UNIVERSITÀ
DEGLI STUDI
DI PADOVA

Università degli Studi di Padova
Dipartimento di Psicologia Generale

SCUOLA DI DOTTORATO DI RICERCA IN PSICOLOGIA
INDIRIZZO SCIENZE COGNITIVE
XXV CICLO

MECHANISMS OF TOP-DOWN VISUAL SPATIAL ATTENTION: COMPUTATIONAL AND BEHAVIORAL INVESTIGATIONS

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This thesis examines the mechanisms underlying visual spatial attention. In particular I focused on top-down or voluntary attention, namely the ability to select relevant information and discard the irrelevant according to our goals. Given the limited processing resources of the human brain, which does not allow to process all the available information to the same degree, the ability to correctly allocate processing resources is fundamental for the accomplishment of most everyday tasks. The cost of misoriented attention is that we could miss some relevant information, with potentially serious consequences.

In the first study (chapter 2) I will address the issue of the neural substrates of visual spatial attention: what are the neural mechanisms that allow the deployment of visual spatial attention? According to the premotor theory orienting attention to a location in space is equivalent to planning an eye movement to the same location, an idea strongly supported by neuroimaging and neurophysiological evidence. Accordingly, in this study I will present a model that can account for several attentional effects without requiring additional mechanisms separate from the circuits that perform sensorimotor transformations for eye movements. Moreover, it includes a mechanism that allows, within the framework of the premotor theory, to explain dissociations between attention and eye movements that may be invoked to disprove it. In the second model presented (chapter 3) I will further investigate the computational mechanisms underlying sensorimotor transformations. Specifically I will show that a representation in which the amplitude of visual responses is modulated by postural signal is both efficient and plausible, emerging also in a neural network model trained through unsupervised learning (i.e., using only signals locally available at the neuron level). Ultimately this result gives additional support to the approach adopted in the first model.

Next, I will present a series of behavioral studies: in the first (chapter 4) I will show that spatial constancy of attention (i.e., the ability to sustain attention at a spatial location across eye movements) is dependent on some properties of the image, namely the presence of continuous visual landmarks at the attended locations. Importantly, this finding helps resolve contrasts between several recent results. In the second behavioral study (chapter 5), I will investigate an often neglected aspect of spatial cueing paradigms, probably the most widely used technique in studies of covert attention: the role of cue predictivity (i.e. the extent to which the spatial cue correctly indicates the location where the target stimulus will appear). Results show that, independently of participant's awareness, changes in predictivity result in changes in spatial validity effects, and that reliable shifts of attention can take place also in the absence of a predictive cue. In sum the results question the appropriateness of using predictive cues for delineating pure voluntary shifts of spatial attention. Finally, in the last study I will use a psychophysiological measure, the diameter of the eye's pupil, to investigate *intensive* aspects of attention. Event-related pupil dilations accurately mirrored changes in visuospatial awareness induced by a dual-task manipulation that consumed attentional resources. Moreover, results of the primary spatial monitoring task revealed a significant rightward bias, indicated by a greater proportion of missed targets in the left hemifield. Interestingly this result mimics the extinction to double simultaneous stimulation (i.e., the failure to respond to a stimulus when it is presented simultaneously with another stimulus) which is often found in patients with unilateral brain damage.

Overall, these studies present an emerging picture of attention as a complex mechanism that even in its volitional aspects is modulated by other non-volitional factors, both external and internal to the individual.

Questa tesi verte sull’indagine dei meccanismi alla base dell'attenzione visuo-spaziale e In particolare sull'attenzione top-down. Con questo termine si intende la capacità di selezionare le informazioni rilevanti e scartare quelle irrilevanti in maniera volontaria e sulla base dei nostri obiettivi. Il cervello umano non è in grado di processare allo stesso livello tutte le informazioni disponibili nell’ambiente in un dato momento, per questo una selezione corretta dell’informazione da elaborare è fondamentale anche per l’esecuzione delle più semplici attività quotidiane. Prestare attenzione ad informazioni irrilevanti può farci trascurare altre informazioni di importanza cruciale, con conseguenze potenzialmente gravi.

Nel primo studio (capitolo 2) I affronterò con un approccio computazionale la questione dei meccanismi neurali che sottendono l’attenzione visuo-spaziale: quali sono le basi neurali dell’attenzione visuo-spaziale? Secondo la teoria premotoria, orientare l'attenzione verso una specifica posizione spaziale equivale a preparare un movimento oculare verso la medesima posizione, un’ipotesi supportata dai risultati di molteplici studi di neuroimaging e neurofisiologici, i quali hanno mostrato una notevole sovrapposizione tra i circuiti dedicati all’attenzione visiva e la programmazione di movimenti oculari. In questo capitolo presenterò un modello computazionale in grado di spiegare diversi effetti attentivi senza richiedere l’aggiunta di meccanismi specifici oltre ai circuiti oculomotori. Inoltre include un meccanismo, modellato sulla base di dati neurofisiologici, che consente di anticipare le conseguenze sensoriali di un movimento oculare sulla rappresentazione spaziale interna al modello, e di spiegare alcune recenti dimostrazioni di dissociazione tra attenzione e movimenti oculari che possono essere utilizzate per confutare la teoria premotoria. Nel capitolo successivo presenterò un secondo modello computazionale (capitolo 3) con lo scopo di investigare ulteriormente i meccanismi computazionali alla base delle trasformazioni sensorimotorie, cioè i processi che traducono l’informazione sensoriale in appropriati comandi motori. In particolare mostrerò che una rappresentazione spaziale costituita da neuroni con campi recettivi retinocentrici ,modulati in ampiezza da un segnale posturale, è sia efficiente (al fine di trasformare l’informazione visiva in coordinate motorie centrate su un effettore) che plausibile, in quanto emerge in un modello di rete neurale addestrato in maniera non supervisionata (usando cioè solo segnali disponibili localmente a livello

del singolo neurone). Questo risultato supporta inoltre l'approccio utilizzato nel primo modello presentato.

Successivamente presenterò una serie di studi comportamentali: nel primo (capitolo 4), mostrerò che la costanza spaziale dell'attenzione visiva rispetto ai movimenti oculari (cioè la capacità di mantenere stabilmente l'attenzione in un punto nello spazio attraverso successivi movimenti oculari), dipende fortemente da alcune proprietà dell'immagine, vale a dire la presenza continua di punti di riferimento visivi. Questo risultato aiuta a risolvere recenti controversie sull'orientamento dell'attenzione durante movimenti oculari. Nel secondo studio comportamentale (capitolo 5), indagherò un aspetto spesso trascurato relativo al paradigma di *cueing* spaziale (probabilmente la tecnica più utilizzata nello studio dell'attenzione spaziale): la predittività del *cue* (cioè la misura in cui il cue spaziale indica correttamente la posizione in cui apparirà lo stimolo bersaglio). I risultati mostrano che, indipendentemente dalla consapevolezza dei partecipanti, variazioni nella predittività producono corrispondenti variazioni degli effetti di validità del cue, e che effetti significativi di validità possono comparire anche in assenza di un cue predittivo o direzionale. Questi risultati mettono in dubbio l'appropriatezza dell'uso di cue predittivi per indagare spostamenti volontari dell'attenzione spaziale. Infine, nell'ultimo studio userò una misura psicofisiologica, il diametro della pupilla, per indagare gli aspetti relativi all'*intensità* del processamento visuospaziale. In particolare mostrerò come dilatazioni della pupilla evento-relate riflettano accuratamente variazioni nella performance in un compito di monitoraggio spaziale provocate dall'aggiunta di un doppio-compito. Inoltre, i risultati del compito primario spaziale rivelano la presenza di un bias consistente verso l'emispazio di destra, indicato da una percentuale maggiore di bersagli omessi nell'emispazio di sinistra. In particolare il pattern di errori rispecchia il fenomeno dell'estinzione (mancata risposta a uno stimolo quando è presentata simultaneamente con un secondo stimolo, tipicamente nell'emispazio opposto) che si trova spesso in pazienti con danno cerebrale unilaterale.

In conclusione, dagli studi presentati emerge un quadro dell'attenzione volontaria visuo-spaziale come un meccanismo complesso, che, anche nei suoi aspetti volitivi è fortemente influenzato da altri fattori, non volitivi, sia esterni che interni all'individuo.

1 INTRODUCTION

"Attention is that state of mind which prepares one to receive impressions.
According to the degree of attention objects make a strong or weak impression.
Attention is requisite even to the simple act of seeing."

Henry Home Kames,
from the appendix of *Elements of Criticism* (1769)

1.1 THE NEED OF SELECTION

We live in a extremely complex visual environment, yet we experience a complete and effortless cognizance of it. However, there are many experimental demonstrations that show how this subjective impression of visual richness is nothing but an illusion: change blindness (Jensen, Yao, Street, & Simons, 2011; O'Regan, Rensink, & Clark, 1999a; Rensink, O'Regan, & Clark, 1997; Simons & Rensink, 2005) and inattentional blindness studies (Mack, 2003; Simons & Chabris, 1999; Simons & Rensink, 2005; Simons, 2000) have clearly shown that we are unable to process all the available visual information to the same degree. Thus, in order to deal with the complexity of the visual world, is essential to operate a selection and attention is the key mechanism that allows the allocation of processing resources to behaviorally relevant information. Orienting attention therefore means improved processing of some relevant information and discarding of other irrelevant information.

Capacity limits in information processing are likely a consequence of the high metabolic costs of neural activity, which largely dominates the overall energy consumption of the brain (Attwell & Laughlin, 2001; Howarth, Gleeson, & Attwell, 2012). The energy cost of a single spike is such that only a very limited fraction of neurons could be concurrently active, perhaps fewer than 1% (Lennie, 2003). Ultimately, energy limitations dictate the need of sparse representational codes (i.e., relying only on a small number of neurons simultaneously active) and flexible allocation of metabolic resources according to task demands, providing a physiological basis for the idea of selective attention as a consequence of the brain's limited processing capacity.

According to a widely accepted model, the biased competition model (Desimone & Duncan, 1995), selection results from competition among relevant stimuli: multiple stimuli present at the same time in the visual field compete for neural representations and attention operates by biasing the competition in favor of neurons that encode the attended stimulus. Interestingly, the opening quote of this chapter indicates that the idea of attention as a requisite for conscious vision, modulating the strength of stimulus representations, is not a recent one, being present almost 300 years ago.

A computational implementation of the biased competition model has been proposed by Reynolds and colleagues (Reynolds, Chelazzi, & Desimone, 1999), and was later refined onto the normalization model of attention (Reynolds & Heeger, 2009), a combination of biased competition and divisive normalization (see also Lee & Maunsell, 2009 for a further model based on normalization). Normalization is a form of gain control that adjusts neurons' responses in proportion to the activity of neighboring neurons, and was first introduced to explain nonlinearities in the responses of V1 simple cells in the presence of multiple stimuli (Heeger, 1992). The normalization model of attention can explain many effects of attentional modulation within a single computational framework, predicting different forms of attentional modulation depending on stimulus and attention field size. However while it offers a far-reaching computational characterization of attentional modulation in visual cortex, it does not make explicit hypotheses about the underlying biophysical mechanisms or neural circuitry, or about the sources of the attentional signals (the attentional field in the model).

1.2 COVER AND OVERT VISUAL-SPATIAL SELECTION

When the information is visual, and the selection is based on space, prioritizing some regions of the visual field and discarding others, we refer to visual-spatial attention. Intuitively, attending to something relevant in the visual field requires *looking* at it, i.e. moving the eyes in order to align high-acuity foveal vision with the target of interests (overt orienting). However attention can be allocated also covertly, without eye movements (Posner, Snyder, & Davidson, 1980).

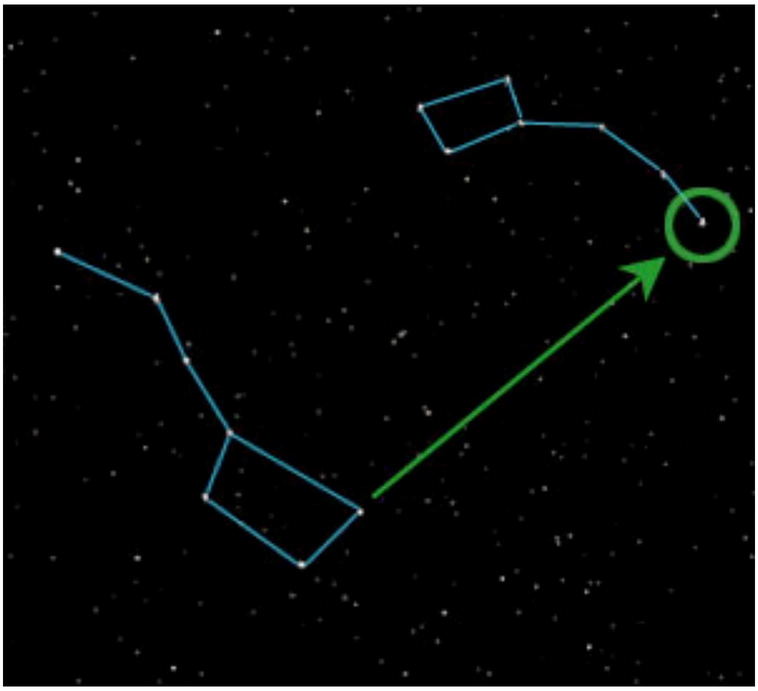

Figure 1 A demonstration of covert orienting of attention. In order to locate the Polaris or North Star, the first step is locating the Big Dipper (Ursa Major), which is usually the most easily recognizable constellation in the night sky. By looking at the two front star of the Big Dipper and directing attention along the imaginary line that depart from these two star, the first bright star encountered is the Polaris (circled in the picture) which is also at the end of the handle of the Little Dipper (Ursa Minor). Remarkably, even the accomplishment of such a simple task requires dissociation between the center of gaze and the focus of attention.

Covert deployment of attention allows an observer to monitor the environment without shifting gaze and can inform subsequent eye movements. Indeed is well established that covert shifts of attention precede gaze shifts (Deubel & Schneider, 1996; Rolfs & Carrasco, 2012). Notably, while eye movements are necessarily sequential, covert shifts of attention can select multiple locations in the visual fields simultaneously, as in the case of sequential eye movements: during the preparation of a sequence of saccades attention is allocated in parallel at all the upcoming targets locations (Baldauf & Deubel, 2008). This has been observed as well for multiple reaching movements (Baldauf & Deubel, 2009; Baldauf, Wolf, & Deubel, 2006).

