive to tangential and radial components of a current source, MEG is only sensitive to sources that are tangentially oriented to the scalp. Magnetic fields do not suffer from distortion across brain tissues, therefore source localization tend to be more accurate than with EEG. Brain magnetic signals are recorded with an array of superconducting quantum interference devices (SQUIDs) set in a helmet device. Head position relative to the sensor array is divergent across participants.

Magnetometers: MEG type of sensor made of a single coil loop that measures the radial component of the magnetic field that flows in or out the head. The cartography of magnetic fields can be seen as a bipolar pattern, with positive and negative maximums arranged symmetrically perpendicular to the source axis, which represent the exit and entry points of the magnetic field in and out the head (figure 20). Deeper sources are seen with the maxima more separated than closer to the skull sources.

Multivariate pattern analysis: Statistical methods to decode brain activity patterns that are distributed across neurons or cortical regions. This analysis includes methods such as pattern classification or stimulus-model-based encoding and decoding.

Neuroimaging: The set of techniques used to measure the structure and function of the brain. Here, we mainly refer to metabolic techniques such as fMRI and PET.

Oscillations: A periodic and continuous (wave-like) variation of a neural signal that reflects rhythmic shifting of neuronal excitability over a wide range of spatial and temporal scales. In general, oscillations can be characterized by their frequency, amplitude and phase. Neural oscillations have been classified into different frequency bands (delta, 1–3 Hz; theta, 4–7 Hz; alpha, 8–13 Hz; beta, 14–30 Hz; gamma, 30–80 Hz; fast, 80–200 Hz; ultra-fast, 200–600 Hz). Because most neuronal connections are local, higher frequency oscillations are confined to a small neuronal space, whereas very large networks are recruited during slow oscillations. In the cortex, LFP power is inversely proportional frequency. The oscillatory phase is defined by the angle of a sinusoidal function that is the momentary deflection of an oscillation (for example, 0° at the peak and 180° at the trough of an oscillation). In networks of synchronized neurons, the oscillatory phase determines the degree of excitability of the neurons

PET: Neuroimaging technique that measures emissions from radioactively labeled metabolically active chemicals previously injected into the bloodstream.

Phase coherence: A measure of phase synchronization between two time-series.

Planar Gradiometers: MEG type of sensor made of two identical coils connected in series. It measures the difference between the magnetic field radial components between the two coils, so it gives the gradient (or spatial derivative) between the two coils. Gradiometers tend to see only close-by sources that is sources for which outgoing and ingoing magnetic fields lead to each coil, which give opposite values on each coil. Cartography of the magnetic field gradients are seen as monopolar patterns with maxima just over the source (figure 20).

Receptive field: Of a neuron is the specific region of the visual field that would trigger the firing of that neuron.

Retinotopic: Organization that respects the topological distribution of stimuli in the retina.

Single-unit recordings: Electrophysiological method that measures the activity of single neurons using microelectrodes. Electrodes can be placed in the extracellular space, measuring neuron spikes or intracellularly providing information about the cell resting potential, postsynaptic potentials and spikes through the soma or axon.

Source reconstruction: Procedure that tries to find the current sources associated to the scalp potentials measured with EEG or MEG. First, it models the potentials associated to hypothetical current dipoles inside the brain, which is called the forward problem. Then, in conjunction with the actual M/EEG measured data, it can be used to estimate the sources that fit these measurements, what has been called the inverse problem. Since the number of current sources is superior to the number of sensors or electrodes the inverse solution is not unique. Several source reconstruction methods are possible such as distributed source models or beamformer algorithms.

Sustained delayed activity: Above baseline brain activity that persists during the maintenance period of a delayed task. It has been associated to the retention of information for short periods of time.

Synchronization: This term refers to different concepts depending on the context. Single-unit studies often use the term synchronization to refer to the correlation between spikes in different regions, or the coupling between spikes and the LFP. M/EEG and LPF studies, usually refer to the coupling between different areas or to enhanced local power. Here, in relation to our results, we use the term synchronization (des) to refer to increases (decreases) in local power.

Time-frequency analysis: Signal decomposition in the space and temporal domains simultaneously. There are a variety of techniques to calculate the time-frequency representation of a two dimensional signal. These include the short-time Fourier transform or the wavelet transform.

TMS: Non-invasive method that uses magnetic fields to stimulate small regions of the brain. In cognitive neuroscience, TMS is used to induce a transient interruption of cortical information processing in a relatively restricted area of the brain

Top-down-signal: Influence of higher-processing areas to lower ones based on previous experience and current goals.

Upstream area: Lower processing region that sends projections to higher areas.

Vogel´s paradigm: This is term is used in reference to a change detection task in which a visual hemifield is cued prior to the encoding phase.

Wavelet transform: It is a time-frequency representation. A wavelet transform is a convolution of a signal with a set of functions which are generated by translations and dilations, called wavelets, of the mother wavelet which is the main function.

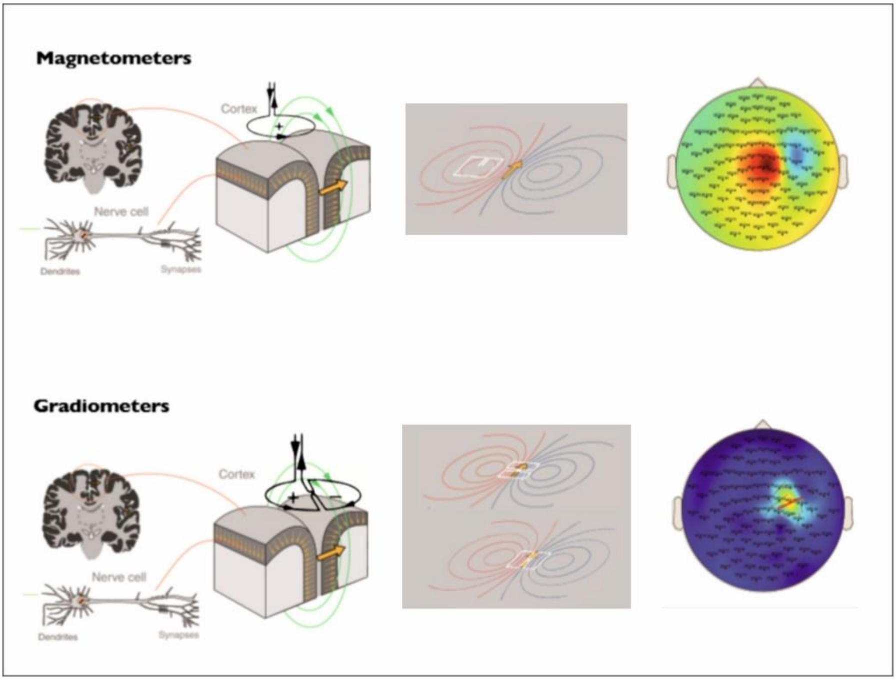

Figure 20. Magnetometers and planar gradiometers. On the left, the geometry of each sensor and the best location to record a tangential source in a sulcus. On the right, the topography arise for each type of sensor. The magnetometers present a bipolar pattern with the current source situated in the middle between of the maximum and minimum. In contrast, the gradiometers record the source just below the sensor.

Bibliography

Bibliography

Albers, A. M., Kok, P., Toni, I., Dijkerman, H. C., & De Lange, F. P. (2013). Shared representations for working memory and mental imagery in early visual cortex. *Current Biology*, *23*(15), 1427–1431. http://doi.org/10.1016/j.cub.2013.05.065

Alvarez, G. A., & Cavanagh, P. (2008). Visual short-term memory operates more efficiently on boundary features than on surface features. *Perception & Psychophysics*, *70*(2), 346–64. Retrieved from http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2621012&tool=pmcentrez&rendertype=abstract

Alvarez, G. A., Gill, J., & Cavanagh, P. (2012). Anatomical constraints on attention: hemifield independence is a signature of multifocal spatial selection. *Journal of Vision*, *12*(5), 9. http://doi.org/10.1167/12.5.9

Anderson, D. E., Ester, E. F., Serences, J. T., & Awh, E. (2013). Attending multiple items decreases the selectivity of population responses in human primary visual cortex. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *33*(22), 9273–82. http://doi.org/10.1523/JNEUROSCI.0239-13.2013

Anderson, D. E., Vogel, E. K., & Awh, E. (2011). Precision in visual working memory reaches a stable plateau when individual item limits are exceeded. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *31*(3), 1128–38. http://doi.org/10.1523/JNEUROSCI.4125-10.2011

Armstrong, K. M., Fitzgerald, J. K., & Moore, T. (2006). Changes in visual receptive fields with microstimulation of frontal cortex. *Neuron*, *50*(5), 791–8. http://doi.org/10.1016/j.neuron.2006.05.010

Astle, D. E., Scerif, G., Kuo, B.-C., & Nobre, A. C. (2009). Spatial selection of features within perceived and remembered objects. *Frontiers in Human Neuroscience*, *3*, 6. http://doi.org/10.3389/neuro.09.006.2009

Awh, E., Anllo-Vento, L., & Hillyard, S. A. (2000). The role of spatial selective attention in working memory for locations: evidence from event-related potentials. *Journal of Cognitive Neuroscience*, *12*(5), 840–7. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11054925

Awh, E., & Jonides, J. (2001). Overlapping mechanisms of attention and spatial working memory. *Trends in Cognitive Sciences*, *5*(3), 119–126. http://doi.org/10.1016/S1364-6613(00)01593-X

Awh, E., Jonides, J., Smith, E. E., Buxton, R. B., Frank, L. R., Love, T., … Gmeindl, L. (1999). Rehearsal in Spatial Working Memory: Evidence From Neuroimaging. *Psychological Science*, *10*(5), 433–437. http://doi.org/10.1111/1467-9280.00182