The parallel allocation of attention to multiple movements targets raises the problem of the coordinate system of visual attention: since visual processing is, at least in its early stages (but likely also in higher level visual cortices, Golomb & Kanwisher, 2011), organized in retinal coordinates, what happens to the multiple foci of attention once the sequence of planned eye movements is started and the first saccade is executed? If their internal representation is retinotopic (i.e., organized in retinal coordinates) to maintain their alignment with relevant targets in the visual field they need to be updated to compensate for the sensory consequences of eye movements. Neural correlates for this updating process, usually referred to as spatial remapping (see fig. 2), have been described initially in single cell studies of parietal and frontal areas involved in attention and eye movements planning (Colby & Goldberg, 1999; Duhamel, Colby, & Goldberg, 1992; Sommer & Wurtz, 2006) and subsequently by neuroimaging studies in human parietal cortex (Heide et al., 2001; Medendorp, Goltz, Vilis, & Crawford, 2003; Merriam, Genovese, & Colby, 2003). While the available evidence clearly converge on the notion of a retinotopic coordinate system for spatial attention (Golomb, Chun, & Mazer, 2008; Golomb & Kanwisher, 2011; Golomb, Nguyen-Phuc, Mazer, McCarthy, & Chun, 2010; Golomb, Pulido, Albrecht, Chun, & Mazer, 2010; Mathôt & Theeuwes, 2010), the issue of the nature of the updating mechanism and the computations involved has been hotly debated in recent years (Burr & Morrone, 2011; Cavanagh, Hunt, Afraz, & Rolfs, 2010; Melcher & Colby, 2008). I will return to this point later: in chapter 2 I will provide a biologically plausible computational account of the remapping process, and in chapter 3 I will report novel behavioral results that help reconcile existing controversy about the allocation of attention across eye movements.

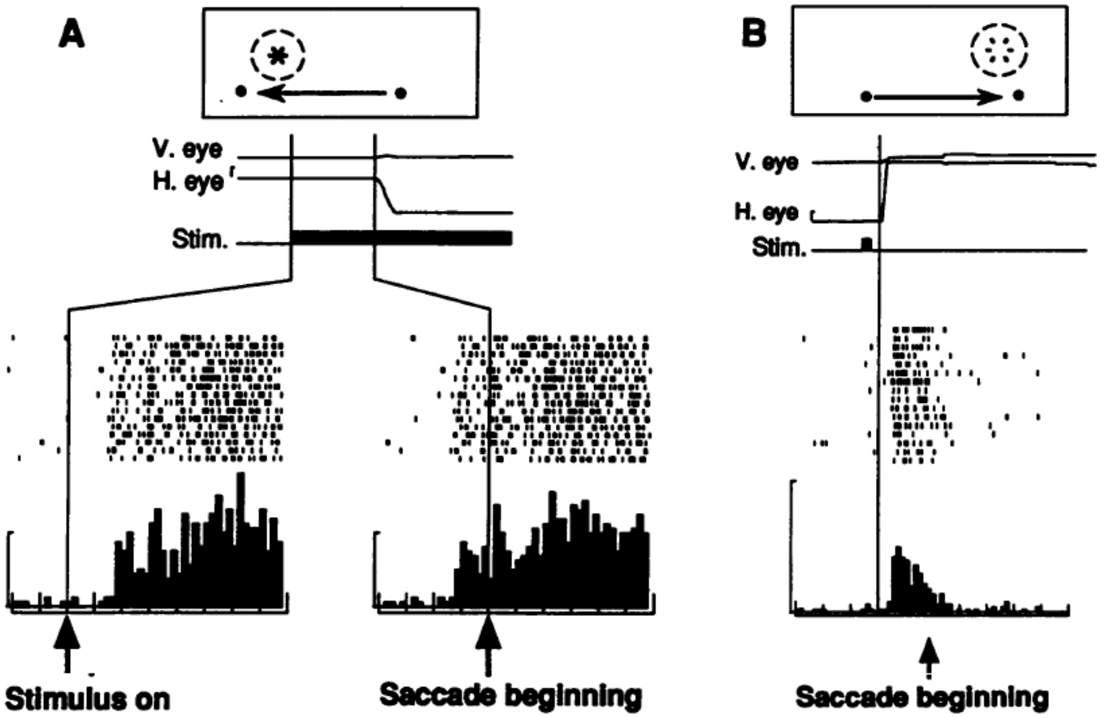

Figure 2 Remapping of neural activity in lateral intraparietal area (LIP). Upper diagrams show the fixation point (dot), visual stimulus (star), receptive field (dashed circle), and saccade (arrow). Time lines below represent the horizontal (H.) and vertical (V.) eye position and the beginning and ending of the stimulus (Stim.); the mark at the left of the bottom histograms represent a level of 100 spikes per second. Left panel (**A**) shows the visual response of a LIP neuron to a stimulus that is initially outside its receptive field, in this condition the new fixation point and the visual stimulus appeared simultaneously. On the basis of the normal visual latency of LIP neurons one would predict the selected neuron to respond to the visual stimulus approximately 70 ms after the saccade has brought the stimulus into its receptive field. However it start responding 150 ms earlier, 80 ms before the onset of the saccade. Right panel (**B**) shows the response of another LIP neuron to a briefly flashed stimulus. In this case the neuron fires after the saccade has brought the location of the stimulus into the receptive field, even though the stimulus is already gone. This finding has been interpreted has the remapping of a visual memory trace in conjunction with eye movements (adapted from Duhamel et al., 1992).

1.3 TOP-DOWN & BOTTOM-UP CONTROL OF VISUAL SPATIAL ATTENTION

Another well established distinction define two different types of spatial attention orienting: one is passive, reflexive and involuntary, the other is active and voluntary. Notably, everyday language is full of idiomatic expressions that explicitly make this distinction: we might say that something unexpected or new 'caught our attention', meaning that our attention has been involuntarily captured. Alternatively, we might ask someone to 'pay attention to the road' while driving, which indicates a voluntary allocation of processing resources to a subset of the perceptual input. They are usually referred to as exogenous, stimulus-driven or bottom-up attention in the former case and endogenous or top-down attention in the latter (see Carrasco, 2011 for a review). The terms 'bottom-up' and 'top-down' refers to the flow of information processing, with sensory input considered 'down' and higher cognitive functions considered 'up'. While this distinction seem sharp, everyday visual cognition is not only a bottom-up process but instead it is permeated with both kinds of processes (see Cavanagh, 2011 for a review) working together to build a coherent representation of the world (e.g., see fig. 3).

Figure 3 Top-down processes in visual cognition. The picture on the left contains only amorphous shapes in white on black that apparently carry very little information, and yet they connect to knowledge about human form, recovering the possible shape of a woman sitting on a bench (from Rock, 1984). Similarly, pictures on the right are portrait (the two male faces are self-potrait) by Giorgio Kienerk (Firenze, 1869 – Fauglia, 1948), probably the first artist that made extensive use of this technique, which he called "macchie senza contorni disegnati" ('patches without contour'). No bottom-up analysis can recover either of the elements in the pictures. No image analysis based on parts or surfaces can work as shadow regions have broken the real object parts into accidental islands of black or white.

For what concerns attention, with respect to the biased competition model (Desimone & Duncan, 1995), bottom-up and top-down refers to the two possible ways to resolve the competition among multiple objects. The competition could be biased by factors inherent in the image, that determines the relative stimuli salience on the basis of multiple perceptual factors, like color, luminance, perceptual grouping, etc. In this case, when the selection is stimulus-driven we refer to it as exogenous or bottom-up orienting of attention. Transient visual changes are also known to elicit a rapid, exogenous orienting response toward the location where the change has occurred. For example, abruptly-appearing letters on a display automatically attract attention and are responded to faster than are gradually-appearing letters (Jonides & Yantis, 1988). When such a visual transient, usually an abrupt-onset visual stimulus called cue, appears about 100 ms before another stimulus (termed target or probe stimulus) in the same spatial location, the latter is processed faster and more accurately (Miller, 1989; Theeuwes, 1991; Watson & Humphreys, 1995), meaning that attention was attracted reflexively to the spatial location of the cue. This procedure is called spatial cueing and has been used extensively in studies of both bottom-up and top-down visual spatial attention (see fig. 4). Exogenous shifts of attention are involuntary and occur also in the case of uninformative and irrelevant cues. The deployment of attention following a visual transient rises and decays quickly, peaking at about 100-120 ms (Carrasco, 2011).

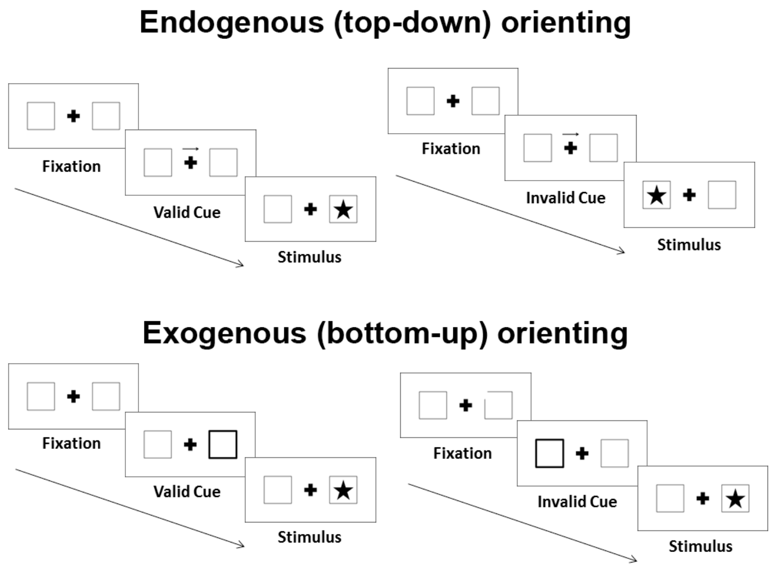

Figure 4 Spatial cueing paradigms. In this popular experimental paradigm a target is preceded by an informative or a non-informative cue that appears at the target location (bottom-up or exogenous attention, lower panel) or centrally, at fixation (top-down or endogenous attention, higher panel). Attentional effects are inferred in terms of reaction time and/or accuracy of target detection difference between valid trials (i.e., with a congruent cue, indicating the true target position) and invalid trials (cue incongruent respect to target position).

On the other hand, when the competition is biased by factors that are related to the observer, like behavioral relevance, expectations, etc., the term top-down attention is used instead. Top-down or endogenous orienting of attention indicates our ability to willfully monitor information at given locations in the visual field that are relevant to our goals. In this thesis I will focus on top-down attention, which is at the basis of our ability to accurately planning and performing any goal-directed action. In spatial cueing experiments, top-down orienting is usually studied by presenting a symbolic cue (usually at the center of the visual field, see fig 4) which indicates where in space participants are required to orient attention (Posner, 1980). Traditionally the study of top-down visual spatial attention has involved predictive cues, i.e. cues that correctly predicted target location in a substantial proportion of the experimental trials (e.g., 75%), with the purpose of giving the participant an incentive to focus attention at the cued location. The underlying assumption is that with a highly predictive cue subjects will learn to use it in order to predict the location of the forthcoming target. This consolidated practice has been supported by the observation that there is a positive correlation between cue predictiveness and the magnitude of attentional effects (e.g., Bartolomeo, Decaix, & Siéroff, 2007; Gottlob, Cheal, & Lyon, 1999; Johnson & Yantis, 1995; Risko & Stolz, 2010). This effect has been called proportion-valid effect and is widely assumed to reflect intentional and strategic control over the orienting of attention. More specifically, as the utility of a cue increases (i.e., as the proportion of valid trials increases), subjects are thought to volitionally allocate more visual attention to the cued location (either by allocating more resources to the cued location or by attending to it more frequently). In chapter 5 I will present results that challenge this view, showing that reliable orienting of attention can emerge even in absence of predictive cues, and that the proportion-valid effect is not related to subjective estimates of cue utility (contrary to what the strategic control account would predict). Our findings thus provide support for an alternative account of the proportion valid effect based on implicit learning (Peterson & Gibson, 2011) and overall question the appropriateness of using highly predictive cues in studies aiming at the investigation of pure voluntary attention.

1.4 NEURAL CIRCUITRY FOR TOP-DOWN ATTENTION: THE PREMOTOR THEORY OF SPATIAL ATTENTION

A fundamental question for the understanding of top-down attention regards its neural substrates: what are the sources of the top-down attentional bias? According to the most classical models, spatial attention was thought of as a dedicated and anatomically distinct supramodal control mechanism (e.g., Mesulam, 1990; Posner & Dehaene, 1994). In contrast with this view, the premotor theory of spatial attention, initially formulated in the late eighties of last century, proposed a tight link between endogenous attention and eye movements (Rizzolatti, Riggio, Dascola, & Umiltá, 1987; Rizzolatti, Riggio, & Sheliga, 1994). Specifically, the premotor theory maintains that top-down orienting of visual spatial attention originates from a weaker activation of the same cortical circuits involved in saccadic eye movement planning. Preparation of a saccade produces, by means of recurrent projections from premotor areas to parietal spatial, a processing facilitation for stimuli located in the same location toward which the motor program is prepared. According to the theory thus a covert shift of attention occurs when an eye movement is prepared but not executed.

The premotor theory was originally formulated on the basis of some behavioral studies, among which the first has been the meridian effect (Rizzolatti et al., 1987). The meridian effect consists in greater costs for processing a target after orienting attention in the opposite hemifield than after orienting in the same hemifield, even if the physical distance from the unattended stimuli and the cued location remains the same. Such an anatomical landmark as the vertical meridian contrasts with the notion of attention as a supramodal control system independent from sensorimotor circuits, while it can be accounted for by assuming that attention derives from saccade preparation: while changes in saccade direction (e.g., changing the motor plan of a leftward saccade into a rightward one) require a radical modification in the motor program, changes in saccade amplitude imply only a minor adjustment of the initial program. Another classical demonstration used vertical saccades together with left/right attentional cues: when participants pay attention to a given spatial location, the trajectory of a saccade directed toward another location deviated contralateral to the attention site (Sheliga, Riggio, & Rizzolatti, 1995). This finding strongly support the idea of a strict coupling between attention and eye movements and suggests that the allocation of spatial attention necessarily activates the eye movement system. The above mentioned studies on pre-saccadic attention shifts also strongly support the premotor theory (Baldauf & Deubel, 2008; Deubel & Schneider, 1996) by showing a consistent coupling between the focus of attention and the saccade endpoint.