Awh, E., & Pashler, H. (2000). Evidence for split attentional foci. *Journal of Experimental Psychology. Human Perception and Performance*, *26*(2), 834–46. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10811179

Axmacher, N., Henseler, M. M., Jensen, O., Weinreich, I., Elger, C. E., & Fell, J. (2010). Cross-frequency coupling supports multi-item working memory in the human hippocampus. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(7), 3228–3233. http://doi.org/10.1073/pnas.0911531107

Baddeley, A. (2003). Working memory: looking back and looking forward. *Nature Reviews. Neuroscience*, *4*(10), 829–39. http://doi.org/10.1038/nrn1201

Bashinski, H. S., & Bacharach, V. R. (1980). Enhancement of perceptual sensitivity as the result of selectively attending to spatial locations. *Perception & Psychophysics*, *28*(3), 241–8. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/7433002

Bauer, M., Kluge, C., Bach, D., Bradbury, D., Heinze, H.-J., Dolan, R. J., & Driver, J. (2012). Cholinergic enhancement of visual attention and neuronal oscillations in the human brain. *Curr.Biol.*, *22*(5), 397–402. http://doi.org/10.1016/j.cub.2012.01.022

Bays, P. M., & Husain, M. (2008). Dynamic shifts of limited working memory resources in human vision. *Science (New York, N.Y.)*, *321*(5890), 851–4. http://doi.org/10.1126/science.1158023

Beauchamp, M. S., Petit, L., Ellmore, T. M., Ingeholm, J., & Haxby, J. V. (2001). A parametric fMRI study of overt and covert shifts of visuospatial attention. *NeuroImage*, *14*(2), 310–321. http://doi.org/10.1006/nimg.2001.0788

Becke, A., Müller, N., Vellage, A., Schoenfeld, M. A., & Hopf, J.-M. (2015). Neural sources of visual working memory maintenance in human parietal and ventral extrastriate visual cortex. *NeuroImage*, *110*, 78–86. http://doi.org/10.1016/j.neuroimage.2015.01.059

Berryhill, M. E., Richmond, L. L., Shay, C. S., & Olson, I. R. (2012). Shifting attention among working memory representations: Testing cue type, awareness, and strategic control. *The Quarterly Journal of Experimental Psychology*, *65*(3), 426–438. http://doi.org/10.1080/17470218.2011.604786

Bertrand, O., & Tallon-Baudry, C. (2000). Oscillatory gamma activity in humans: a possible role for object representation. *International Journal of Psychophysiology : Official Journal of the International Organization of Psychophysiology*, *38*(3), 211–223. http://doi.org/10.1016/S0167-8760(00)00166-5

Bichot, N. P., Rossi, A. F., & Desimone, R. (2005). Parallel and serial neural mechanisms for visual search in macaque area V4. *Science (New York, N.Y.)*, *308*(5721), 529–534. http://doi.org/10.1126/science.1109676

Bles, M., Schwarzbach, J., De Weerd, P., Goebel, R., & Jansma, B. M. (2006). Receptive field size-dependent attention effects in simultaneously presented stimulus displays. *NeuroImage*, *30*(2), 506–511. http://doi.org/10.1016/j.neuroimage.2005.09.042

Bollinger, J., Rubens, M. T., Zanto, T. P., & Gazzaley, A. (2010). Expectation-driven changes in cortical functional connectivity influence working memory and long-term memory performance. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *30*(43), 14399–14410. http://doi.org/10.1523/JNEUROSCI.1547-10.2010

Bonnefond, M., & Jensen, O. (2012). Alpha oscillations serve to protect working memory maintenance against anticipated distracters. *Current Biology*, *22*(20), 1969–1974. http://doi.org/10.1016/j.cub.2012.08.029

Bonnefond, M., & Jensen, O. (2015). Gamma Activity Coupled to Alpha Phase as a Mechanism for Top-Down Controlled Gating. *Plos One*, *10*(6), e0128667. http://doi.org/10.1371/journal.pone.0128667

Bosman, C. a., Schoffelen, J. M., Brunet, N., Oostenveld, R., Bastos, A. M., Womelsdorf, T., … Fries, P. (2012). Attentional Stimulus Selection through Selective Synchronization between Monkey Visual Areas. *Neuron*, *75*(5), 875–888. http://doi.org/10.1016/j.neuron.2012.06.037

Brady, T. F., Konkle, T., & Alvarez, G. A. (2011). A review of visual memory capacity: Beyond individual items and toward structured representations. *Journal of Vision*, *11*(5), 4. http://doi.org/10.1167/11.5.4

Buffalo, E. a, Fries, P., Landman, R., Buschman, T. J., & Desimone, R. (2011). Laminar differences in gamma and alpha coherence in the ventral stream. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(27), 11262–11267. http://doi.org/10.1073/pnas.1011284108/-/DCSupplemental.www.pnas.org/cgi/doi/10.1073/pnas.1011284108

Buffalo, E. a, Fries, P., Landman, R., Liang, H., & Desimone, R. (2010). A backward progression of attentional effects in the ventral stream. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(1), 361–365. http://doi.org/10.1073/pnas.0907658106

Busch, N. a, & Herrmann, C. S. (2003). Object-load and feature-load modulate EEG in a short-term memory task. *Neuroreport*, *14*(13), 1721–1724. http://doi.org/10.1097/00001756-200309150-00013

Buschman, T. J., & Miller, E. K. (2007). of Attention in the Prefrontal and. *Science*, *315*(Ci), 1860–1862. http://doi.org/10.1126/science.1138071

Capilla, A., Schoffelen, J. M., Paterson, G., Thut, G., & Gross, J. (2014). Dissociated ??-band modulations in the dorsal and ventral visual pathways in visuospatial attention and perception. *Cerebral Cortex*, *24*(2), 550–561. http://doi.org/10.1093/cercor/bhs343

Capotosto, P., Babiloni, C., Romani, G. L., & Corbetta, M. (2009). Frontoparietal cortex controls spatial attention through modulation of anticipatory alpha rhythms. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *29*(18), 5863–5872. http://doi.org/10.1523/JNEUROSCI.0539-09.2009

Cardin, J. A., Carlén, M., Meletis, K., Knoblich, U., Zhang, F., Deisseroth, K., … Moore, C. I. (2009). Driving fast-spiking cells induces gamma rhythm and controls sensory responses. *Nature*, *459*(7247), 663–7. http://doi.org/10.1038/nature08002

Carrasco, M. (2012). Visual attention : The past 25 years, *51*(13), 1484–1525. http://doi.org/10.1016/j.visres.2011.04.012.Visual

Cavada, C., & Goldman-Rakic, P. S. (1989). Posterior parietal cortex in rhesus monkey: I. Parcellation of areas based on distinctive limbic and sensory corticocortical connections. *The Journal of Comparative Neurology*, *287*(4), 393–421. http://doi.org/10.1002/cne.902870402

Chalk, M., Herrero, J. L., Gieselmann, M. a., Delicato, L. S., Gotthardt, S., & Thiele, A. (2010). Attention Reduces Stimulus-Driven Gamma Frequency Oscillations and Spike Field Coherence in V1. *Neuron*, *66*(1), 114–125. http://doi.org/10.1016/j.neuron.2010.03.013

Chelazzi, L., Duncan, J., Miller, E. K., & Desimone, R. (1998). Responses of neurons in inferior temporal cortex during memory-guided visual search. *Journal of Neurophysiology*, *80*(6), 2918–40. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9862896

Cohen, J. D., Perlstein, W. M., Braver, T. S., Nystrom, L. E., Noll, D. C., Jonides, J., & Smith, E. E. (1997). Temporal dynamics of brain activation during a working memory task. *Nature*, *386*(6625), 604–8. http://doi.org/10.1038/386604a0

Constantinidis, C., Franowicz, M. N., & Goldman-Rakic, P. S. (2001). The sensory nature of mnemonic representation in the primate prefrontal cortex. *Nature Neuroscience*, *4*(3), 311–316. http://doi.org/10.1038/85179

Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. a., … Shulman, G. L. (1998). A common network of functional areas for attention and eye movements. *Neuron*, *21*(4), 761–773. http://doi.org/10.1016/S0896-6273(00)80593-0

Corbetta, M., Kincade, J. M., & Shulman, G. L. (2002). Neural systems for visual orienting and their relationships to spatial working memory. *Journal of Cognitive Neuroscience*, *14*(3), 508–523. http://doi.org/10.1162/089892902317362029

Corbetta, M., Kincade, J., Ollinger, J., McAvoy, M., & Shulman, G. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nat Neurosci*, *3*(3), 292–297. http://doi.org/10.1038/73009

Corbetta, M., Miezin, F. M., Shulman, G. L., & Petersen, S. E. (1993). A PET study of visuospatial attention. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *13*(3), 1202–26. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/8441008

Courtney, S. M., Ungerleider, L. G., Keil, K., & Haxby, J. V. (1997). Transient and sustained activity in a distributed neural system for human working memory. *Nature*. http://doi.org/10.1038/386608a0

Cowan, N. (2001). The magical number 4 in short-term memory: a reconsideration of mental storage capacity. *The Behavioral and Brain Sciences*, *24*(1), 87–114; discussion 114–85. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11515286

Curtis, C. E. (2006). Prefrontal and parietal contributions to spatial working memory. *Neuroscience*, *139*(1), 173–180. http://doi.org/10.1016/j.neuroscience.2005.04.070

Curtis, C. E., Rao, V. Y., & D'Esposito, M. (2004). Maintenance of spatial and motor codes during oculomotor delayed response tasks. *The Journal of Neuroscience :*

The Official Journal of the Society for Neuroscience, *24*(16), 3944–52. http://doi.org/10.1523/JNEUROSCI.5640-03.2004

Desimone, R. (1995). Neural Mechanisms of Selective Visual Attention. *Annual Review of Neuroscience*, *18*(1), 193–222. http://doi.org/10.1146/annurev.neuro.18.1.193

Doesburg, S. M., Green, J. J., McDonald, J. J., & Ward, L. M. (2009). From local inhibition to long-range integration: A functional dissociation of alpha-band synchronization across cortical scales in visuospatial attention. *Brain Research*, *1303*, 97–110. http://doi.org/10.1016/j.brainres.2009.09.069

Doesburg, S. M., Roggeveen, A. B., Kitajo, K., & Ward, L. M. (2008). Large-scale gamma-band phase synchronization and selective attention. *Cerebral Cortex*, *18*(2), 386–396. http://doi.org/10.1093/cercor/bhm073

Downing, C. J. (1988). Expectancy and visual-spatial attention: effects on perceptual quality. *Journal of Experimental Psychology. Human Perception and Performance*, *14*(2), 188–202. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/2967876

Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review*, *96*(3), 433–58. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/2756067

Eckhorn, R., Bauer, R., Jordan, W., Brosch, M., Kruse, W., Munk, M., & Reitboeck, H. J. (1988). Coherent oscillations: a mechanism of feature linking in the visual cortex? Multiple electrode and correlation analyses in the cat. *Biological Cybernetics*, *60*(2), 121–30. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/3228555

Eimer, M., & Kiss, M. (2010). An electrophysiological measure of access to representations in visual working memory. *Psychophysiology*, *47*(1), 197–200. http://doi.org/10.1111/j.1469-8986.2009.00879.x

Emrich, S. M., Riggall, A. C., Larocque, J. J., & Postle, B. R. (2013). Distributed Patterns of Activity in Sensory Cortex Reflect the Memory, *33*(15), 6516–6523. http://doi.org/10.1523/JNEUROSCI.5732-12.2013

Engel, a K., Fries, P., & Singer, W. (2001). Dynamic predictions: oscillations and synchrony in top-down processing. *Nature Reviews. Neuroscience*, *2*(10), 704–716. http://doi.org/10.1038/35094565

Engel, a K., Kreiter, a K., König, P., & Singer, W. (1991). Synchronization of oscillatory neuronal responses between striate and extrastriate visual cortical areas of the cat. *Proceedings of the National Academy of Sciences of the United States of America*, *88*(14), 6048–6052. http://doi.org/10.1073/pnas.88.14.6048

Ester, E. F., Anderson, D. E., Serences, J. T., & Awh, E. (2013). A neural measure of precision in visual working memory. *Journal of Cognitive Neuroscience*, *25*(5), 754–61. http://doi.org/10.1162/jocn_a_00357

Feredoes, E., Heinen, K., Weiskopf, N., Ruff, C., & Driver, J. (2011). Causal evidence for frontal involvement in memory target maintenance by posterior brain areas during distracter interference of visual working memory, *108*(42). http://doi.org/10.1073/pnas.1106439108

Foxe, J. J., Simpson, G. V, & Ahlfors, S. P. (1998). Parieto-occipital approximately 10 Hz activity reflects anticipatory state of visual attention mechanisms. *Neuroreport*, *9*(17), 3929–3933.

Fries, P. (2005). A mechanism for cognitive dynamics: Neuronal communication through neuronal coherence. *Trends in Cognitive Sciences*, *9*(10), 474–480. http://doi.org/10.1016/j.tics.2005.08.011

Fries, P. (2009). Neuronal gamma-band synchronization as a fundamental process in cortical computation. *Annual Review of Neuroscience*, *32*, 209–224. http://doi.org/10.1146/annurev.neuro.051508.135603

Fries, P., Nikolić, D., & Singer, W. (2007). The gamma cycle. *Trends in Neurosciences*, *30*(7), 309–316. http://doi.org/10.1016/j.tins.2007.05.005

Fries, P., Reynolds, J. H., Rorie, a E., & Desimone, R. (2001). Modulation of oscillatory neuronal synchronization by selective visual attention. *Science (New York, N.Y.)*, *291*(5508), 1560–1563. http://doi.org/10.1126/science.1055465

Fries, P., Schröder, J.-H., Roelfsema, P. R., Singer, W., & Engel, A. K. (2002). Oscillatory neuronal synchronization in primary visual cortex as a correlate of stimulus selection. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *22*(9), 3739–3754. http://doi.org/20026318

Fries, P., Womelsdorf, T., Oostenveld, R., & Desimone, R. (2008). The effects of visual stimulation and selective visual attention on rhythmic neuronal synchronization in macaque area V4. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *28*(18), 4823–4835. http://doi.org/10.1523/JNEUROSCI.4499-07.2008

Funahashi, S., Bruce, C. J., & Goldman-Rakic, P. S. (1989). Mnemonic coding of visual space in the monkey's dorsolateral prefrontal cortex. *Journal of Neurophysiology*, *61*(2), 331–49. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/2918358

Fuster, J. M., & Alexander, G. E. (1971). Neuron activity related to short-term memory. *Science (New York, N.Y.)*, *173*(3997), 652–4. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/4998337

Fuster, J. M., & Jervey, J. P. (1981). Inferotemporal neurons distinguish and retain behaviorally relevant features of visual stimuli. *Science (New York, N.Y.)*, *212*(4497), 952–955. http://doi.org/10.1126/science.7233192

Gazzaley, A., Cooney, J. W., McEvoy, K., Knight, R. T., & D'Esposito, M. (2005). Top-down enhancement and suppression of the magnitude and speed of neural activity. *Journal of Cognitive Neuroscience*, *17*(3), 507–17. http://doi.org/10.1162/0898929053279522

Gazzaley, A., & Nobre, A. C. (2012). Top-down modulation: bridging selective attention and working memory. *Trends in Cognitive Sciences*, *16*(2), 129–35. http://doi.org/10.1016/j.tics.2011.11.014

Gevins, A., Smith, M. E., McEvoy, L., & Yu, D. (1997). High-resolution EEG mapping of cortical activation related to working memory: Effects of task difficulty, type of processing, and practice. *Cerebral Cortex*, *7*(4), 374–385. http://doi.org/10.1093/cercor/7.4.374

Gitelman, D. R., Nobre, a C., Parrish, T. B., LaBar, K. S., Kim, Y. H., Meyer, J. R., & Mesulam, M. M. (1999). A large-scale distributed network for covert spatial attention. *Brain*, *122*(6), 1093–1106.

Goldman-Rakic, P. S. (1995). Cellular basis of working memory. *Neuron*, *14*(3), 477–85. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/7695894

Gould, I. C., Rushworth, M. F., & Nobre, A. C. (2011a). Indexing the graded allocation of visuospatial attention using anticipatory alpha oscillations. *Journal of Neurophysiology*, *105*(3), 1318–1326. http://doi.org/10.1152/jn.00653.2010

Gould, I. C., Rushworth, M. F., & Nobre, A. C. (2011b). Indexing the graded allocation of visuospatial attention using anticipatory alpha oscillations. *Journal of Neurophysiology*, *105*(3), 1318–1326. http://doi.org/10.1152/jn.00653.2010

Gray, C. M., & Singer, W. (1989). Stimulus-specific neuronal oscillations in orientation columns of cat visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *86*(5), 1698–1702. http://doi.org/10.1073/pnas.86.5.1698

Green, J. J., & McDonald, J. J. (2006). An event-related potential study of supramodal attentional control and crossmodal attention effects. *Psychophysiology*, *43*(2), 161–71. http://doi.org/10.1111/j.1469-8986.2006.00394.x

Gregoriou, G. G., Gotts, S. J., Zhou, H., & Desimone, R. (2009a). High-frequency, long-range coupling between prefrontal and visual cortex during attention. *Science (New York, N.Y.)*, *324*(5931), 1207–1210. http://doi.org/10.1126/science.1171402

Gregoriou, G. G., Gotts, S. J., Zhou, H., & Desimone, R. (2009b). Long-range neural coupling through synchronization with attention. *Progress in Brain Research* (Vol. 176). Elsevier. http://doi.org/10.1016/S0079-6123(09)17603-3

Gregoriou, G. G., Rossi, A. F., Ungerleider, L. G., & Desimone, R. (2014). Lesions of prefrontal cortex reduce attentional modulation of neuronal responses and synchrony in V4. *Nature Neuroscience*, *17*(7), 1003–11. http://doi.org/10.1038/nn.3742

Griffin, I. C., & Nobre, A. C. (2003). Orienting attention to locations in internal representations. *Journal of Cognitive Neuroscience*, *15*(8), 1176–1194. http://doi.org/10.1162/089892903322598139

Grimault, S., Robitaille, N., Grova, C., Lina, J.-M., Dubarry, a-S., & Jolicoeur, P. (2009). Oscillatory activity in parietal and dorsolateral prefrontal cortex during retention in visual short-term memory: Additive effects of spatial attention and memory load. *Human Brain Mapping*, *30*(10), 3378–3392. http://doi.org/10.1002/hbm.20759

Gruber, T., Müller, M. M., Keil, A., & Elbert, T. (1999). Selective visual-spatial attention alters induced gamma band responses in the human EEG. *Clinical Neurophysiology : Official Journal of the International Federation of Clinical Neurophysiology*, *110*(12), 2074–85. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10616112

Gunseli, E., van Moorselaar, D., Meeter, M., & Olivers, C. N. L. (2015). The reliability of retro-cues determines the fate of noncued visual working memory representations. *Psychonomic Bulletin & Review*. http://doi.org/10.3758/s13423-014-0796-x