In more recent years, a vast amount of brain-imaging and neurophysiological studies gave strong support to the idea that planning eye movements and orienting visuospatial attention share overlapping brain mechanisms. Neurophysiological data strongly support the premotor theory indicating that spatial attention is related to eye-movement planning structures, including the frontal eye fields (FEF; Moore, Armstrong, & Fallah, 2003; Moore & Fallah, 2001, 2004; Moore, 2006) and the superior colliculus (SC; Ignashchenkova, Dicke, Haarmeier, & Thier, 2004; Kustov & Robinson, 1996). Reversible inactivation of FEF, both in monkeys (Moore & Fallah, 2004; Wardak, Ibos, Duhamel, & Olivier, 2006) and humans (see Chambers & Mattingley, 2005 for a review) affects the orienting of spatial attention. Neurons in the intraparietal sulcus (IPs) generate action-oriented representations of space and are also crucially involved in the top–down (endogenous) control of spatial attention (Colby & Goldberg, 1999). Neural activity in the lateral intraparietal area (LIP), an area within the IPs that codes for impending saccades (Andersen, 1989; Paré & Wurtz, 2001; Pierrot-Deseilligny, Rivaud, Gaymard, Müri, & Vermersch, 1995) and has been described as representing the space explored by eye movements (Berman & Colby, 2009), depends on the spatial and temporal dynamics of attention (Bisley & Goldberg, 2003). Since it represents only salient targets (Gottlieb, Kusunoki, & Goldberg, 2005; Gottlieb, Kusunoki, & Goldberg, 1998; Kusunoki, Gottlieb, & Goldberg, 2000), it has been suggested that LIP neurons generate a saliency map of the visual environment (Fecteau & Munoz, 2006; Goldberg, Bisley, Powell, & Gottlieb, 2006). Remarkably, it has been showed that LIP neurons have mutually suppressive interactions, spatially arranged in a center-surround scheme (with wide inhibitory surround), providing thus a neural substrate for spatial competition among multiple stimuli (Falkner, Krishna, & Goldberg, 2010).

Coherently with neurophysiological results, neuroimaging studies indicate that top–down orienting of spatial attention in humans recruits a network of cortical areas, including the IPs and the FEF (see fig. 4), that largely overlap with the network of regions involved in the control of saccadic eye movements (Corbetta et al., 1998; Corbetta & Shulman, 2002). Although the competition among stimuli is ultimately resolved within the visual cortex, it has been shown that the source of the biasing signal comes from a network of areas in frontal and parietal cortex (Kastner & Ungerleider, 2001; Kastner & Ungerleider, 2000; Simpson et al., 2011; Szczepanski, Konen, & Kastner, 2010). Another recent fMRI study (Bressler, Tang, Sylvester, Shulman, & Corbetta, 2008) used Granger causality measures (a concept of causality based on temporal precedence and predictability, see Roebroeck, Formisano, & Goebel, 2005) to infer functional connectivity among different areas in a visuospatial attention task. Results suggest that during covert, voluntary orienting of visual spatial attention FEF and IPS modulate visual occipital cortex, and FEF modulates IPS (Bressler et al., 2008), supporting thus the idea of the oculomotor network as the source for the top-down biasing signal. To summarize, the available evidence converges in showing a strong overlap between the network of brain regions involved in top-down orienting of spatial attention and sensorimotor transformations for saccadic movements (Beauchamp, Petit, Ellmore, Ingeholm, & Haxby, 2001; Corbetta et al., 1998; Nobre, Gitelman, Dias, & Mesulam, 2000), providing thus strong support to the idea of a causal link between oculomotor control and covert visual selection, which is at the core of the premotor theory.

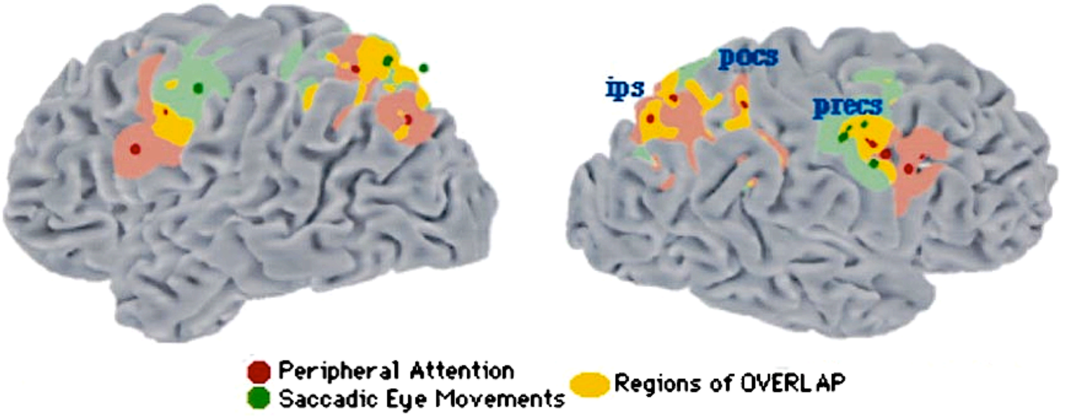

Fig. 4 A meta analysis of imaging studies. In yellow are represented the area of overlap between eye movements and orienting of attention. From Corbetta et al, 1998.

1.4.1 THE PREMOTOR THEORY OF SPATIAL ATTENTION: A COMMENT ON SMITH & SCHENK (2012)[1]

Despite the amount of experimental evidence that support it, the idea of a strong link between visual-spatial attention and eye movements has been long debated since the first proposal of the premotor theory of spatial attention (Rizzolatti et al., 1987). In their recent contribution, Smith and Schenk (Smith & Schenk, 2012) review experimental results in favor and against premotor theory and conclude that the overall evidence is not consistent with the idea of equivalence between attention and motor planning. However, at least two points in Smith and Schenk article are problematic. First, when discussing the issue of the overlap between neural circuitry subtending attention and eye movements, the authors question the view of microstimulation studies of FEF (e.g., Moore et al., 2003) as an evidence of attentional modulation driven by the motor system, on the basis of the notion that FEF contains multiple overlapping neuronal populations (visual, visuo-motor, and motor neurons) and is thus not possible to determine precisely whether the resulting attentional modulation derives from visual or motor signals. While this is an important word of caution in the interpretation of those results, it is fundamental to remind that these cell classes are not strictly distinct, but instead appear to fall on a continuum between purely visual and purely

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[1] Smith, D.T., & Schenk, T. (2012). The premotor theory of attention: time to move on?

movement neurons (Bruce & Goldberg, 1985). Even though this functional scheme has been useful in characterizing neural activity in FEF, it is unlikely that within this area specialized subpopulations operate independently. Moreover, Smith and Schenk fail to mention another relevant microstimulation study (Cavanaugh & Wurtz, 2004) which has targeted the intermediate layer of the superior colliculus (SC), an area even more closely tied to saccade generation. In this study SC stimulation improved monkey’s performance in a change blindness paradigm. Notably, it is highly unlikely that stimulation in this study triggered a visual signal: visual stimulation, acting as a visual cue (e.g., a phosphene) presented at the time of a change in the visual scene, should reduce the ability to detect the change (O’Regan et al., 1999) while results show exactly the opposite pattern (improved performance). On the whole, we believe there is compelling evidence that common neural circuits underlie the planning of saccades and the covert selection of visual stimuli. Obviously at some point the mechanisms involved in covert and overt orienting must diverge, at least at the point in which the eyes are moved or held fixed, and indeed some studies showed suppression of activity in some pure movement neurons in FEF and SC during covert orienting (Ignashchenkova et al., 2004; Thompson, Biscoe, & Sato, 2005) suggesting that the divergence starts at the single neuron level within these areas, a result that in any case does not question per se the idea of a common origin for spatial attention and eye movements, which is at the core of the premotor theory.

Second, when discussing the link between action preparation and covert attention the authors invoke the physiological process of remapping (Duhamel et al., 1992) as an alternative mechanisms that could account for the coupling between oculomotor activity and attention shifts. More specifically, they argue that saccade targets are not really ‘attended’ but are processed more efficiently because some neurons, anticipating the sensory consequences of an eye movement, start responding to stimuli at the saccade endpoint and thus “as there are relatively more of these receptors the relative signal-to-noise ratio of the stimulus at the saccade endpoint is greatly enhanced”. However, this hypothesis is highly unlikely given the available neurophysiological and psychophysical data: first, it implies a shifting receptive field model of remapping, which has been recently challenged (Cavanagh et al., 2010). The main point against the shifting receptive field model is the remapping of memory activity (Umeno & Goldberg, 2001): in this case at the time of the remapping there is no activity on the retina or in earlier visual cortices, hence the only source for remapping is a transfer of activity from other cells through horizontal connections. Furthermore, a recent study (Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011) which investigated the functional correlates of predictive remapping in humans through a double-step saccade task, showed that briefly before the eyes start moving, attention drawn to the targets of upcoming saccades also shifted to those retinal locations that the targets would cover after the eyes had moved, facilitating future movements. Specifically, in this study improved visual processing at the remapped (or future retinotopic) location of the second saccade target was associated with speeded execution of the second eye movements. These results strongly support the idea of a strict coupling between oculomotor programming and covert attention orienting, and suggest that motor programming is both sufficient and necessary for spatial attention. Moreover, in that study Rolfs and colleagues investigated also remapping in single saccades and found also an increasing performance at fixation starting shortly before the saccade, indicating remapping of attention to the fovea. This is exactly the opposite of what Smith and Schenk hypothesis would suggest: if, as they suggest, the presaccadic perceptual benefit is due to receptors that normally respond to foveal stimulation starting to respond to stimulation at the saccade endpoint, it would follow that the relative decrease of receptors responding to foveal stimulation in the pre-saccadic interval should produce a reduced visual performance at fixation (or at least not an improvement).

These novel findings indicate that oculomotor preparation and attention are strictly coupled and internally represented by neural activity in the same spatial maps, coherently with previous studies showing that deployment of covert attention can affect saccade latencies (e.g., Tanaka & Shimojo, 2001; Walker, Kentridge, & Findlay, 1995) and saccade trajectories (Kustov & Robinson, 1996; Sheliga et al., 1995; Van der Stigchel & Theeuwes, 2005). Accordingly, spatial remapping is best described as a mechanism that maintains activity in saccade-attention maps (organized in retinal coordinates) aligned with the corresponding targets (world coordinates). It is thus straightforward why this mechanism operates only during overt shifts: as pointed out by Berman and Colby (Berman & Colby, 2009), with a covert shift of attention nothing moves on the retina and there is no need for remapping. Coherently with this view in chapter 2 I will present a computational model of spatial attention and saccadic planning that represents an improvement of the original premotor theory because it takes into account the remapping mechanism, which is implemented in the model as a transfer of activation through lateral connections among simulates parietal neurons. Specifically, we demonstrate that this updating mechanism allows the premotor theory to account for recent reports of dissociations between attention and eye movements (Golomb et al., 2008; Golomb, Marino, Chun, & Mazer, 2011; Golomb, Pulido, et al., 2010; Mathôt & Theeuwes, 2010).

In conclusion, the issue about the source of attentional signals is central for the understanding of the mechanisms of selective visual attention. The premotor theory provided an explicit hypothesis to this issue, by maintaining that visual spatial attention originates from the activation of the same cortical circuits involved in saccadic planning. Remarkably, this proposal of a tight link between oculomotor programming and covert orienting has undoubtedly stimulated research in the field for over 20 years, has anticipated many later neurophysiological and behavioral findings, and, as I argued, still holds against more recent results. Ultimately, debates like these are useful in reminding the importance of interdisciplinary work in neuroscience, and specifically the importance of linking neurophysiological findings with plausible computational mechanisms in order to explain behavioral phenomena.

1.5 ATTENTION AND SENSORIMOTOR TRANSFORMATIONS: COMPUTATIONAL APPROACHES

The premotor theory of spatial attention maintains that spatial attention originates in sensorimotor circuits involved in eye movements planning. There is evidence that pre-motor allocation of visual attention precedes also other types of movements, like reaching movements, as demonstrated by studies showing improved visual discrimination at target locations of manual movements (Baldauf & Deubel, 2009, 2010; Baldauf et al., 2006; Deubel & Schneider, 2003; Jonikaitis & Deubel, 2011). It has been shown that in the early stages of motor planning reaching targets are represented in retinotopic or eye-centered coordinates (Beurze, Van Pelt, & Medendorp, 2006; Desmurget, Pélisson, Rossetti, & Prablanc, 1998) and that, similarly to saccade targets also the retinotopic representation of reach targets is updated across eye movements (Henriques, Klier, Smith, Lowy, & Crawford, 1998; Medendorp, Beurze, Van Pelt, & Van Der Werf, 2008; Thompson & Henriques, 2011). However, before the actual execution, goal directed action requires also a transformation between different reference frames (Cohen & Andersen, 2002): this is evident in the case of reaching movements because the reference frame in which stimuli are encoded (eye-centered) is different from those of the motor effector (hand-centered). The neural substrates of sensorimotor transformations are attributed to the posterior parietal cortex (PPC) (Andersen, 1989; Colby & Goldberg, 1999), which combines multiple sensory and postural inputs and has been described as a sensorimotor interface for visually guided movements (Buneo & Andersen, 2006).