Haegens, S., Händel, B. F., & Jensen, O. (2011). Top-down controlled alpha band activity in somatosensory areas determines behavioral performance in a discrimination task. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *31*(14), 5197–5204. http://doi.org/10.1523/JNEUROSCI.5199-10.2011

Haegens, S., Nacher, V., Luna, R., Romo, R., & Jensen, O. (2011). -Oscillations in the monkey sensorimotor network influence discrimination performance by rhythmical inhibition of neuronal spiking. *Proceedings of the National Academy of Sciences*, *108*(48), 19377–19382. http://doi.org/10.1073/pnas.1117190108

Haegens, S., Osipova, D., Oostenveld, R., & Jensen, O. (2010). Somatosensory working memory performance in humans depends on both engagement and disengagement of regions in a distributed network. *Human Brain Mapping*, *31*(1), 26–35. http://doi.org/10.1002/hbm.20842

Han, X., Berg, A. C., Oh, H., Samaras, D., & Leung, H. C. (2013). Multi-voxel pattern analysis of selective representation of visual working memory in ventral temporal and occipital regions. *NeuroImage*, *73*, 8–15. http://doi.org/10.1016/j.neuroimage.2013.01.055

Hanslmayr, S., Aslan, A., Staudigl, T., Klimesch, W., Herrmann, C. S., & Bäuml, K. H. (2007). Prestimulus oscillations predict visual perception performance between and within subjects. *NeuroImage*, *37*(4), 1465–1473. http://doi.org/10.1016/j.neuroimage.2007.07.011

Hanslmayr, S., Klimesch, W., Sauseng, P., Gruber, W., Doppelmayr, M., Freunberger, R., & Pecherstorfer, T. (2005). Visual discrimination performance is related to decreased alpha amplitude but increased phase locking. *Neuroscience Letters*, *375*(1), 64–8. http://doi.org/10.1016/j.neulet.2004.10.092

Harrison, S. a, & Tong, F. (2009). Decoding reveals the contents of visual working memory in early visual areas. *Nature*, *458*(7238), 632–635. http://doi.org/10.1038/nature07832

Heinze, H. J., Mangun, G. R., Burchert, W., Hinrichs, H., Scholz, M., Münte, T. F., … Hundeshagen, H. (1994). Combined spatial and temporal imaging of brain activity during visual selective attention in humans. *Nature*, *372*(6506), 543–6. http://doi.org/10.1038/372543a0

Hillyard, S. a, & Anllo-Vento, L. (1998). Event-related brain potentials in the study of visual selective attention. *Proceedings of the National Academy of Sciences of the United States of America*, *95*(3), 781–787. http://doi.org/10.1073/pnas.95.3.781

Hollingworth, A., & Maxcey-Richard, A. M. (2013). Selective maintenance in visual working memory does not require sustained visual attention. *Journal of Experimental Psychology. Human Perception and Performance*, *39*(4), 1047–58. http://doi.org/10.1037/a0030238

Hoogenboom, N., Schoffelen, J. M., Oostenveld, R., & Fries, P. (2010). Visually induced gamma-band activity predicts speed of change detection in humans. *NeuroImage*, *51*(3), 1162–1167. http://doi.org/10.1016/j.neuroimage.2010.03.041

Hopf, J. M., & Mangun, G. R. (2000). Shifting visual attention in space: an electrophysiological analysis using high spatial resolution mapping. *Clinical Neurophysiology : Official Journal of the International Federation of Clinical Neurophysiology*, *111*(7), 1241–1257. http://doi.org/S1388-2457(00)00313-8 [pii]

Howard, M. W., Rizzuto, D. S., Caplan, J. B., Madsen, J. R., Lisman, J., Aschenbrenner-Scheibe, R., … Kahana, M. J. (2003). Gamma Oscillations Correlate with Working Memory Load in Humans. *Cerebral Cortex*, *13*(12), 1369–1374. http://doi.org/10.1093/cercor/bhg084

Irwin, D. E. (1991). Information integration across saccadic eye movements. *Cognitive Psychology*, *23*(3), 420–56. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/1884598

Janczyk, M., & Berryhill, M. E. (2014). Orienting attention in visual working memory requires central capacity: decreased retro-cue effects under dual-task conditions. *Attention, Perception & Psychophysics*, *76*(3), 715–24. http://doi.org/10.3758/s13414-013-0615-x

Jensen, O., Gelfand, J., Kounios, J., & Lisman, J. E. (2002). Oscillations in the alpha band (9-12 Hz) increase with memory load during retention in a short-term memory task. *Cerebral Cortex (New York, N.Y. : 1991)*, *12*(8), 877–882.

Jensen, O., Gips, B., Bergmann, T. O., & Bonnefond, M. (2014). Temporal coding organized by coupled alpha and gamma oscillations prioritize visual processing. *Trends in Neurosciences*, *37*(7), 357–369. http://doi.org/10.1016/j.tins.2014.04.001

Jensen, O., & Mazaheri, A. (2010). Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Frontiers in Human Neuroscience*, *4*(November), 186. http://doi.org/10.3389/fnhum.2010.00186

Jokisch, D., & Jensen, O. (2007). Modulation of gamma and alpha activity during a working memory task engaging the dorsal or ventral stream. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *27*(12), 3244–3251. http://doi.org/10.1523/JNEUROSCI.5399-06.2007

Jolicoeur, P., Brisson, B., & Robitaille, N. (2008). Dissociation of the N2pc and sustained posterior contralateral negativity in a choice response task. *Brain Research*, *1215*, 160–72. http://doi.org/10.1016/j.brainres.2008.03.059

Jongen, E. M. M., Smulders, F. T. Y., & Van Der Heiden, J. S. H. (2007). Lateralized ERP components related to spatial orienting: Discriminating the direction of attention from processing sensory aspects of the cue. *Psychophysiology*, *44*(6), 968–986. http://doi.org/10.1111/j.1469-8986.2007.00557.x

Jonides, J., Lacey, S. C., & Nee, D. E. (2015). Processes of Working Memory in Mind and Brain WORKING MEMORY IN THE MIND. *Society*, *14*(1), 12–15.

Jonides, J., Smith, E. E., Koeppe, R. a, Awh, E., Minoshima, S., & Mintun, M. a. (1993). Spatial Working-Memory in Humans As Revealed By Pet. *Nature*, *363*(6430), 623–625. http://doi.org/10.1038/363623a0

Kastner, S., Pinsk, M. a, De Weerd, P., Desimone, R., & Ungerleider, L. G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Ne*, *22*(4), 751–761.

Kastner, S., & Ungerleider, L. G. (2000). M ECHANISMS OF V ISUAL A TTENTION IN THE H UMAN C ORTEX *, 315–341.

Kastner, S., & Ungerleider, L. G. (2001). ScienceDirect - Neuropsychologia : The neural basis of biased competition in human visual cortex, *39*, 1263–1276. Retrieved from http://www.sciencedirect.com/science?_ob=ArticleURL&_udi=B6T0D-43YH3SD-3&_user=10&_coverDate=12/31/2001&_rdoc=1&_fmt=high&_orig=gateway&_origin=gateway&_sort=d&_docanchor=&view=c&_acct=C000050221&_version=1&_urlVersion=0&_userid=10&md5=977827dbf2b301372fd

Kastner, S., Weerd, D., P., D., R, Ungerleider, L. C. G., De Weerd, P., & Desimone, R. (1998). Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. *Science*, *282*(5386), 108–111.

Keil, a, Müller, M. M., Ray, W. J., Gruber, T., & Elbert, T. (1999). Human gamma band activity and perception of a gestalt. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *19*(16), 7152–7161.

Kelly, S. P., Gomez-Ramirez, M., & Foxe, J. J. (2009). The strength of anticipatory spatial biasing predicts target discrimination at attended locations: A high-density EEG study. *European Journal of Neuroscience*, *30*(11), 2224–2234. http://doi.org/10.1111/j.1460-9568.2009.06980.x

Kelly, S. P., Lalor, E. C., Reilly, R. B., & Foxe, J. J. (2006). Increases in alpha oscillatory power reflect an active retinotopic mechanism for distracter suppression during sustained visuospatial attention. *Journal of Neurophysiology*, *95*(6), 3844–3851. http://doi.org/10.1152/jn.01234.2005

Kiebel, S. J., & Friston, K. J. (2004a). Statistical parametric mapping for event-related potentials (II): a hierarchical temporal model. *NeuroImage*, *22*(2), 503–20. http://doi.org/10.1016/j.neuroimage.2004.02.013

Kiebel, S. J., & Friston, K. J. (2004b). Statistical parametric mapping for event-related potentials: I. Generic considerations. *NeuroImage*, *22*(2), 492–502. http://doi.org/10.1016/j.neuroimage.2004.02.012

Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in Cognitive Sciences*, *16*(12), 606–617. http://doi.org/10.1016/j.tics.2012.10.007

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Research Reviews*, *53*(1), 63–88. http://doi.org/10.1016/j.brainresrev.2006.06.003

Kornblith, S., Buschman, T. J., & Miller, E. K. (2015). Stimulus Load and Oscillatory Activity in Higher Cortex. *Cerebral Cortex (New York, N.Y. : 1991)*. http://doi.org/10.1093/cercor/bhv182

Kravitz, D. J., Saleem, K. S., Baker, C. I., & Mishkin, M. (2011). A new neural framework for visuospatial processing. *Nature Reviews. Neuroscience*, *12*(4), 217–30. http://doi.org/10.1038/nrn3008

Kravitz, D. J., Saleem, K. S., Baker, C. I., Ungerleider, L. G., & Mishkin, M. (2013). The ventral visual pathway: An expanded neural framework for the processing of object quality. *Trends in Cognitive Sciences*, *17*(1), 26–49. http://doi.org/10.1016/j.tics.2012.10.011

Kubota, K., & Niki, H. (1971). Prefrontal cortical unit activity and delayed alternation performance in monkeys. *Journal of Neurophysiology*, *34*(3), 337–47. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/4997822

Kuo, B.-C., Stokes, M. G., & Nobre, A. C. (2012). Attention Modulates Maintenance of Representations in Visual Short-term Memory. *Journal of Cognitive Neuroscience*, *24*(1), 51–60. http://doi.org/10.1162/jocn_a_00087

Lakatos, P., Shah, A. S., Knuth, K. H., Ulbert, I., Karmos, G., & Schroeder, C. E. (2005). An oscillatory hierarchy controlling neuronal excitability and stimulus processing in the auditory cortex. *Journal of Neurophysiology*, *94*(3), 1904–1911. http://doi.org/10.1152/jn.00263.2005

Landman, R., Spekreijse, H., & Lamme, V. A. F. (2003). Large capacity storage of integrated objects before change blindness. *Vision Research*, *43*(2), 149–64. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12536137

Lara, A. H., & Wallis, J. D. (2014). Executive control processes underlying multi-item working memory. *Nature Neuroscience*, *17*(6), 876–83. http://doi.org/10.1038/nn.3702

LaRocque, J. J., Lewis-Peacock, J. a, Drysdale, A. T., Oberauer, K., & Postle, B. R. (2013). Decoding attended information in short-term memory: an EEG study. *Journal of Cognitive Neuroscience*, *25*(1), 127–42. http://doi.org/10.1162/jocn_a_00305

Larocque, J. J., Lewis-Peacock, J. a, & Postle, B. R. (2014). Multiple neural states of representation in short-term memory? It’s a matter of attention. *Frontiers in Human Neuroscience*, *8*(January), 5. http://doi.org/10.3389/fnhum.2014.00005

Lebedev, M. a., Messinger, A., Kralik, J. D., & Wise, S. P. (2004). Representation of attended versus remembered locations in prefrontal cortex. *PLoS Biology*, *2*(11). http://doi.org/10.1371/journal.pbio.0020365

Lee, S.-H., Kravitz, D. J., & Baker, C. I. (2013). Goal-dependent dissociation of visual and prefrontal cortices during working memory. *Nature Neuroscience*, *16*(8), 997–9. http://doi.org/10.1038/nn.3452

Lepsien, J., & Nobre, A. C. (2006). Cognitive control of attention in the human brain: Insights from orienting attention to mental representations. *Brain Research*, *1105*(1), 20–31. http://doi.org/10.1016/j.brainres.2006.03.033

Lepsien, J., & Nobre, A. C. (2007). Attentional modulation of object representations in working memory. *Cerebral Cortex*, *17*(9), 2072–2083. http://doi.org/10.1093/cercor/bhl116

Lepsien, J., Thornton, I., & Nobre, A. C. (2011). Modulation of working-memory maintenance by directed attention. *Neuropsychologia*, *49*(6), 1569–1577. http://doi.org/10.1016/j.neuropsychologia.2011.03.011

Lewis-Peacock, J. a., & Postle, B. R. (2012). Decoding the internal focus of attention. *Neuropsychologia*, *50*(4), 470–478. http://doi.org/10.1016/j.neuropsychologia.2011.11.006

Linden, D. E. J., Bittner, R. a., Muckli, L., Waltz, J. a., Kriegeskorte, N., Goebel, R., … Munk, M. H. J. (2003). Cortical capacity constraints for visual working memory: Dissociation of fMRI load effects in a fronto-parietal network. *NeuroImage*, *20*(3), 1518–1530. http://doi.org/10.1016/j.neuroimage.2003.07.021

Lisman, J. E., & Idart, M. a. P. (1995). Oscillatory Subcycles phorylated with each quantum of released Informational input. *Science*, *267*(March), 1512–1515.

Luck, S. J., Chelazzi, L., Hillyard, S. a, & Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *Journal of Neurophysiology*, *77*(1), 24–42.

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature*, *390*(6657), 279–81. http://doi.org/10.1038/36846

Luck, S. J., & Vogel, E. K. (2013). Visual working memory capacity: From psychophysics and neurobiology to individual differences. *Trends in Cognitive Sciences*, *17*(8), 391–400. http://doi.org/10.1016/j.tics.2013.06.006

Ma, W. J., Husain, M., & Bays, P. M. (2014). Changing concepts of working memory. *Nature Neuroscience*, *17*(3), 347–356. http://doi.org/10.1038/nn.3655

Machizawa, M., Goh, C., & Driver, J. (2012). Human visual short-term memory precision can be varied at will when the number of retained items is low., (Experiment 1). http://doi.org/10.1177/0956797611431988

Magen, H., Emmanouil, T. A., McMains, S. a., Kastner, S., & Treisman, A. (2009). Attentional demands predict short-term memory load response in posterior parietal cortex. *Neuropsychologia*, *47*(8-9), 1790–1798. http://doi.org/10.1016/j.neuropsychologia.2009.02.015

Makovsik, T., & Jiang, Y. V. (2007). Distributing versus focusing attention in visual short-term memory. *Psychonomic Bulletin & Review*, *14*(6), 1072–1078. http://doi.org/10.3758/BF03193093

Makovski, T., Sussman, R., & Jiang, Y. V. (2008). Orienting attention in visual working memory reduces interference from memory probes. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *34*(2), 369–80. http://doi.org/10.1037/0278-7393.34.2.369

Mallat, S. (1998) A Wavelet Tour of Signal Processing. Academic Press, San Diego, CA.

Mangun, G. R., Hinrichs, H., Scholz, M., Mueller-Gaertner, H. W., Herzog, H., Krause, B. J., … Heinze, H. J. (2001). Integrating electrophysiology and neuroimaging of spatial selective attention to simple isolated visual stimuli. *Vision Research*, *41*(10-11), 1423–1435. http://doi.org/10.1016/S0042-6989(01)00046-3

Manza, P., Hau, C. L. V., & Leung, H.-C. (2014). Alpha power gates relevant information during working memory updating. *The Journal of Neuroscience*, *34*(17), 5998–6002. http://doi.org/10.1523/JNEUROSCI.4641-13.2014

Marshall, T. R., O'Shea, J., Jensen, O., & Bergmann, T. O. (2015). Frontal eye fields control attentional modulation of alpha and gamma oscillations in contralateral occipitoparietal cortex. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *35*(4), 1638–47. http://doi.org/10.1523/JNEUROSCI.3116-14.2015

Martínez, a, Anllo-Vento, L., Sereno, M. I., Frank, L. R., Buxton, R. B., Dubowitz, D. J., … Hillyard, S. a. (1999). Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nature Neuroscience*, *2*(4), 364–369. http://doi.org/10.1038/7274

Matsukura, M., Luck, S. J., & Vecera, S. P. (2007). Attention effects during visual short-term memory maintenance: protection or prioritization? *Perception & Psychophysics*, *69*(8), 1422–34. Retrieved from http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2150741&tool=pmcentrez&rendertype=abstract

Matsukura, M., & Vecera, S. P. (2015). Selection of multiple cued items is possible during visual short-term memory maintenance. *Attention, Perception & Psychophysics*, *77*(5), 1625–46. http://doi.org/10.3758/s13414-015-0836-2

Mazaheri, A., & Jensen, O. (2008). Asymmetric amplitude modulations of brain oscillations generate slow evoked responses. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *28*(31), 7781–7787. http://doi.org/10.1523/JNEUROSCI.1631-08.2008

Mazaheri, A., & Jensen, O. (2010). Rhythmic pulsing: linking ongoing brain activity with evoked responses. *Frontiers in Human Neuroscience*, *4*(October), 177. http://doi.org/10.3389/fnhum.2010.00177

McElree, B. (2001). Working memory and focal attention. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *27*(3), 817–35. Retrieved from http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3077110&tool=pmcentrez&rendertype=abstract

McMains, S. a, Fehd, H. M., Emmanouil, T.-A., & Kastner, S. (2007). Mechanisms of feature- and space-based attention: response modulation and baseline increases.

Journal of Neurophysiology, *98*(4), 2110–2121. http://doi.org/10.1152/jn.00538.2007

McNab, F., & Dolan, R. J. (2014). Dissociating distractor-filtering at encoding and during maintenance. *Journal of Experimental Psychology. Human Perception and Performance*, *40*(3), 960–7. http://doi.org/10.1037/a0036013

Mehta, a D., Ulbert, I., & Schroeder, C. E. (2000). Intermodal selective attention in monkeys. I: distribution and timing of effects across visual areas. *Cerebral Cortex (New York, N.Y. : 1991)*, *10*(4), 343–358. http://doi.org/10.1093/cercor/10.4.343

Miller, B. T., & D'Esposito, M. (2005). Searching for "the top" in top-down control. *Neuron*, *48*(4), 535–538. http://doi.org/10.1016/j.neuron.2005.11.002

Miller, E. K., Li, L., & Desimone, R. (1993). Activity of neurons in anterior inferior temporal cortex during a short-term memory task. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *13*(4), 1460–1478.