Spatial representation for motor planning has been shown to rely on PPC neurons whose activity approximates a multiplicative combination of visual and posture signal (Andersen, Essick, & Siegel, 1985; Brotchie, Andersen, Snyder, & Goodman, 1995). Computational and connectionist studies have proved to be particularly valuable in disclosing the computational mechanisms that underlie the translation of sensory inputs to motor outputs: the seminal study of Zipser and Andersen (Zipser & Andersen, 1988) was the first to show how a measured property of real neurons (gain modulation of visual responses by eye position) could underlie a specific non-trivial computation (coordinate transformation). Multiplicative gain modulation was later formally expressed in the basis function (BF) approach, an application of the theory of nonlinear function approximations to sensorimotor tranformations (Poggio, 1990; Pouget & Sejnowski, 1995). In the BF approach single units compute the product of nonlinear functions (i.e., Gaussian and sigmoidal functions) of their inputs, and a linear combination of their outputs is sufficient to approximate any arbitrary function of their inputs. Notably, encoding space with BFs renders it possible to reduce nonlinear coordinate transformations into simple linear mappings, since the resulting representation encodes spatial locations in a format that contains implicitly any frame of reference that can be derived from the input variables (Pouget & Snyder, 2000; Pouget, Deneve, & Duhamel, 2002). Moreover, it has been shown that adding lateral connections among BF processing units (i.e., recurrent BF networks) can provide additional interesting properties like short-term memory (Pouget & Snyder, 2000), the ability to filter out noise in sensory inputs (Deneve, Latham, & Pouget, 2001) or to predict the sensory consequences of motor actions by integrating sensory signals with motor commands (Denève, Duhamel, & Pouget, 2007).

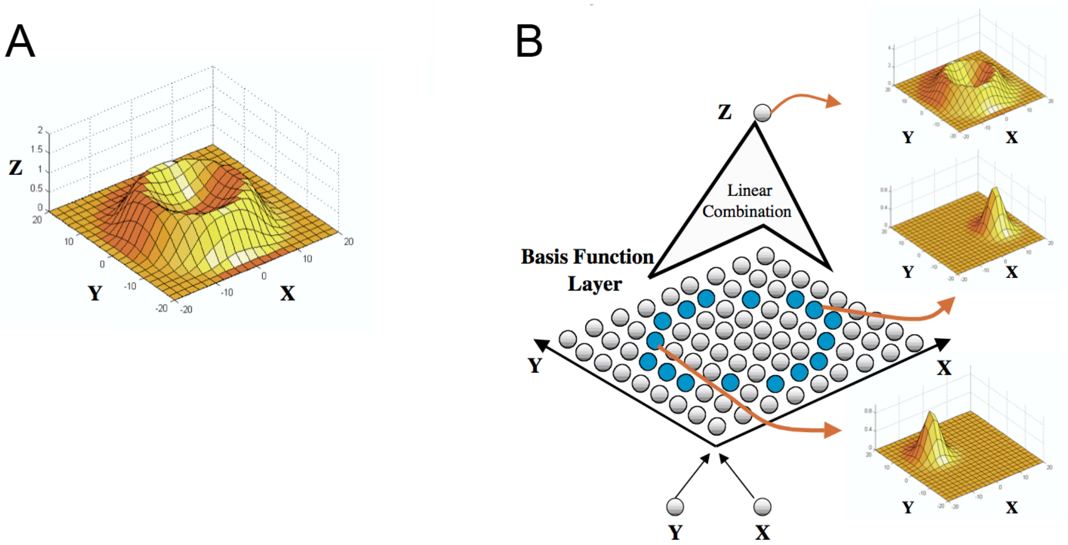

Figure 5 An example of approximation of nonlinear functions through basis functions units. The complex non linear function $z = e^{\left(-\left(x^2+y^2-100\right)^2/1000\right)}$ represented in panel **A** and its approximation in a BF neural network using Gaussian basis functions (panel **B**). The basis function units are organized so as to form a map in the x–y plane. On the right two representative response functions of these basis function units are represented. The activity of the output unit is obtained by taking a linear sum of the basis function units. In this example, the weights of the blue units onto the output unit are set to one, whereas all the other units have a weight of zero. As a result, the output unit mathematically sums a set of Gaussian functions arranged along a circle in the x–y plane. This leads to the response function (top-right), which is similar to the circular ridge defined by the original function in panel A (adapted from Pouget & Snyder, 2000).

Recurrent BF neural networks also exhibit several characteristics that make them particularly suited also for modeling spatial attention. In particular, as I will show in chapter 2, lateral connections within a BF layer of units can implement competitive interactions that can account for attentional costs and benefits emerging in attention experiments using the spatial cueing paradigm (e.g., Posner et al., 1980). This approach provides a biologically plausible implementation of spatial attention in sensorimotor circuits (in agreement with the premotor theory) that can explain *spatial* aspects of visual attention orienting, like the distance effect (Umiltà, Mucignat, Riggio, Barbieri, & Rizzolatti, 1994) and the updating of the attentional foci across eye movements (Cavanagh et al., 2010; Golomb et al., 2008). Note that it does not address the same issues of the normalization model of attention (Reynolds & Heeger, 2009), which aim to explain the attentional modulation of neuronal responses in visual cortices.

The plausibility of the BF approach has been however questioned, because it gives rise to theoretical problems like the combinatorial explosion (the number of neurons required increases exponentially with the number of signals being integrated, for further discussion see Pouget & Snyder, 2000). In chapter 3 I will present a computational model of sensorimotor tranformations in the PPC that shows how gain modulation can emerge in a generative model that simply learns to efficiently encode the sensory data without supervision. This strongly supports the view of gain modulation as an efficient coding strategy for multisensory integration, and suggests that it could subserve a broader class of nonlinear transformations.

1.6 CAPACITY OF VISUAL SPATIAL ATTENTION

In everyday life we are often required to perform several tasks simultaneously. Under these conditions often the performance of one or both tasks degrade (Pashler, 1994), an effect typically interpreted in terms of shared attentional resources. In the last chapter of the thesis I will use a measure that can be easily derived from eyetracking recordings to estimate such 'intensive' aspects of attention (Kahneman, 1973): the size of the eye's pupil. It has long been know that the diameter of human pupil enlarges with increasing effort during the execution of a task (Ahern & Beatty, 1979; Hess & Polt, 1964; Nunnally, Knott, Duchnowski, & Parker, 1967). Previous investigation that reported significant effect of mental effort on the diameter of the eye's pupil involved increasing load on working memory (Beatty, 1982; Granholm, Asarnow, Sarkin, & Dykes, 1996; Jainta & Baccino, 2010; Kahneman & Beatty, 1966; Kahneman, Peavler, & Onuska, 1968), memory strength of individual items (Van Rijn, Dalenberg, Borst, & Sprenger, 2012), processing load and complexity of the visual stimulation (Porter, Troscianko, & Gilchrist, 2007; Privitera, Renninger, Carney, Klein, & Aguilar, 2010; Young, Han, & Wu, 1993), semantic incongruences (Just & Carpenter, 1993; Nuthmann & van der Meer, 2005), arousal and interest or emotional value of the stimuli (Bradley, Miccoli, Escrig, & Lang, 2008; Laeng & Falkenberg, 2007; Nunnally, Knott, & Duchnowski, 1967; Partala & Surakka, 2003; Rieger & Savin-Williams, 2012; Stanners, Coulter, Sweet, & Murphy, 1979), higher risk, reward or uncertainty in decision making (Bijleveld, Custers, & Aarts, 2009; Einhäuser, Koch, & Carter, 2010; Gilzenrat, Nieuwenhuis, Jepma, & Cohen, 2010; Jepma & Nieuwenhuis, 2011; Preuschoff, 't Hart, & Einhäuser, 2011) or complexity of the response set (Gabay, Pertzov, & Henik, 2011; Moresi et al., 2008). However an investigation of the effect of 'pure' top-down attentional load in visual processing is still missing. Therefore in the last study of the present thesis I will examine whether changes in pupil size could reflect 'pure' top-down attentional load when measured in a dual task paradigm that allows to control other confounding influences (e.g., bottom-up factors, number of target stimuli, working memory load, etc.). Additionally, our paradigm includes a primary task consisting in the detection of lateralized targets, in order to investigate eventual load-related effects on attentional and visuospatial asymmetries across hemifield (Dodds et al., 2008; Hellige, 1996; O'Connell, Schneider, Hester, Mattingley, & Bellgrove, 2011; Peers, Cusack, & Duncan, 2006; Pérez et al., 2009).

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2 PAYING ATTENTION THROUGH EYE MOVEMENTS: A COMPUTATIONAL INVESTIGATION OF THE PREMOTOR THEORY OF SPATIAL ATTENTION

2.1 INTRODUCTION

The premotor theory of spatial attention (Rizzolatti, Riggio, & Sheliga, 1994; Rizzolatti, Riggio, Dascola, & Umiltà, 1987; Umiltà, Riggio, Dascola, & Rizzolatti, 1991) maintains that endogenous (i.e., top-down) orienting of visuospatial attention originates from the activation of the cortical circuits involved in saccadic planning. Preparation of a saccadic movement produces, by means of recurrent projections from premotor areas to parietal spatial maps, a processing facilitation for stimuli located in the region of space towards which the motor program is prepared. Planning a saccade is equivalent to shifting attention in space, because a covert movement of attention occurs when an eye movement is prepared, but not executed. In contrast, other theories of spatial attention postulate the existence of specific attention mechanisms that modulate the activity of information processing systems (see, e.g., Mesulam, 1990).

Neurophysiological data strongly support the premotor theory indicating that spatial attention is related to eye-movement planning structures, including the frontal eye fields (FEF) (Moore & Fallah, 2001; Moore & Fallah, 2004; Moore, Amstrong, & Fallah, 2003) and the superior colliculus (SC) (Kustov & Robinson, 1996; Ignashchenkova, Dicke, Haarmeier, & Thier, 2004; Muller, Philiastides, & Newsome, 2005). Reversible neurodisruption of FEF, both in monkeys (Moore & Fallah, 2004; Vardak, Ibos, Duhamel, & Olivier, 2006) and humans (see Chambers & Mattingley, 2005, for review), affects the orienting of spatial attention. Neurons in the intraparietal sulcus (IPs) generate action-oriented representations of space and are also crucially involved in the top-down (endogenous) control of spatial attention (see Colby & Goldberg, 1999, for review). Neural activity in the lateral intraparietal area (LIP) depends on the spatial and temporal dynamics of attention (Bisley & Goldberg, 2003) and represents only salient targets, suggesting that LIP neurons generate a saliency map of the visual environment.

Neuroimaging studies indicate that top-down control of spatial attention in humans recruits a network of cortical areas including the IPs and the FEF (see Corbetta & Shulman, 2002, for review). That is, the network of brain regions involved in endogenous orienting of spatial attention largely overlaps with the network sub-serving sensorimotor transformations for saccadic movements (Corbetta, Akbudak, Conturo, Snyder, Ollinger, & Drury, 1998; Nobre, Gitelman, Dias, & Mesulam, 2000; Beauchamp, Petit, Ellmore, Ingeholm, & Haxby, 2001).

Recent behavioral data, however, challenge the premotor theory by showing dissociations between attention and eye movements. Golomb, Chun, and Mazer (2008) directly addressed the issue of how the topography of visuospatial attention reorganizes after an eye movement. They developed a gaze-contingent paradigm in which participants performed an eye movement while keeping in memory the location of a spatial cue. Maintaining a location in memory, indeed, amounts to voluntary deploy spatial attention to the memorized location (see Awh & Jonides, 2001, for review). Results demonstrated that attention can be maintained on the location of a spatial cue while moving the eyes elsewhere. This should not be possible if control of eye movements and control of attention were tightly coupled. More specifically, the study revealed facilitation effects at both retinotopic and spatiotopic coordinates of the attended location around the time of an intervening saccade. Retinotopic facilitation prevailed for 100-200 ms after the eye movement, even though this location was task-irrelevant. Conversely, at later delays, the attentional benefit prevailed at the spatial, task-relevant, coordinates of the attended location.

These findings were replicated under different experimental manipulations (Golomb, Pulido, Albrecht, Chun, & Mazer, 2010; Golomb, Marino, Chun, & Mazer, 2011) and corroborated by neuroimaging evidence (Golomb, Nguyen-Phuc, Mazer, McCarthy, & Chun, 2010). According to Golomb and collegues (Golomb et al., 2008), these results imply that the basic coordinate system of spatial attention is retinotopic and it must be updated to compensate for intervening eye movements. However, the data are also consistent with the alternative hypothesis that spatial attention operates on two saliency maps (one retinotopic and the other spatiotopic) with different time courses (see also Astle, 2009).

Spatial updating of attended locations is consistent with single-cell studies showing that LIP neurons update the representation of visual space across eye movements (Duhamel, Colby, & Goldberg, 1992). LIP neurons have retinotopic receptive fields (RFs), and carry visual and visual memory signals. Spatial representations in LIP, however, are not simply retinotopic. Indeed, remembered target locations are remapped in the coordinates of the new fixation point after an eye movement. Some LIP neurons, moreover, anticipate the retinal consequences of intended eye movements by becoming transiently responsive to stimuli presented in their post-saccadic RF (i.e., *predictive remapping*).

Remapping in LIP updates the internal representation of visual space in conjunction with eye movements. This process requires a mechanism that produces a shift of activity from the original coordinate frame to the postsaccadic frame using oculomotor information. A corollary discharge (CD) of the saccadic command is supposed to originate in the SC, from which it gets to the FEF via the mediodorsal thalamus (see Sommer & Wurtz, 2008, for review). FEF neurons in turn are functionally coupled with LIP (Ferraina, Pare, & Wurtz, 2002). CD signals may also reach LIP neurons without crossing the FEF, via the lateral pulvinar nucleus (Clower, West, Lynch, & Strick, 2001). This distributed network is supposed to fulfill the computation of vector subtraction, which permits to achieve spatial remapping without requiring an explicit supraretinal representation of target location. However, how the brain performs this computation remains unknown.

In the seminal paper by Duhamel et al. (1992), remapping was attributed to shifting RFs. This account implies that each LIP cell should be connected to all locations on the retina through interneurons. During fixation, only the retinal location that corresponds to the classic RF can be accessed, whereas all the other locations are gated. Around the time of an eye movement, all RFs shift from their default location to the appropriate offset location, which depends on the current saccade target. The shifting RF model has been recently challenged on the basis of two compelling arguments (see Cavanagh, Hunt, Afraz, & Rolfs, 2010, for discussion). The first one takes advantage of cross-modal anticipatory responses, which are analogous to predictive remapping. In this case, no shifting RFs can be invoked, because rewiring should take place between different modalities. Second, the updating of remembered spatial locations in LIP rules out the hypothesis of shifting RFs, because at the time of remapping there is no activity on the retina or in earlier visual cortices. Cavanagh et al. (2010) argue that the only source for remapping must be a transfer of information from currently active cells that hold spatial locations in memory. This mechanism requires that horizontal connections can transfer activation across LIP cells using a corollary signal of the upcoming saccade.

If remapping involves activation transfer across a saliency map, one important question is what kind of connectivity might be involved. Quaia, Optican, and Goldberg (1998) proposed a computational model of LIP-FEF interactions that performed spatial remapping through horizontal connections in LIP. However, the model required specific connectivity and operations at the dendritic level, which are difficult to implement in a biological circuit. Horizontal connections were used also by Xing and Andersen (2000a) to model spatial updating in LIP. The connection weights, however, were computed using an optimization procedure with specific constraints. Moreover, the model included a set of memory units that stored one spatial location at a time. That is, it required as many memory buffers as targets to be stored. More recently, Keith and Crawford (2008) trained a back-propagation network to perform a double saccade task. After learning, the network achieved spatial remapping by means of a lateral displacement in the hidden units' RFs. However, back-propagation is not considered biologically plausible, because learning employs signals that are non-locally available. Moreover, the model has a feed-forward architecture, while bidirectional propagation is a critical computational principle in the cerebral cortex (O'Reilly, 1998), where recurrent connections are ubiquitous.

Unlike back-propagation models, basis function (BF) networks with recurrent connectivity can be readily mapped onto parietal circuits (Pouget & Snyder, 2000, for a review). Indeed, the properties of posterior parietal neurons that combine sensory and posture signals suggest that they may serve as BFs with which the brain computes coordinate transformations. BFs are processing units that compute the product of nonlinear functions, which form their basis set, and a linear combination of their outputs is sufficient to approximate any arbitrary function of their inputs (Poggio & Girosi, 1990; Pouget & Sejnowsky, 1997). It follows that encoding space with BFs renders it possible to reduce nonlinear coordinate transformations to simple linear mappings. The resulting BF representation encodes spatial locations in a format that contains implicitly any frame of reference that can be derived from the input variables: for instance, a BF map that combines visual information with eye position contains a head-centered frame that can be read out with a simple linear transformation of the activity of the BF units (Pouget & Sejnowsky, 1997). One drawback of the BF approach is the problem known as the curse of dimensionality: BF representations are subject to combinatorial explosion, because the number of units increases exponentially with the number of inputs being combined (for further discussion see Pouget & Snyder, 2000). Nevertheless, the high redundancy of a BF representation can be exploited to optimally filter out noise in the sensory input (Deneve, Latham, & Pouget, 2001).

The BF approach is consistent with neurophysiological evidence showing that the activity of many parietal neurons involved in sensorimotor transformations approximates a multiplicative combination of sensory and posture signals (Andersen, Essick, & Siegel, 1985; Andersen, 1989). Cell encoding with multiplicative interaction of independent variables (i.e., gain-field coding) is considered as a major computational principle of nonlinear neuronal processing (Salinas & Their, 2000, for a review). Computational studies determined how and under what conditions coordinate transformations can be performed by gain modulated neurons (Salinas & Abbott, 1995). How neurons combine their inputs in a directly multiplicative manner remains unclear, even though a number of cellular mechanisms have been proposed (see Brozović, Abbott, & Andersen, 2008). At the network level, gain modulation can arise as a consequence of learning rules that adjust the strength of synaptic connections in order to achieve specific coordinate transformations (Zipser & Andersen, 1988; Xing & Andersen, 2000a-b; Smith & Crawford, 2005). Moreover, multiplicative responses can arise through population effects in a recurrent network with excitatory connections between similarly tuned neurons and inhibitory connections between differently tuned neurons (Salinas & Abbott, 1996). As a consequence, BFs can be seen as building blocks that simulate the activity of single gain modulated neurons or population effects within many parietal cells.

Notably, recurrent BF networks are well suited for implementing internal forward models (Denève, Duhamel, & Pouget, 2007) that describe how sensory inputs are modified as a result of motor action. Growing empirical evidence suggests that the brain integrates sensory and motor signals using such internal models to perform a variety of tasks, such as predicting sensory information and optimal motor control (Wolpert, Gharamani, & Jordan, 1995; Kawato, 1999; Desmurget & Grafton, 2000; Todorov, 2004). Because retinotopic representations change in a predictable way if the parameters of an eye movement are known, an internal forward model may be used for achieving spatial remapping across saccades (Vaziri, Diedrichsen, & Shadmehr, 2006).

The present study aims to investigate whether a recurrent model of saccadic planning can account for attentional effects without requiring additional or specific mechanisms separate from the circuits that perform sensorimotor transformations for eye movements. Accordingly, attention orienting is implemented in terms of feedback effects due to saccadic planning and is explicitly concerned with action-oriented representations. The model builds on the BF approach and includes a circuit that achieves spatial remapping using an internal forward model of how visual signals are modified as a result of saccadic movements. The latter circuit provides new insight into how remapping operations may be implemented in parietal cortex and accounts for dissociations between attention and eye movements observed in gaze-contingent paradigms.

2.2 METHOD

2.2.1 OVERVIEW OF THE MODEL

In the spirit of a nested incremental modeling approach (Perry, Ziegler, & Zorzi, 2007), the model is built upon previous computational work on modeling sensorimotor transformations using BFs (Pouget & Sejnowski, 1997; Pouget & Snyder, 2000, for a review). The architecture of the model (Figure 1) consists of a BF map, which simulates the activity of LIP neurons, and a motor map that simulates saccadic planning in FEF through population coding. Each map has lateral connections that generate local excitation and long-range inhibition. This allows memory activity in the absence of visual input and competition between different population codes (Compte, Brunel, Goldman-Rakic, & Wang, 2000; Wang, 2001).

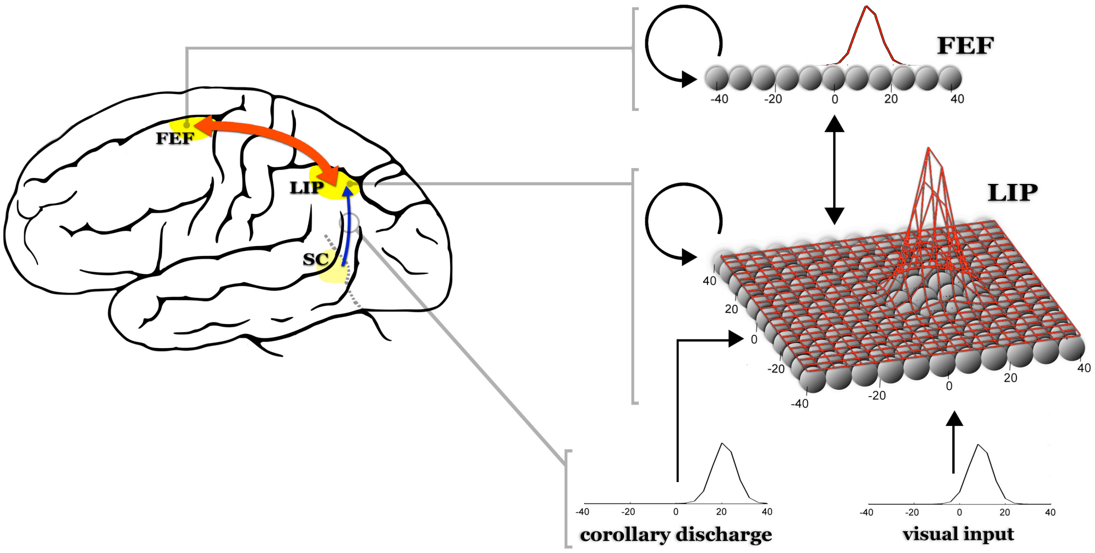

Figure 1. Recurrent neural network model for spatial attention. The model contains a radial basis function map (LIP) for retinal position and oculomotor command, and a motor map (FEF) encoding saccadic plans through population coding. Neurons in the LIP map combine visual and motor signals (i.e., retinal information and a corollary discharge of saccadic commands) to represent oculomotor space. Lateral connectivity in LIP implements an internal model that predicts the sensory consequences of saccadic movements. Each map has lateral connections with local excitation and long range inhibition.

The BF map combines population codes representing retinal (*r*) and oculomotor (*c*) signals. As the neuron tuning curves are Gaussians centered at (*r, c*), this layer is a two-dimensional radial BF map for retinal position and oculomotor command. Neurons are arranged topographically (e.g., Patel et al., 2010) along the corresponding axis and are connected so as to estimate the remapped position of a memorized visual target across eye movements. As a result, given visual input *r* and oculomotor command *c*, the corresponding hill of activity in LIP will shift to the fixation neuron (i.e., coding for a *0*° motor command) with preferred retinal position $r - c$. This recurrent connectivity implements an internal forward model that predicts the visual consequences of saccadic movements.

LIP neurons are reciprocally connected with FEF neurons through topographical projections. That is, a LIP neuron with preferred retinal position *r* is connected preferentially with a FEF neuron that codes for the corresponding target location. In agreement with the premotor theory, feedback of FEF activity to LIP neurons allows a motor program to generate endogenous, top-down attentional signals through the recruitment of neurons located upstream in parietal spatial maps. Moreover, the implementation of the circuit responsible for spatial remapping renders it possible to investigate the role of perisaccadic updating in attention orienting.

2.2.2 RECURRENT MODEL: IMPLEMENTATION DETAILS

The LIP map is composed of 441 neurons that generate a representation of the oculomotor space by combining multiplicatively population codes of retinal (*r*) and oculomotor (*c*) signals. LIP activity is also driven by recurrent lateral connectivity and by feedback signals from the FEF layer. The activity of each LIP neuron is updated according to the following equation:

$$\frac{dx_i^{LIP}}{dt} = f\left(G(r)_i + \sum_j w_{ij} x_j^{LIP} + \sum_l q_{il} x_l^{FEF} - \zeta x_i^{LIP} \right) G(c)_i \tag{1}$$

where *f* is the logistic function, $G(r)_i$ is the retinal signal, x_j^{LIP} is the activity of other LIP neurons received through the w_{ij} lateral connection weights, x_l^{FEF} is the activity of FEF neurons that is received through the q_{il} connection weights, and ζ is the neuron's passive decay of activation (set to 0.1). $G(c)_i$ is the oculomotor signal, which represents the corollary discharge of the current eye movement, and its multiplicative interaction with the other signals produces the typical gain modulation of a BF map. Visual and motor tuning curves are Gaussian functions of *r* and *c*, respectively, both defined in retinal coordinates:

$$G(r)_i = e^{-\frac{(r - r_i)^2}{2\sigma^2}} \tag{2}$$

$$G(c)_i = e^{-\frac{(c - c_i)^2}{2\sigma^2}} \tag{3}$$

where r_i and c_i, which are uniformly spread between -40° and +40° in increments of 4°, indicate the preferred retinal location and preferred oculomotor command of neuron *i*, respectively. The width of the Gaussians, σ, is kept fixed to 5°. Intraparietal neurons, indeed, have narrow spatial tuning, with a modal response field radius smaller than 5° (Platt & Glimcher, 1998).

Recurrent connectivity within LIP implements an internal forward model of how visual information is modified as a result of saccadic movements. To achieve this computation, the neuron with preferred target location *r* and oculomotor command *c* connects neurons with preferred retinal location and oculomotor command close to *r-c* and 0°, respectively. The strength of these connections follows a Gaussian profile centered on (*r-c*, 0°). The lateral weight w_{ij} that connects the presynaptic neuron *i* to the postsynaptic neuron *j* within the LIP map is given by:

$$w_{ij} = k\left(\theta_i e^{-\frac{((r_i - c_i) - r_j)^2 + c_j^2}{2\sigma^2}} + \rho_{ij}\right) - \varphi \tag{4}$$

where κ and φ determine the strength of excitatory and inhibitory connections respectively ($\kappa = 3.6$; $\varphi = 0.75$). ϑ_i modulates the connection weight as a function of the preferred motor command of the presynaptic neuron *i*:

$$\theta_i = -\alpha\, e^{\frac{\frac{-(c_i^2)}{\sigma^2}}{2}} + \beta \tag{5}$$

where α and β are set to 2.5 and 1.9, respectively. This allows sustaining memory activity during remapping and gradually decreasing it as remapping approaches its completion without altering the computational properties of the internal model. Finally, ρ_{ij} ensures that all neurons with the same preferred target location have reciprocal excitatory connections:

$$\rho_{ij} = e^{\left(-abs(c_i) - \frac{(r_i - r_j)^2}{2\sigma^2}\right)} \tag{6}$$

LIP neurons are bidirectionally connected with FEF neurons. The LIP neuron with preferred target location *r* is connected to FEF neurons with preferred motor command *m* close to *r*. The strength of the connection q_{il} between the LIP neuron *i* and the FEF neuron *l* is given by a Gaussian function of the difference between r_i and m_l:

$$q_{il} = e^{-\frac{(r_i - m_l)^2}{2\sigma^2}} - \varphi \tag{7}$$

where φ (set to 0.75) determines the value of the inhibitory component of the connections.

The FEF map is composed of 21 neurons that generate a motor map for saccadic planning. Similarly to the LIP layer, motor fields' centers of FEF neurons are uniformly spread between -40° and +40° in increments of 4°. The activity of each FEF neuron is updated according to the following equation:

$$\frac{dx_i^{FEF}}{dt} = f\left(G(m)_i + \sum_n v_{in} x_n^{FEF} + \sum_l q_{il} x_l^{LIP} - 2\zeta x_i^{FEF} \right) \quad (8)$$

where f is the logistic function, x_n^{FEF} is the activity of other FEF neurons received through the v_{in} lateral connection weights, x_l^{LIP} is the activity of LIP neurons that is received through the q_{il} connection weights, and ζ is the neuron's passive decay of activation (set to 0.1). $G(m)_i$ is a Gaussian function of the planned oculomotor program, which is always set to 0 except in the case of saccadic planning and attention orienting.