Mishkin, M., & Ungerleider, L. G. (1982). Contribution of striate inputs to the visuospatial functions of parieto-preoccipital cortex in monkeys. *Behavioural Brain Research*, *6*(1), 57–77. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/7126325

Mitchell, D. J., & Cusack, R. (2008). Flexible, capacity-limited activity of posterior parietal cortex in perceptual as well as visual short-term memory tasks. *Cerebral Cortex (New York, N.Y. : 1991)*, *18*(8), 1788–98. http://doi.org/10.1093/cercor/bhm205

Mo, J., Schroeder, C. E., & Ding, M. (2011). Attentional modulation of alpha oscillations in macaque inferotemporal cortex. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *31*(3), 878–882. http://doi.org/10.1523/JNEUROSCI.5295-10.2011

Moore, T., & Armstrong, K. M. (2003). Selective gating of visual signals by microstimulation of frontal cortex. *Nature*, *421*(6921), 370–3. http://doi.org/10.1038/nature01341

Moore, T., & Fallah, M. (2001). Control of eye movements and spatial attention. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(3), 1273–1276. http://doi.org/10.1073/pnas.021549498

Moran, & Desimone. (n.d.). Selective Attention Gates Visual Processing in the Extrastriate Cortex - Moran_Desimone1985.pdf.

Moratti, S., Méndez-Bértolo, C., Del-Pozo, F., & Strange, B. A. (2014). Dynamic gamma frequency feedback coupling between higher and lower order visual cortices underlies perceptual completion in humans. *NeuroImage*, *86*, 470–9. http://doi.org/10.1016/j.neuroimage.2013.10.037

Motter, B. C. (1993). Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli. *Journal of Neurophysiology*, *70*(3), 909–919. http://doi.org/0022-3077/93

Müller, M. M., Bosch, J., Elbert, T., Kreiter, a, Sosa, M. V, Sosa, P. V, & Rockstroh, B. (1996). Visually induced gamma-band responses in human electroencephalographic activity--a link to animal studies. *Experimental Brain Research. Experimentelle Hirnforschung. Experimentation Cerebrale*, *112*(1), 96–102. http://doi.org/10.1007/BF00227182

Müller, M. M., Gruber, T., & Keil, a. (2000). Modulation of induced gamma band activity in the human EEG by attention and visual information processing. *International Journal of Psychophysiology : Official Journal of the International Organization of Psychophysiology*, *38*(3), 283–299. http://doi.org/10.1016/S0167-8760(00)00171-9

Munneke, J., Belopolsky, A. V., & Theeuwes, J. (2012). Shifting Attention within Memory Representations Involves Early Visual Areas. *PLoS ONE*, *7*(4), e35528. http://doi.org/10.1371/journal.pone.0035528

Munneke, J., Heslenfeld, D. J., & Theeuwes, J. (2008). Directing attention to a location in space results in retinotopic activation in primary visual cortex. *Brain Research*, *1222*, 184–191. http://doi.org/10.1016/j.brainres.2008.05.039

Murray, S. O. (2008). The effects of spatial attention in early human visual cortex are stimulus independent. *Journal of Vision*, *8*(10), 2.1–11. http://doi.org/10.1167/8.10.2.Introduction

Niki, H., & Watanabe, M. (1976). Prefrontal unit activity and delayed response: relation to cue location versus direction of response. *Brain Research*, *105*(1), 79–88. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/1252960

Nobre, a C., Sebestyen, G. N., Gitelman, D. R., Mesulam, M. M., Frackowiak, R. S., & Frith, C. D. (1997). Functional localization of the system for visuospatial attention using positron emission tomography. *Brain : A Journal of Neurology*, *120 (Pt 3*, 515–533. http://doi.org/10.1093/brain/120.3.515

Nobre, a C., Sebestyen, G. N., & Miniussi, C. (2000). The dynmamics of shifting visuospatial attention revearled by event-related potentials. *Neuropsychologia*, *38*, 964–974.

Nobre, A. C., Coull, J. T., Maquet, P., Frith, C. D., Vandenberghe, R., & Mesulam, M. M. (2004). Orienting attention to locations in perceptual versus mental representations. *Journal of Cognitive Neuroscience*, *16*(3), 363–73. http://doi.org/10.1162/089892904322926700

Nolte, G. (2003). The magnetic lead field theorem in the quasi-static approximation and its use for magnetoencephalography forward calculation in realistic volume conductors. *Physics in Medicine and Biology*, *48*(22), 3637–52. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/14680264

Nunez, P. L., Wingeier, B. M., & Silberstein, R. B. (2001). Spatial-temporal structures of human alpha rhythms: Theory, microcurrent sources, multiscale measurements, and global binding of local networks. *Human Brain Mapping*, *13*(3), 125–164. http://doi.org/10.1002/hbm.1030

Oberauer, K. (2002). Access to information in working memory: exploring the focus of attention. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *28*(3), 411–21. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12018494

Offen, S., Schluppeck, D., & Heeger, D. J. (2009). The role of early visual cortex in visual short-term memory and visual attention. *Vision Research*, *49*(10), 1352–1362. http://doi.org/10.1016/j.visres.2007.12.022

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, *9*(1), 97–113. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/5146491

Osipova, D., Hermes, D., & Jensen, O. (2008). Gamma power is phase-locked to posterior alpha activity. *PLoS ONE*, *3*(12), e3990. http://doi.org/10.1371/journal.pone.0003990

Palmer, J. (1990). Attentional limits on the perception and memory of visual information. *Journal of Experimental Psychology. Human Perception and Performance*, *16*(2), 332–50. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/2142203

Palva, S., & Palva, J. M. (2007). New vistas for alpha-frequency band oscillations. *Trends in Neurosciences*, *30*(4), 150–8. http://doi.org/10.1016/j.tins.2007.02.001

Pasternak, T., & Greenlee, M. W. (2005). Working memory in primate sensory systems. *Nature Reviews. Neuroscience*, *6*(2), 97–107. http://doi.org/10.1038/nrn1603

Pertzov, Y., Bays, P. M., Joseph, S., & Husain, M. (2013). Rapid forgetting prevented by retrospective attention cues. *Journal of Experimental Psychology. Human Perception and Performance*, *39*(5), 1224–31. http://doi.org/10.1037/a0030947

Pesaran, B., Pezaris, J. S., Sahani, M., Mitra, P. P., & Andersen, R. a. (2002). Temporal structure in neuronal activity during working memory in macaque parietal cortex. *Nature Neuroscience*, *5*(8), 805–811. http://doi.org/10.1038/nn890

Pessoa, L., Gutierrez, E., Bandettini, P. a., & Ungerleider, L. G. (2002). Neural Correlates of Visual Working Memory. *Neuron*, *35*(5), 975–987. http://doi.org/10.1016/S0896-6273(02)00817-6

Petrides, M. (2000). The role of the mid-dorsolateral prefrontal cortex in working memory. *Experimental Brain Research*, *133*(1), 44–54. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10933209

Pfurtscheller, G., & Lopes Da Silva, F. H. (1999). Event-related EEG/MEG synchronization and desynchronization: Basic principles. *Clinical Neurophysiology*, *110*(11), 1842–1857. http://doi.org/10.1016/S1388-2457(99)00141-8

Pfurtscheller, G., Stancák, a., & Neuper, C. (1996). Event-related synchronization (ERS) in the alpha band - An electrophysiological correlate of cortical idling: A review. *International Journal of Psychophysiology*, *24*(1-2), 39–46. http://doi.org/10.1016/S0167-8760(96)00066-9

Poch, C., Campo, P., & Barnes, G. R. (2014). Modulation of alpha and gamma oscillations related to retrospectively orienting attention within working memory. *European Journal of Neuroscience*, *40*(2), 2399–2405.

Posner, M. I. (1980). Orienting of attention. *The Quarterly Journal of Experimental Psychology*, *32*(1), 3–25. http://doi.org/10.1080/00335558008248231

Postle, B. R. (2006). Working memory as an emergent property of the mind and brain. *Neuroscience*, *139*(1), 23–38. http://doi.org/10.1016/j.neuroscience.2005.06.005

Postle, B. R., Awh, E., Jonides, J., Smith, E. E., & D'Esposito, M. (2004). The where and how of attention-based rehearsal in spatial working memory. *Cognitive Brain Research*, *20*(2), 194–205. http://doi.org/10.1016/j.cogbrainres.2004.02.008

Postle, B. R., & Druzgal, T. J. (2003). Special Issue Seeking the Neural Substrates of Visual. *Cortex*, *3*(39), 927–946. http://doi.org/10.1016/S0010-9452(08)70871-2

PribramKH,AhumadaA,HartogJ,RoosL.1964.Aprogressreportontheneurologicalprocessesdisturbed by frontal lesions in primates. In The Frontal Cortex and Behavior, ed. JM Warren, K Akert, pp. 28–55. New York: McGraw-Hill

Ranganath, C., DeGutis, J., & D'Esposito, M. (2004). Category-specific modulation of inferior temporal activity during working memory encoding and maintenance. *Cognitive Brain Research*, *20*(1), 37–45. http://doi.org/10.1016/j.cogbrainres.2003.11.017

Ray, W. J., & Cole, H. W. (1985). EEG alpha activity reflects attentional demands, and beta activity reflects emotional and cognitive processes. *Science (New York, N.Y.)*, *228*(4700), 750–752. http://doi.org/10.1126/science.3992243

Rerko, L., Souza, A. S., & Oberauer, K. (2014). Retro-cue benefits in working memory without sustained focal attention. *Memory & Cognition*, *42*(5), 712–28. http://doi.org/10.3758/s13421-013-0392-8

Reynolds, J. H., & Chelazzi, L. (2004). Attentional modulation of visual processing. *Annual Review of Neuroscience*, *27*, 611–647. http://doi.org/10.1146/annurev.neuro.26.041002.131039

Reynolds, J. H., Chelazzi, L., & Desimone, R. (1999). Competitive mechanisms subserve attention in macaque areas V2 and V4. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *19*(5), 1736–1753.