Lateral connections in FEF generate local excitation and long-range inhibition. The strength of the lateral connection v_{ij} from the FEF neurons i to the FEF neuron j depends on the difference between their motor fields' centers, m_i and m_j, according to the following equation:

$$v_{ij} = \tau e^{-\frac{(m_i - m_j)^2}{2\sigma^2}} - \lambda\, e^{-\frac{(m_i - m_j)^2}{2\varsigma\sigma^2}} \quad (9)$$

where τ and λ determine the values of excitatory and inhibitory region, and ς controls the width of the inhibitory region ($\tau = 1.15$, $\lambda = 0.47$, $\varsigma = 10$).

Continuous time was discretized in the simulations and the time constant (*dt*) was set to 0.01 for all simulations.

2.3 RESULTS

2.3.1 OCULAR PERTURBATION TASK

Before simulating attention tasks, we tested the ability of the model in performing spatial remapping by implementing a saccadic task that required to foveate a remembered spatial location after an ocular perturbation (usually evoked by electrical stimulation of the SC). Each trial started with presentation of a random visual target (*r*). After its offset, we simulated an ocular perturbation by generating a random CD signal (*c*). We decoded FEF activity using the center of mass method (Zemel, Dayan, & Pouget, 1998) and we measured the error of the system (i.e., distance between expected and decoded target location) when the difference in decoded target location between two successive states was less than 0.005° (i.e., when the network has settled into a stable state). We computed the root mean square error (*RMSE*) as performance index over 300 runs with random values of *r* and *c*. The *RMSE* (1.9°) was less than half of the interpeak distance in FEF, indicating that the model accurately planned the movement required to acquire the remembered target location after ocular perturbation.

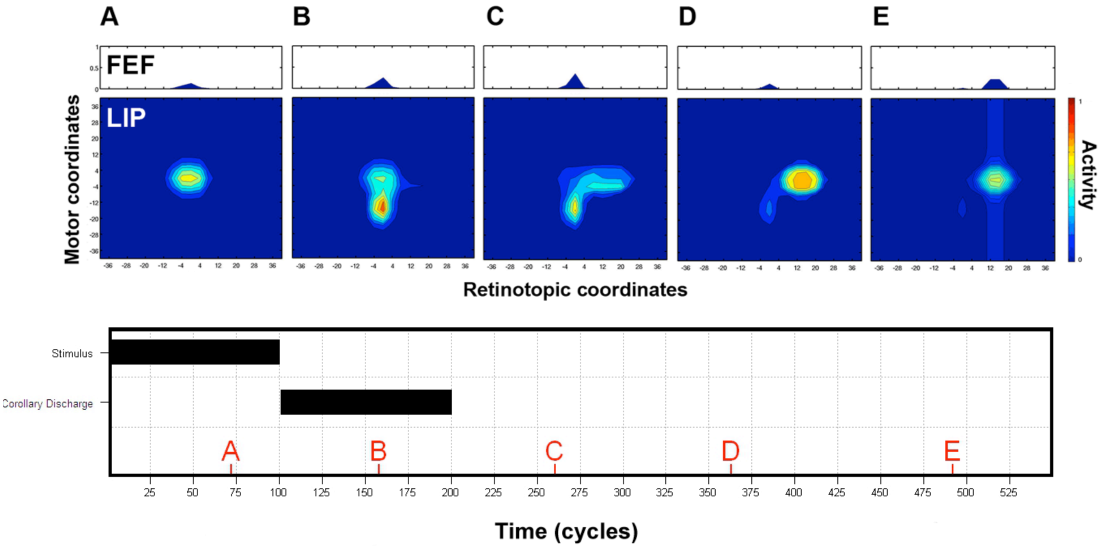

Figure 2. Snapshots of the temporal dynamics of simulated LIP (bottom) and FEF (top) neurons during the ocular perturbation task. (a) Activity profiles immediately after the onset of a visual target presented at 2°on the left from fixation. After an ocular perturbation, which shifts the eye 18° to the left, the corresponding CD signal is combined with the memory trace of the target location (b-c). The lateral connectivity in LIP, which implements the internal forward model, drives the hill of activity to the remapped location (16°to the right on the retinal axis and fixation position on motor axis) (d-e). Note that activity in FEF reflects the changes in LIP activity. The bottom panel represents the detailed temporal sequence of events during the trial, with letters on the lower line indicating the exact timing of the activity snapshots.

The analysis of the response properties of simulated LIP neurons showed that retinotopic representations were remapped in the coordinates of the new fixation point after ocular perturbation. Figure 2 shows the temporal evolution of the network activity. When a visual target is briefly presented to the model, a two-dimensional pattern of activity builds-up in the LIP map. The hill of activity is centered at the corresponding position along the retinal axis and at 0° (corresponding to fixation) along the motor axis. After ocular perturbation, the CD signal modulates the activity in LIP recruiting those neurons that are selective for the corresponding motor vector. Then, the lateral connections, which implement the internal forward model, start to transfer the activity to the fixation neurons that code the remapped location along the retinal axis. As a result, the remapped representations in LIP are coded by those neurons whose visual RFs would have been stimulated if the visual target had still been present. This is consistent with the finding that many LIP neurons code for impending saccades (e.g., Colby, Duhamel, & Goldberg, 1996). FEF activity at the end of the remapping process encodes target position in the coordinates of the new fixation point.

2.3.2 SPATIAL CUEING PARADIGM

The premotor theory maintains that motor planning generates top-down signals that produce a processing facilitation for stimuli located in the region of space toward which the motor plan was prepared. We tested this basic claim by implementing a spatial cueing paradigm (Posner, 1980), which requires detecting as fast as possible a visual target. In endogenous cueing, participants voluntarily orient to the spatial location indicated by a cognitive cue and the target can be presented at the cued location (valid trials) or at a different location (invalid trials). In neutral condition, the cognitive cue does not indicate where to orient attention. Typically, valid trials give rise to faster RTs with respect to neutral trials (attentional benefits), while invalid trials give rise to slower RTs (attentional costs).

We simulated attention orienting by generating a saccadic plan in the FEF map and feeding back the activity to the LIP map. The saccadic plan could be directed toward one of two spatial locations (-4° and 4° eccentricity), similarly to the classical spatial cueing paradigm (Posner, 1980). After a random delay (within the range 300-600 cycles), we presented a visual target in the location corresponding to the planned saccade (valid condition) or in the other location (invalid condition). In order to measure attentional benefits and costs, we included a baseline condition in which attention orienting did not precede target presentation. We measured the number of cycles required for reaching the threshold value of 0.7 in FEF (the same response criterion was used in all subsequent simulations) as an index of RT for target detection. The target remained on until the end of the trial because, with the current set of parameters, this allowed proper build-up of activation in FEF to reach response threshold. We performed 10 runs with 60 trials each (20 valid trials, 20 invalid trials and 20 neutral trials).

A repeated-measures ANOVA on mean RTs showed a significant main effect of condition (valid, invalid, baseline) [*F*(2, 27) = 15474, *p* < .0001]. The valid condition produced faster responses than the baseline condition [265 vs. 378 cycles; *t* (9) = 216.12, *p* < .0001], which in turn produced faster responses than the invalid condition [378 vs. 399 cycles; *t* (9) = 24.27, *p* < .0001], indicating robust attentional effects for selected spatial locations in the absence of eye movements. The RT benefit observed for valid trials depends on the spatial correspondence between top-down signals (from FEF) and bottom-up signals (from the visual target) in the LIP map. In contrast, top-down and bottom-up signals are spatially misaligned during invalid trials, thereby generating two different hills of activity in LIP. The competition between these population codes through lateral connectivity slows down target detection and is responsible for the incurred RT cost.

Behavioral studies have shown that attentional costs increase as a function of the distance between target and cued location (Umiltà, Mucignat, Riggio, Barbieri, & Rizzolatti, 1994). This distance effect was attributed to the time required to reorient attention from the cued location after target presentation. To investigate the presence of a distance effect in the model, we repeated the previous simulations by adding two peripheral positions (-8° and 8°). This allowed presenting the target at four different distances from the cued location (4°, 8°, 12°, 16°), as in the study of Umiltà and colleagues (see Figures 3B and 3C). A repeated-measures ANOVA on mean RTs with distance (0°, 4°, 8°, 12°, 16°) as factor yielded a significant main effect [*F*(5, 54) = 14243, *p* < .0001]. Planned comparisons (two-tailed *t* tests) revealed that the attentional cost varied reliably as a function of the distance from the cued location (all *ps* < .0001; see Figure 3A). Notably, the distance effect in the model emerges from lateral connectivity that generates local excitation and long-range inhibition, without requiring any additional mechanism.

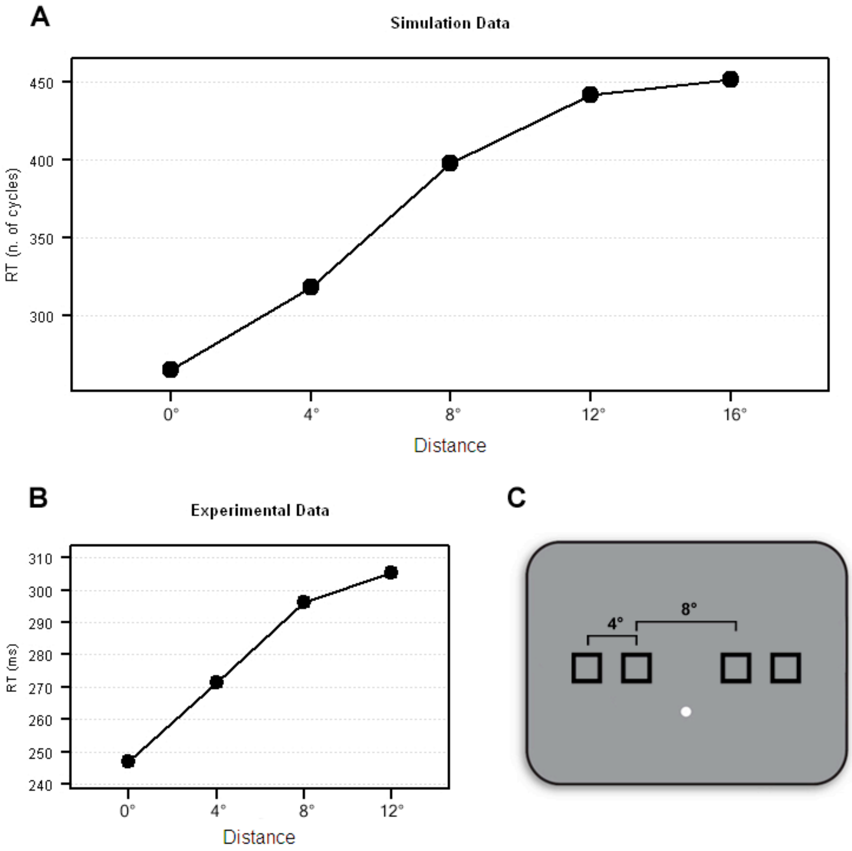

Figure 3. Distance effect. Attentional costs increase as a function of distance from the cued position. (**A**) Simulation data. (**B**) Experimental data (Umiltà et al., 1994). (**C**) Schematic representation of the possible target positions in the simulated spatial cueing paradigm.

2.3.3 GAZE-CONTINGENT PARADIGM

To investigate the role of spatial remapping in attention orienting, we implemented a gaze-contingent paradigm similar to that used by Golomb et al. (2008). Following the initial phase of attention orienting (up to and including a 100-cycle fixed delay), we simulated an intervening saccade by generating a second saccadic plan in the FEF map. Because the intervening saccade was an overt eye movement, the corresponding CD signal was delivered to the network. After a variable delay (50, 100, 200, 300, 400, 500, or 600 cycles), we presented the detection target, which lasted until the end of the trial. The target could appear at the spatiotopic coordinates of the attended location (spatiotopic condition), at its retinotopic coordinates (retinotopic condition), or in two control locations (see Figure 4), which were chosen to be equidistant from the cued position both in retinotopic and in spatiotopic coordinates. We measured the number of cycles required for reaching the threshold value in FEF as an index of RT for target detection. To assess attentional facilitation, we computed the differences in RT when the target occurred in the spatiotopic or retinotopic locations compared to average RT between the two control locations.

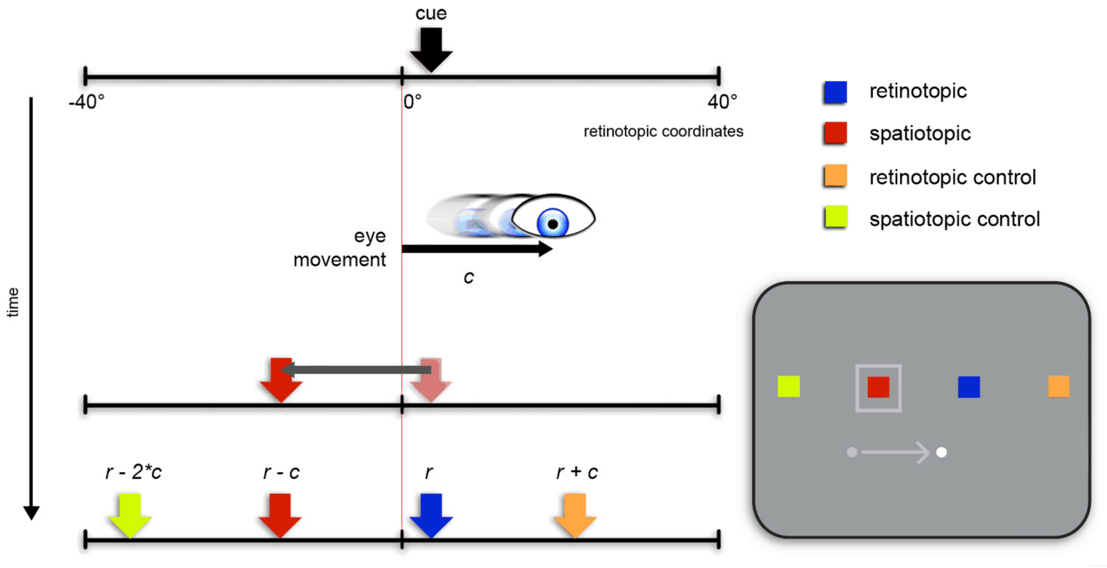

Figure 4. Schematic example of target presentation in the simulated gaze-contingent paradigm. Given initial orienting to a cue location r and intervening eye movement c, we measured the latency for target detection at 4 different locations: r (retinotopic condition); r - c (spatiotopic condition); r + c (retinotopic control); r - 2c (spatiotopic control), where c is the eye movements amplitude. The bottom right panel shows the same 4 locations as they appear on the display (i.e., spatiotopic coordinates). Since we did not implemented a modulation of visual acuity by eccentricity, the greater eccentricity of control positions is not relevant in the model.

We performed 10 runs with 20 offset trials for each delay and condition. Mean RT differences were computed for each run and then entered into a repeated-measures ANOVA with delay (50, 100, 200, 300, 400, 500, and 600 cycles) and condition (retinotopic vs. spatiotopic) as factors. There was no effect of condition [$F(1, 9) = 2.09$, $p = 0.18$], but there was a significant effect of delay [$F(1, 9) = 64.356$, $p < .0001$], and a significant interaction [$F(1, 9) = 17.82$, $p < .001$]. We then conducted planned t tests to compare retinotopic and spatiotopic conditions at different delays and to assess whether spatiotopic or retinotopic locations were significantly facilitated compared with the control baseline (0 cycles RT difference). All t tests were Bonferroni corrected for multiple comparisons ($p < .0024$) and two-tailed.

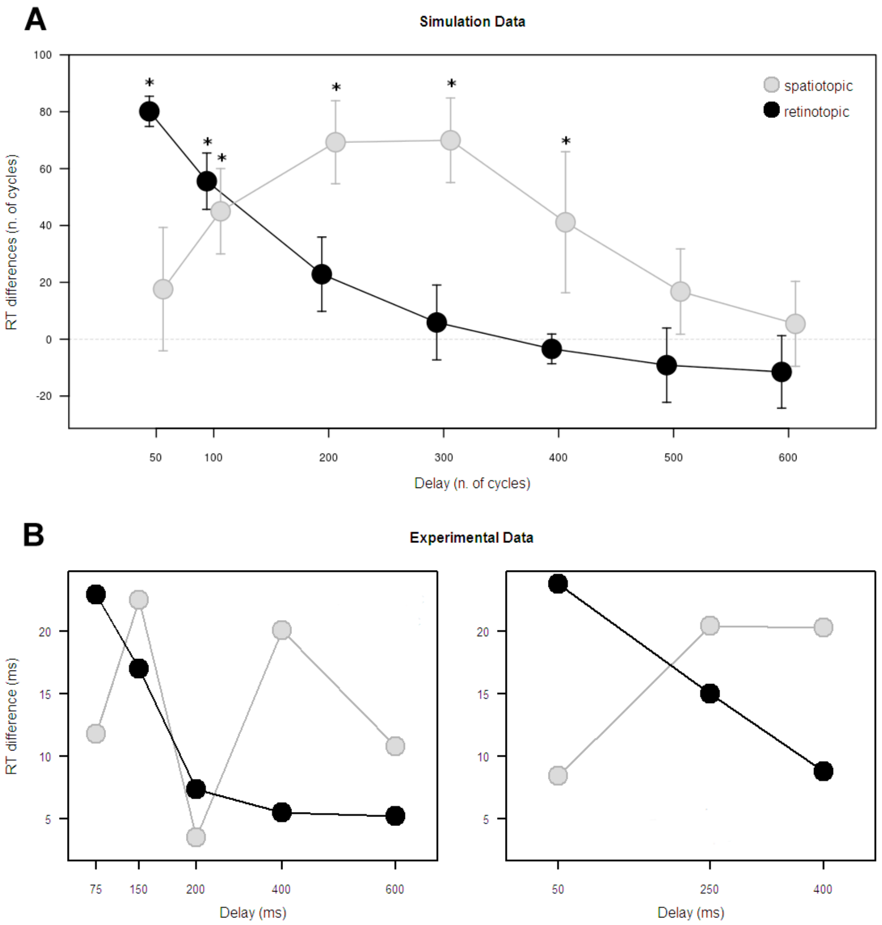

Figure 5. Attentional facilitation in a gaze-contingent paradigm. Attentional facilitation is shown as the difference in RT for targets appearing in the spatiotopic and retinotopic locations compared with the control location baseline. Positive values reflect faster RTs than at control locations; error bars indicates 95% confidence intervals and asterisks indicate values significantly different from 0 after Bonferroni correction for multiple comparisons. (a) Simulation data. Facilitation is plotted as a function of delay between saccadic planning and target onset. (b) Experimental data from Golomb et al. (2008; Saccade Task) on the left, and from Golomb et al. (2011) on the right. Facilitation is plotted as a function of delay between the end of the intervening saccade and target onset.

The interaction depended on a different time course of facilitation between retinotopic and spatiotopic conditions (see Figure 5A). Retinotopic facilitation was strongest at the 50-cycles delay and then rapidly decreased, whereas spatiotopic facilitation reached its peak at later delays (200 - 300 cycles). Target detection was significantly faster at the retinotopic coordinates of the attended location until the 100-cycles delay. At this delay, retinotopic facilitation matched spatiotopic facilitation, which prevailed at longer delays (200-400 cycles).

These results are consistent with the empirical data (see Figure 5, panels B) reported by Golomb et al. (2008, 2011) showing early facilitation effects at the eye-centered coordinates of the attended location and later benefits at its spatial coordinates. Our simulations well predict the interplay between retinotopic and spatiotopic facilitation during the first 200 ms after the eye movement (note that the number of cycles is not intended to directly map onto a millisecond-scale). Figure 6 shows the temporal evolution of the network activity throughout a trial of the gaze contingent paradigm. After an eye movement, the hill of activity in LIP generated by attention orienting is shifted to the remapped location. If the delay between eye movement and target onset is sufficiently long to allow completion of the spatial updating, the activity profile in LIP becomes aligned with the bottom-up visual signal of a target presented at the spatiotopic location. Conversely, a target presented at the retinotopic location is spatially misaligned with the LIP memory activity, thereby generating a competition between the two population codes.

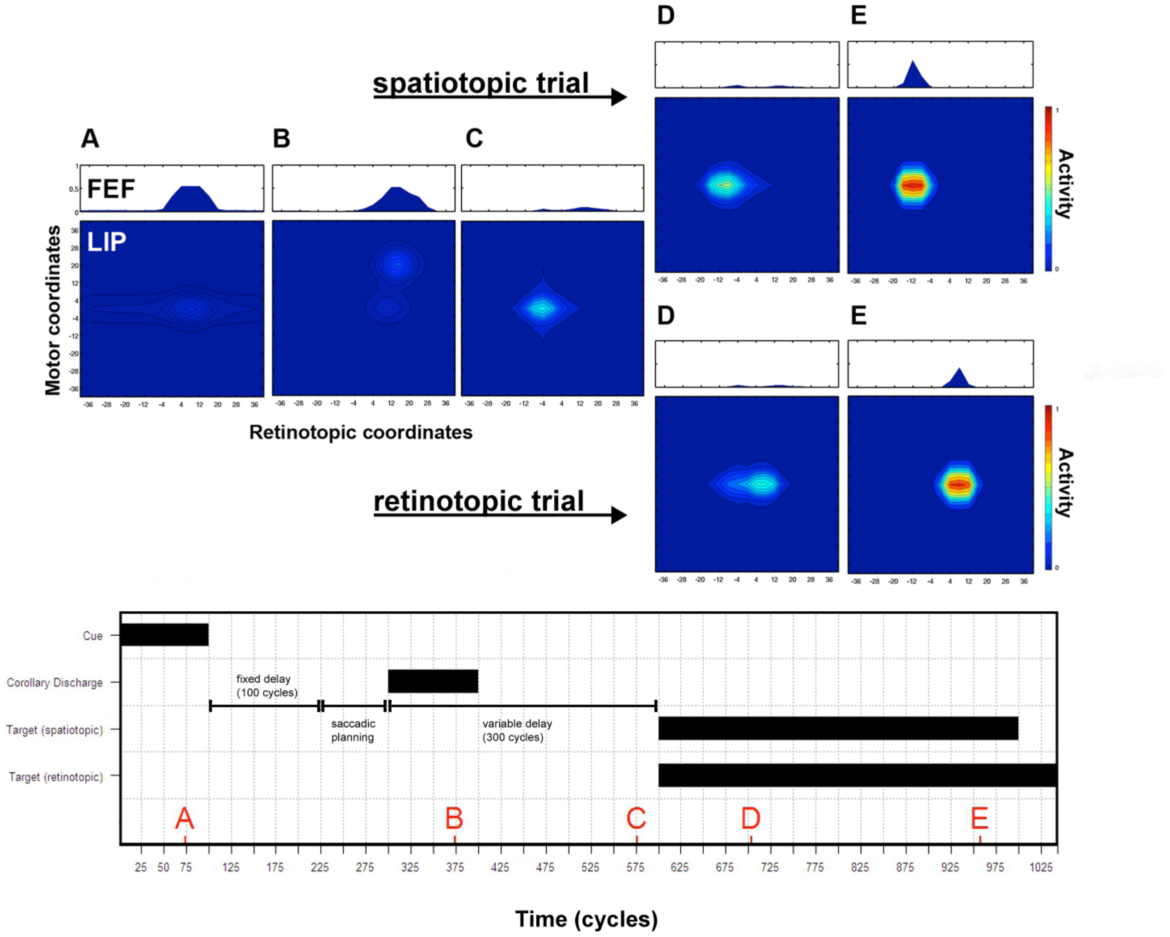

Figure 6. Snapshots of the temporal dynamics of simulated LIP (bottom) and FEF (top) neurons in the gaze contingent task. (a) Activity profiles during the initial phase of attention orienting (attention is cued to a position 8° to the right of fixation). After a fixed delay of 100 cycles, and the build-up of a saccadic plan in FEF (20° to the right), the corresponding CD signal is combined with the memory trace of the cued position (b). The lateral connectivity in LIP drives the hill of activity to the remapped location (c). After a variable delay (here 300 cycles), the target is presented in the spatiotopic (upper row) or in the retinotopic position (lower row) (d). The build-up of activity for target detection (e) (which is achieved when activity in FEF reaches a threshold value) is facilitated in the spatiotopic trial, because the activity profile in LIP is aligned with bottom-up signals from the visual target. In contrast, top-down and bottom-up signals are spatially misaligned in the retinotopic trial, thereby generating competition between the two population codes and slowing down the RT for target detection. The bottom panel represents the detailed temporal sequence of events during the trials, with letters on the lower line indicating the exact timing of the activity snapshots. The right edge of the black bar representing the target does not indicate an offset, but the time required to reach the detection threshold, which occurred earlier in the spatiotopic trial.

2.4 DISCUSSION

We examined whether a recurrent model of saccadic planning can account for attentional effects without requiring additional or specific mechanisms separate from the circuits that perform sensorimotor transformations for eye movements. The model employs BFs to simulate posterior parietal neurons involved in the representation of oculomotor space and incorporates a circuit responsible for updating remembered spatial locations across eye movements. Spatial remapping is achieved by means of horizontal connections among intraparietal neurons that implement an internal, forward model of how an eye movement modifies visual information. This forward model combines the sensory inflow with the motor outflow to estimate the consequences of motor commands on the internal representation of salient locations.

Previous computational studies showed that spatial remapping can be implemented in a recurrent sensory map by integrating an eye velocity signal (Droulez & Berthoz, 1991) or an eye position signal (Krommenhoek, Van Opstal, Gielen, & Van Gisbergen, 1993). Recurrent connections among simulated LIP neurons were used to model spatial updating in parietal cortex. However, specific connectivity and computations at the dendritic level (Quaia, Optician, & Goldberg, 1998) or a dedicated memory buffer, which stores the location of one target at a time (Xing & Andersen, 2000a), were required. In contrast, sensorimotor transformations, short-term memory, and spatial updating are handled in our model by the same computational units, which resemble the properties of posterior parietal neurons (for further discussion on the biological plausibility of the BF approach see Pouget & Snyder, 2000). More recently, Keith and Crawford (2008) proposed a network model with feed-forward architecture that performs spatial updating by means of a lateral displacement in the hidden units' RFs. However, as noted in the Introduction, the hypothesis of shifting RFs is inconsistent with the empirical data on cross-modal anticipatory responses and on the updating of remembered spatial locations in LIP (see Cavanagh et al., 2010, for a thorough discussion).

Simulations of the spatial cueing paradigm showed the typical pattern of results reported in behavioral studies with regular attentional benefits and costs. Contrary to previous computational accounts of spatial attention (Mozer, 1991; Cohen, Romero, Servan-Schreiber, & Farah 1994; Phaf, Van der Heijden, & Hudson, 1990), the model does not require any separate subsystem (e.g., specific nodes or unspecified "bias") to generate top-down attentional effects. Indeed, attentional facilitation depends only on feedback effects from premotor neurons to parietal neurons located downstream. Of course this demonstration does not rule out the possibility that other types of attentional mechanisms may also exist in the brain.

In addition to simulate attentional orienting in absence of eye movements, we implemented a gaze-contingent paradigm in which an eye shift is interposed between attentional allocation and target presentation. The model predicts that, after an eye movement, visuospatial attention is remapped in the coordinate of the new fixation point without requiring top-down reorienting signals. This automatic updating takes time and the native attentional code in retinotopic coordinates persists around the time of the eye movement. Indeed, simulations showed a processing facilitation at the retinotopic coordinates of the attended location immediately after an intervening saccade. As retinotopic facilitation decreases, spatiotopic facilitation increases and prevails at longer delays. These results are consistent with recent empirical studies devoted to investigating the allocation of spatial attention across eye movements (Golomb et al., 2008; Golomb et al., 2010; Golomb et al. 2010, Golomb et al. 2011; Mathôt & Theeuwes, 2010).