Reynolds, J. H., Pasternak, T., & Desimone, R. (2000). Attention increases sensitivity of V4 neurons. *Neuron*, *26*(3), 703–14. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10896165

Riggall, a. C., & Postle, B. R. (2012). The Relationship between Working Memory Storage and Elevated Activity as Measured with Functional Magnetic Resonance Imaging. *Journal of Neuroscience*, *32*(38), 12990–12998. http://doi.org/10.1523/JNEUROSCI.1892-12.2012

Rihs, T. a, Michel, C. M., & Thut, G. (2007). Mechanisms of selective inhibition in visual spatial attention are indexed by alpha-band EEG synchronization. *The European Journal of Neuroscience*, *25*(2), 603–10. http://doi.org/10.1111/j.1460-9568.2007.05278.x

Rihs, T. a., Michel, C. M., & Thut, G. (2009). A bias for posterior ??-band power suppression versus enhancement during shifting versus maintenance of spatial attention. *NeuroImage*, *44*(1), 190–199. http://doi.org/10.1016/j.neuroimage.2008.08.022

Rizzolatti, G., Riggio, L., Dascola, I., & Umiltá, C. (1987). Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. *Neuropsychologia*, *25*(1A), 31–40. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/3574648

Romei, V., Gross, J., & Thut, G. (2010). On the role of prestimulus alpha rhythms over occipito-parietal areas in visual input regulation: correlation or causation? *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *30*(25), 8692–8697. http://doi.org/10.1523/JNEUROSCI.0160-10.2010

Rowe, J. B., Toni, I., Josephs, O., Frackowiak, R. S., & Passingham, R. E. (2000). The prefrontal cortex: response selection or maintenance within working memory? *Science (New York, N.Y.)*, *288*(5471), 1656–1660. http://doi.org/10.1109/SSBI.2002.1233973

Ruchkin, D. S., Grafman, J., Cameron, K., & Berndt, R. S. (2003). Working memory retention systems: a state of activated long-term memory. *The Behavioral and Brain Sciences*, *26*(6), 709–728; discussion 728–777. http://doi.org/10.1017/S0140525X03000165

Rutman, A. M., Clapp, W. C., Chadick, J. Z., & Gazzaley, A. (2009). Early top-down control of visual processing predicts working memory performance. *Journal of Cognitive Neuroscience*, *22*(6), 1224–34. http://doi.org/10.1162/jocn.2009.21257

Salinas, E., & Sejnowski, T. J. (2001). Correlated neuronal activity and the flow of neural information. *Nature Reviews. Neuroscience*, *2*(8), 539–50. http://doi.org/10.1038/35086012

Salmela, V. R., Lähde, M., & Saarinen, J. (2012). Visual working memory for amplitude-modulated shapes. *Journal of Vision*, *12*(6), 2. http://doi.org/10.1167/12.6.2

Sauseng, P., Feldheim, J. F., Freunberger, R., & Hummel, F. C. (2011). Right prefrontalTMS disrupts interregional anticipatory EEG alpha activity during shifting of visuospatial attention. *Frontiers in Psychology*, *2*(OCT), 241. http://doi.org/10.3389/fpsyg.2011.00241

Sauseng, P., Klimesch, W., Doppelmayr, M., Pecherstorfer, T., Freunberger, R., & Hanslmayr, S. (2005a). EEG alpha synchronization and functional coupling during top-down processing in a working memory task. *Human Brain Mapping*, *26*(2), 148–155. http://doi.org/10.1002/hbm.20150

Sauseng, P., Klimesch, W., Heise, K. F., Gruber, W. R., Holz, E., Karim, a a, … Hummel, F. (2009). Brain oscillatory substrates of visual short-term memory capacity: Supplementary Materials. *Current Biology*, *19*(21), 1846–1852. http://doi.org/10.1016/j.cub.2009.08.062

Sauseng, P., Klimesch, W., Stadler, W., Schabus, M., Doppelmayr, M., Hanslmayr, S., … Birbaumer, N. (2005b). A shift of visual spatial attention is selectively associated with human EEG alpha activity. *European Journal of Neuroscience*, *22*(11), 2917–2926. http://doi.org/10.1111/j.1460-9568.2005.04482.x

Scheeringa, R., Petersson, K. M., Oostenveld, R., Norris, D. G., Hagoort, P., & Bastiaansen, M. C. M. (2009). Trial-by-trial coupling between EEG and BOLD identifies networks related to alpha and theta EEG power increases during working memory maintenance. *NeuroImage*, *44*(3), 1224–1238. http://doi.org/10.1016/j.neuroimage.2008.08.041

Sekihara, K., Nagarajan, S. S., Poeppel, D., & Marantz, A. (2004). Asymptotic SNR of scalar and vector minimum-variance beamformers for neuromagnetic source reconstruction. *IEEE Transactions on Bio-Medical Engineering*, *51*(10), 1726–34. http://doi.org/10.1109/TBME.2004.827926

Serences, J. T., Ester, E. F., Vogel, E. K., & Awh, E. (2009). Stimulus-specific delay activity in human primary visual cortex. *Psychological Science : A Journal of the American Psychological Society / APS*, *20*(2), 207–214. http://doi.org/10.1111/j.1467-9280.2009.02276.

Sheremata, S. L., Bettencourt, K. C., & Somers, D. C. (2010). Hemispheric asymmetry in visuotopic posterior parietal cortex emerges with visual short-term memory load. *The Journal of Neuroscience : The Official Journal of the Society for*

Neuroscience, 30(38), 12581–12588. http://doi.org/10.1523/JNEUROSCI.2689-10.2010

Sheremata, S., & Shomstein, S. (2014). Hemifield asymmetries differentiate VSTM for single- and multiple-feature objects. *Attention, Perception & Psychophysics*, 76(6), 1609–19. http://doi.org/10.3758/s13414-014-0689-0

Siegel, M., Donner, T. H., Oostenveld, R., Fries, P., & Engel, A. K. (2008). Neuronal Synchronization along the Dorsal Visual Pathway Reflects the Focus of Spatial Attention. *Neuron*, *60*(4), 709–719. http://doi.org/10.1016/j.neuron.2008.09.010

Siegel, M., Engel, A. K., & Donner, T. H. (2011). Cortical network dynamics of perceptual decision-making in the human brain. *Frontiers in Human Neuroscience*, *5*(February), 21. http://doi.org/10.3389/fnhum.2011.00021

Sligte, I. G., Scholte, H. S., & Lamme, V. A. F. (2008). Are there multiple visual short-term memory stores? *PloS One*, *3*(2), e1699. http://doi.org/10.1371/journal.pone.0001699

Sokolov, A., Lutzenberger, W., Pavlova, M., Preissl, H., Braun, C., & Birbaumer, N. (1999). Gamma-band MEG activity to coherent motion depends on task-driven attention. *Neuroreport*, *10*(10), 1997–2000. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10424663

Soto, D., Humphreys, G. W., & Rotshtein, P. (2007). Dissociating the neural mechanisms of memory-based guidance of visual selection. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(43), 17186–91. http://doi.org/10.1073/pnas.0703706104

Souza, A. S., Rerko, L., & Oberauer, K. (2014). Unloading and reloading working memory: attending to one item frees capacity. *Journal of Experimental Psychology. Human Perception and Performance*, *40*(3), 1237–56. http://doi.org/10.1037/a0036331

Spaak, E., Bonnefond, M., Maier, A., Leopold, D. a., & Jensen, O. (2012). Layer-specific entrainment of gamma-band neural activity by the alpha rhythm in monkey visual cortex. *Current Biology*, *22*(24), 2313–2318. http://doi.org/10.1016/j.cub.2012.10.020

Sperling, G. (1960). The information available in brief visual presentations. Psychological Monographs, 74, 1–29.

Spitzer, H., Desimone, R., & Moran, J. (1988). Increased attention enhances both behavioral and neuronal performance. *Science (New York, N.Y.)*, *240*(4850), 338–40. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/3353728

Sreenivasan, K. K., Curtis, C. E., & D'Esposito, M. (2014). Revisiting the role of persistent neural activity during working memory. *Trends in Cognitive Sciences*, *18*(2), 82–89. http://doi.org/10.1016/j.tics.2013.12.001

Sreenivasan, K. K., Gratton, C., Vytlacil, J., & D'Esposito, M. (2014). Evidence for working memory storage operations in perceptual cortex. *Cognitive, Affective, & Behavioral Neuroscience*, *14*(1), 117–128. http://doi.org/10.3758/s13415-013-0246-7

Stam, C. J., Pijn, J. P., Suffczynski, P., & Lopes da Silva, F. H. (1999). Dynamics of the human alpha rhythm: evidence for non-linearity? *Clinical Neurophysiology : Official Journal of the International Federation of Clinical Neurophysiology*, *110*(10), 1801–13. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10574295

Stokes, M. G. (2011). Top-down visual activity underlying VWM and preparatory attention. *Neuropsychologia*, *49*(6), 1425–1427. http://doi.org/10.1016/j.neuropsychologia.2011.02.004

Thatcher, R. W., McAlaster, R., Lester, M. L., Horst, R. L., & Cantor, D. S. (1983). Hemispheric EEG asymmetries related to cognitive functioning in children. In A. Perecuman, Cognitie Processing in the Right Hemisphere (pp. 125–145). New York: Academic Press.

Tallon-Baudry, C., & Bertrand, O. (1999). Oscillatory gamma activity in humans and its role in object representation. *Trends in Cognitive Sciences*, *3*(4), 151–162. http://doi.org/10.1016/S1364-6613(99)01299-1

Tallon-Baudry, C., Bertrand, O., Delpuech, C., & Pernier, J. (1996). Stimulus specificity of phase-locked and non-phase-locked 40 Hz visual responses in human. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *16*(13), 4240–4249.

Tallon-Baudry, C., Bertrand, O., Peronnet, F., & Pernier, J. (1998). Induced gamma-band activity during the delay of a visual short-term memory task in humans. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *18*(11), 4244–4254.

Tanoue, R. T., Jones, K. T., Peterson, D. J., & Berryhill, M. E. (2013). Differential frontal involvement in shifts of internal and perceptual attention. *Brain Stimulation*, *6*(4), 675–682. http://doi.org/10.1016/j.brs.2012.11.003

Taylor, K., Mandon, S., Freiwald, W. a., & Kreiter, a. K. (2005). Coherent oscillatory activity in monkey area v4 predicts successful allocation of attention. *Cerebral Cortex*, *15*(9), 1424–1437. http://doi.org/10.1093/cercor/bhi023

Thiebaut de Schotten MT, Dell'Acqua F, Forkel SJ, Simmons A, Vergani F, MurphyDG,CataniM (2011) Alateralizedbrainnetworkforvisuospatial attention. Nat Neurosci 14:1245–1246. CrossRef Medline

Thut, G., Nietzel, A., Brandt, S. a, & Pascual-Leone, A. (2006). Alpha-band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *26*(37), 9494–9502. http://doi.org/10.1523/JNEUROSCI.0875-06.2006

Tiesinga, P. H., Fellous, J.-M., Salinas, E., José, J. V, & Sejnowski, T. J. Inhibitory synchrony as a mechanism for attentional gain modulation. *Journal of Physiology, Paris*, *98*(4-6), 296–314. http://doi.org/10.1016/j.jphysparis.2005.09.002

Todd, J. J., & Marois, R. (2004). Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature*, *428*(6984), 751–754. http://doi.org/10.1038/nature02466

Trapp, S., & Lepsien, J. (2012). Attentional orienting to mnemonic representations: Reduction of load-sensitive maintenance-related activity in the intraparietal sulcus. *Neuropsychologia*, *50*(12), 2805–2811. http://doi.org/10.1016/j.neuropsychologia.2012.08.003

Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, *12*(1), 97–136. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/7351125

Tuladhar, A. M., Ter Huurne, N., Schoffelen, J. M., Maris, E., Oostenveld, R., & Jensen, O. (2007). Parieto-occipital sources account for the increase in alpha activity with working memory load. *Human Brain Mapping*, *28*(8), 785–792. http://doi.org/10.1002/hbm.20306

Ungerleider, L. G., Gaffan, D., & Pelak, V. S. (1989). Projections from inferior temporal cortex to prefrontal cortex via the uncinate fascicle in rhesus monkeys. *Experimental Brain Research*, *76*(3), 473–84. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/2792241

Van de Ven, V., Jacobs, C., & Sack, a. T. (2012). Topographic Contribution of Early Visual Cortex to Short-Term Memory Consolidation: A Transcranial Magnetic Stimulation Study. *Journal of Neuroscience*, *32*(1), 4–11. http://doi.org/10.1523/JNEUROSCI.3261-11.2012

Van Dijk, H., van der Werf, J., Mazaheri, A., Medendorp, W. P., & Jensen, O. (2010). Modulations in oscillatory activity with amplitude asymmetry can produce cognitively relevant event-related responses. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(2), 900–905. http://doi.org/10.1073/pnas.0908821107

Verghese, P. (2001). Visual search and attention: a signal detection theory approach. *Neuron*, *31*(4), 523–35. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11545712

Vogel, E. K., & Machizawa, M. G. (2004). Vogel2004, *428*(April), 1997–2000. http://doi.org/10.1038/nature02447

Vogel, E. K., McCollough, A. W., & Machizawa, M. G. (2005). Neural measures reveal individual differences in controlling access to working memory. *Nature*, *438*(7067), 500–503. http://doi.org/10.1038/nature04171

Von der Malsburg, C. (1995). Binding in models of perception and brain function. *Current Opinion in Neurobiology*, *5*(4), 520–6. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/7488855

Von Stein, a, Chiang, C., & König, P. (2000). Top-down processing mediated by interareal synchronization. *Proceedings of the National Academy of Sciences of the United States of America*, *97*(26), 14748–14753. http://doi.org/10.1073/pnas.97.26.14748

Voytek, B., Canolty, R. T., Shestyuk, A., Crone, N. E., Parvizi, J., & Knight, R. T. (2010). Shifts in gamma phase-amplitude coupling frequency from theta to alpha over posterior cortex during visual tasks. *Frontiers in Human Neuroscience*, *4*(October), 191. http://doi.org/10.3389/fnhum.2010.00191

Webster, M. J., Bachevalier, J., & Ungerleider, L. G. Connections of inferior temporal areas TEO and TE with parietal and frontal cortex in macaque monkeys. *Cerebral Cortex (New York, N.Y. : 1991)*, *4*(5), 470–83. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/7530521

Wiegand, I., Töllner, T., Habekost, T., Dyrholm, M., Müller, H. J., & Finke, K. (2014). Distinct neural markers of TVA-based visual processing speed and short-term storage capacity parameters. *Cerebral Cortex (New York, N.Y. : 1991)*, *24*(8), 1967–78. http://doi.org/10.1093/cercor/bht071

Wilken, P., & Ma, W. J. (2004). A detection theory account of change detection. *Journal of Vision*, *4*(12), 1120–35. http://doi.org/10:1167/4.12.11

Williams, M., & Woodman, G. F. (2012). Directed forgetting and directed remembering in visual working memory. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *38*(5), 1206–20. http://doi.org/10.1037/a0027389

Wilson, F. A., Scalaidhe, S. P., & Goldman-Rakic, P. S. (1993). Dissociation of object and spatial processing domains in primate prefrontal cortex. *Science (New York, N.Y.)*, *260*(5116), 1955–8. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/8316836

Womelsdorf, T., & Fries, P. (2007). The role of neuronal synchronization in selective attention. *Current Opinion in Neurobiology*, *17*(2), 154–160. http://doi.org/10.1016/j.conb.2007.02.002

Womelsdorf, T., Fries, P., Mitra, P. P., & Desimone, R. (2006). Gamma-band synchronization in visual cortex predicts speed of change detection. *Nature*, *439*(7077), 733–736. http://doi.org/10.1038/nature04258

Womelsdorf, T., Schoffelen, J.-M., Oostenveld, R., Singer, W., Desimone, R., Engel, A. K., & Fries, P. (2007). Modulation of neuronal interactions through neuronal synchronization. *Science (New York, N.Y.)*, *316*(5831), 1609–1612. http://doi.org/10.1126/science.1139597

Woodman, G. F., Vogel, E. K., & Luck, S. J. (2012). Flexibility in Visual Working Memory: Accurate Change Detection in the Face of Irrelevant Variations in Position. *Visual Cognition*, *20*(1), 1–28. http://doi.org/10.1080/13506285.2011.630694

Worden, M. S., Foxe, J. J., Wang, N., & Simpson, G. V. (2000). Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *20*(6), RC63.

Worsley, K. J., Marrett, S., Neelin, P., Vandal, A. C., Friston, K. J., & Evans, A. C. (1996). A unified statistical approach for determining significant signals in images of cerebral activation. *Human Brain Mapping*, *4*(1), 58–73. http://doi.org/10.1002/(SICI)1097-0193(1996)4:1<58::AID-HBM4>3.0.CO;2-O

Xing, Y., Ledgeway, T., McGraw, P. V, & Schluppeck, D. (2013). Decoding working memory of stimulus contrast in early visual cortex. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *33*(25), 10301–11. http://doi.org/10.1523/JNEUROSCI.3754-12.2013

Xu, Y., & Chun, M. M. (2006). Dissociable neural mechanisms supporting visual short-term memory for objects. *Nature*, *440*(7080), 91–95. http://doi.org/10.1038/nature04262

Yamagishi, N., Goda, N., Callan, D. E., Anderson, S. J., & Kawato, M. (2005). Attentional shifts towards an expected visual target alter the level of alpha-band oscillatory activity in the human calcarine cortex. *Cognitive Brain Research*, *25*(3), 799–809. http://doi.org/10.1016/j.cogbrainres.2005.09.006

Zanto, T. P., & Gazzaley, A. (2009). Neural suppression of irrelevant information underlies optimal working memory performance. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *29*(10), 3059–3066. http://doi.org/10.1523/JNEUROSCI.4621-08.2009

Zanto, T. P., Rubens, M. T., Bollinger, J., & Gazzaley, A. (2010). Top-down modulation of visual feature processing: The role of the inferior frontal junction. *NeuroImage*, *53*(2), 736–745. http://doi.org/10.1016/j.neuroimage.2010.06.012

Zanto, T. P., Rubens, M. T., Thangavel, A., & Gazzaley, A. (2011). Causal role of the prefrontal cortex in top-down modulation of visual processing and working memory. *Nature Neuroscience*, *14*(5), 656–661. http://doi.org/10.1038/nn.2773

Zhang, W., & Luck, S. J. (2008). Discrete fixed-resolution representations in visual working memory. *Nature*, *453*(7192), 233–235. http://doi.org/10.1038/nature06860

Zokaei, N., Manohar, S., Husain, M., & Feredoes, E. (2013). Causal Evidence for a Privileged Working Memory State in Early Visual Cortex. *Journal of Neuroscience*, *34*(1), 158–162. http://doi.org/10.1523/JNEUROSCI.2899-13.2014

Zokaei, N., Ning, S., Manohar, S., Feredoes, E., & Husain, M. (2014). Flexibility of representational states in working memory. *Frontiers in Human Neuroscience*, *8*(November), 1–12. http://doi.org/10.3389/fnhum.2014.00853

Zumer, J. M., Scheeringa, R., Schoffelen, J.-M., Norris, D. G., & Jensen, O. (2014). Occipital alpha activity during stimulus processing gates the information flow to object-selective cortex. *PLoS Biology*, *12*(10), e1001965. http://doi.org/10.1371/journal.pbio.1001965