It has to be noted that Golomb and colleagues (2008) failed to observe spatiotopic facilitation when participants were asked to retain a location in retinotopic coordinates. Building on this result, they argued that the updating of spatial attention occurs only when its spatiotopic coordinates are task relevant. However, other recent studies challenge this conclusion (Howe, Drew, Pinto, & Horowitz, 2011; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011). In particular, Howe and colleagues demonstrated that the attentional system automatically tracks visual objects in spatiotopic coordinates and compensates for ongoing eye movements. Moreover, Rolfs and colleagues have shown that the topography of attention is modified before a saccade in order to compensate for an intervening eye movement, preserving the alignment of the attentional focus with the corresponding target. Taken together, these results suggest that spatiotopic updating is automatic, even though spatiotopic facilitation may be affected by task demands. More generally, the automaticity of a neural process does not necessarily imply the presence of a behavioral effect.

Our computational model represents a fundamental improvement of the premotor theory of attention, because it takes into account the mechanism responsible for updating attended locations across saccades. During execution of a saccadic movement, a CD signal of the motor command is combined with the internal representation of the attended location, which is remapped in the coordinates of the new fixation point. This allows the brain to align spatial attention with the external space, thus producing spatiotopic facilitation effects. As a result, our simulations suggest that the ability to keep attention at a spatial location while moving the eyes elsewhere is a consequence of the computations performed by parietal neurons to achieve spatial remapping. That is, the interactions between top-down orienting and spatial remapping account for behavioral dissociations between attention and eye movements that one may invoke to challenge the premotor theory. The model predicts that, while top-down selection depends on topographic projections from premotor neurons, the updating of selected locations involves an internal forward model that combine oculomotor information with visual memory signals.

The premotor theory of attention has also been questioned on the basis of a neurophysiological dissociation between attentional selection and saccadic preparation in FEF (Sato, & Schall, 2003; Juan, Shorter-Jacobi, & Schall, 2004; Thompson, Biscoe, & Sato, 2005), which hinges upon the existence of two subpopulations of neurons with distinct visual and motor properties (for review see Awh, Armstrong, & Moore, 2006). However, it should be noted that, even though visual activity in FEF does not drive saccadic-related activity, the selection of potential saccade targets by FEF visual neurons remains an essential part of saccade planning (for further discussion see Thompson, Biscoe, & Sato, 2005). Moreover, all those studies that showed a dissociation between orienting of spatial attention and saccadic preparation in FEF employed a singleton search task (see also Awh, Armstrong, & Moore, 2006). This type of task is known to evoke stimulus-driven (i.e., exogenous) rather than endogenous orienting of attention. However, the premotor theory was introduced to explain endogenous orienting and from the beginning it was made clear that it did not apply to exogenous orienting (e.g., Rizzolatti, Riggio, & Sheliga, 1994). Thus, these results do not invalidate the premotor theory, but reinforce a fundamental distinction between endogenous and exogenous orienting**,** which is also endorsed by the broader model of attention orienting proposed by Corbetta and Schulman (2002).

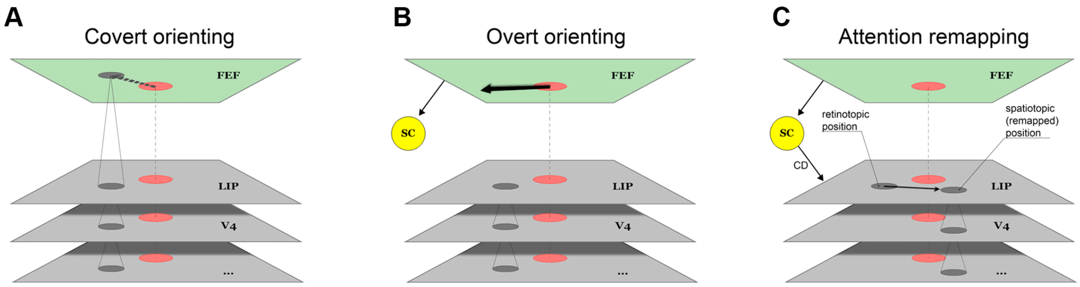

Fig. 7. Revision of the premotor theory of spatial attention. The premotor theory maintains that preparation of an eye movement produces a processing facilitation on neurons located upstream by means of topographic projections from FEF neurons. This allows the brain to select salient spatial locations (a). If an eye movement intervenes (b), an oculomotor signal coming from SC neurons modulates the activity in posterior parietal maps. As a result, selected locations are remapped in the coordinates of the new fixation point (c). Red patches indicate the position of fixation and black patches indicate the selected spatial location within each retinotopically organized map.

From our revision of the premotor theory (see Figure 7), it emerges that spatial attention does not merely reflect the consequences of oculomotor preparation (overt orienting), but also the outcome of an internal, dynamic estimate of how a saliency map of the visual world is modified as a result of oculomotor action (attention remapping).

In conclusion, the model provides new insights into how spatial remapping may be implemented in parietal cortex and offers a computational framework for recent proposals that link visual stability with remapping of attention pointers (Cavanagh et al., 2010). The updating of attended locations in parietal spatial maps may contribute to the perception of a stable visual world despite continuous changes in retinal representations across eye movements.

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3 SPACE CODING FOR SENSORIMOTOR TRANSFORMATIONS CAN EMERGE THROUGH UNSUPERVISED LEARNING

3.1 INTRODUCTION

Programming goal-directed motor behavior requires a series of computational steps, ranging from the sensory acquisition of the target to the generation of the motor command, including a transformation between different coordinate reference frames. Such transformation is mandatory because the reference frames of the sensory input usually differ from those of motor effectors. The neural substrates of sensorimotor transformations are undisputedly attributed to the posterior parietal cortex (PPC) (Colby and Goldberg, 1999). The PPC has been the subject of extensive research since a seminal neurophysiological investigation (Mountcastle et al., 1975) describing how its neural activity, characterized by both sensory and motor properties, is related to eye and limb movements; crucially, the PPC has been described as a sensorimotor interface for the generation of visually guided movements (Buneo and Andersen 2006). PPC neurons are functionally segregated for different types of movement (Fig. 1). In particular, the intraparietal sulcus (IPS) represents the cross-road where different sensory inputs converge to encode specific motor programs (Buneo and Andersen, 2006). The IPS contains several distinct sub-regions, each one devoted to a specific task: for instance, the lateral intraparietal area (LIP) is specialized for saccadic eye movements, the medial intraparietal area (MIP) is specialized for reaching, the anterior intraparietal area (AIP) is involved in grasping (Sakata and Taira, 1994).

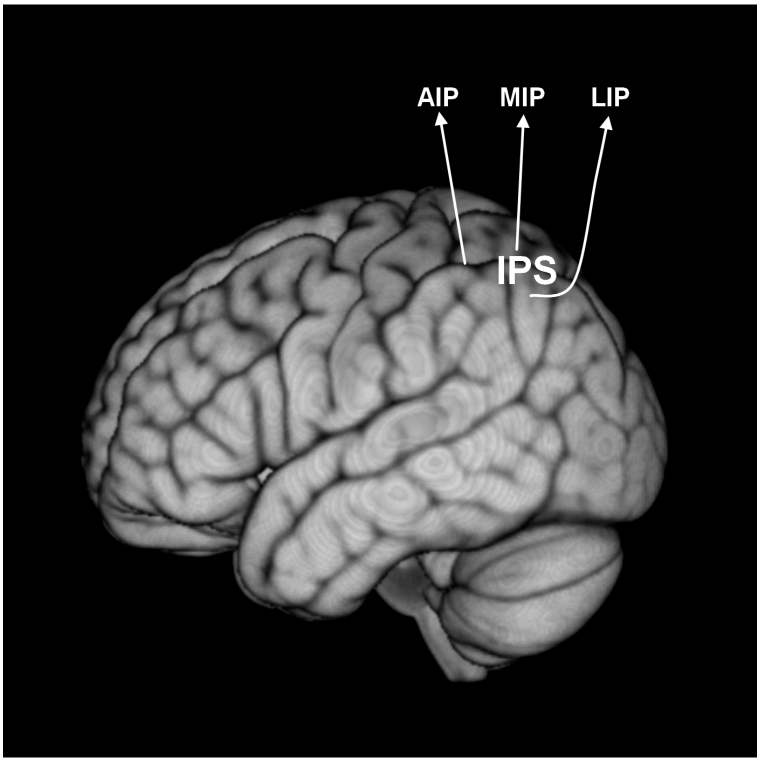

Figure 1 The PPC of the human brain. In particular, three regions of the intraparietal sulcus (IPS) are crucially involved in sensorimotor transformations: anterior (AIP), medial (MIP) and lateral (LIP) intraparietal areas

Spatial representations for motor programming are distributed in a group of PPC neurons whose activity approximates a multiplicative combination of visual and posture signals (Andersen et al. 1985). Such interplay between information coming from different modalities, usually termed gain modulation, can be generally described as a change in response amplitude of a neuron independently of its selectivity or receptive field characteristics. Computational investigations allowed to confirm the crucial role of gain modulation in sensorimotor transformations. In a seminal work (Zipser and Andersen, 1988), a multi-layer neural network was trained with the back-propagation algorithm to transform retinal signal into head-centered coordinates. Notably, the hidden neurons of the network developed gain-fields similar to those described in parietal cortex. In another computational investigation (Mazzoni and Andersen, 1991), a neural network was trained to represent visual space in head-centered coordinates with a reinforcement learning rule, which is more biologically plausible: also in this case, the authors found gain-fields in the hidden neurons. Thus, these studies show that gain modulation might provide an efficient solution to the coordinate transformation problem.

Here we present a computational model mimicking the sensorimotor transformations occurring in PPC. The model combines multiple sensory and posture input signals into a different spatial reference frame that drives the motor programming. The model is based on a Restricted Boltzmann Machine (RBM) (Hinton et al., 2006), a stochastic recurrent neural network that learns a generative model of the input data without supervision and discovers internal representations that are both distributed and non-linearly related to the input.

3.2 METHOD

The model is based on a RBM, which is formed by one layer of visible (sensory) neurons and one layer of hidden neurons (feature detectors) connected by bidirectional symmetric weights (Fig. 2). The visible neurons simulated the activity of the cortical areas interconnected with PPC while hidden neurons were supposed to develop an internal representation of input data during the learning phase. The RBM was trained with the Contrastive-Divergence learning algorithm (Hinton and Salakhutdinov, 2006) to learn a generative model of the data without supervision (i.e., maximizing the likelihood of reconstructing the data) starting from a given state of the feature detectors and using the weights $w_{i,j}$ in a top-down direction. First, given an input vector v_i^+, the feature detectors h_j^+ ("positive" phase) are activated; then, starting from a stochastically selected binary state of the feature detectors (using their state h_j^+ as a probability to activate them), the input vector v_i^- is inferred and used in turn to reactivate the feature detectors h_j^- ("negative" phase). The weights $w_{i,j}$ are updated with a small learning fraction ε of the difference between input-output correlations measured in the positive phase and the negative phase:

$$\Delta w_{ij} = \varepsilon \left(v_i^+ h_j^+ - v_i^- h_j^- \right)$$

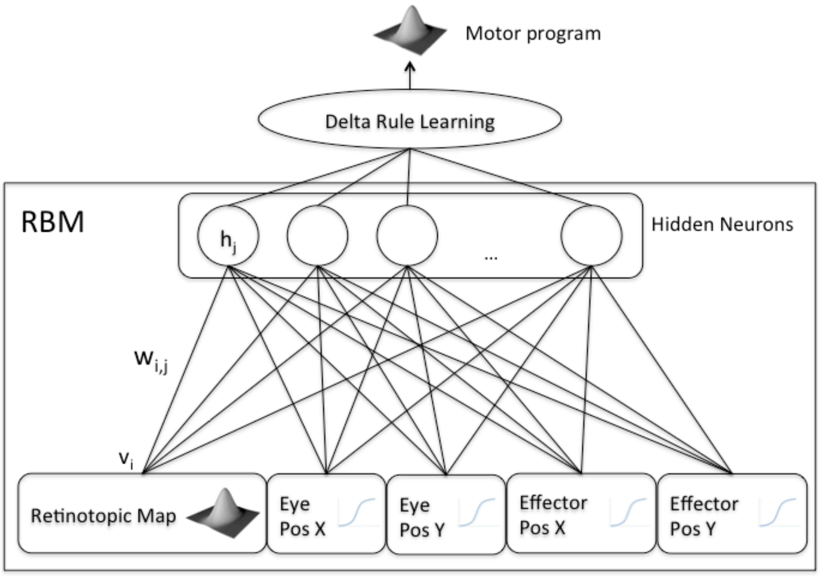

Figure 2 Model architecture. The RBM was used to learn without supervision a distributed nonlinear representation of the sensory input in the hidden layer. Delta rule learning was then used to compute the motor program from the activity of the hidden neurons

The visible layer was composed of 357 neurons:

A retinotopic map consisting in a square matrix of 17x17 neurons with Gaussian tuning functions. Visual receptive fields were uniformly spread between -9° and +9° in increments of 3°, both in the horizontal and vertical dimensions;

Four postural maps (each one consisting in 17 neurons) encoding the horizontal and vertical position of the eye and the horizontal and vertical position of an effector (e.g., hand). The neurons used a sigmoid activation function to encode position between -18° and 18°, in steps of 3°.

This input representation is broadly consistent with neurophysiological data (Pouget and Snyder, 2000). The hidden layer was composed of 250 neurons and its activity reflected a distributed nonlinear encoding of the sensory input. The recurrent architecture was characterized by bidirectional connectivity between layers. The training set presented for each training epoch consisted in 520 patterns balanced for each visual and postural position. In the learning phase, the training set was presented for a total of 3000 epochs.

After training, the activity of the hidden neurons was used to compute a motor program through a simple linear projection and delta rule learning. The motor program was a population code on a map of 35x35 neurons that coded the target position in coordinates centered on the effector. The model's performance was tested by computing the average motor error, consisting in the difference between expected and actual output. In order to achieve reliable results, we trained 10 networks with different initial random weights.

Activity in the hidden layer was analyzed with the approach that is usually adopted in neurophysiological studies to detect the presence of gain modulation in parietal neurons: the modulation of the visual receptive field of each hidden neuron was mapped by recording its response to each target location as a function of eye and effector positions. For each postural position, the normalized ratio between maximum and minimum volume profiles (changing a postural position at a time) was computed. The postural positions that generated the maximum volume profile have been set as constant values for the invariant postural positions. Thus, for each hidden neuron, four values indicating the gain modulation index (GMI) were obtained.

3.3 RESULTS

The average motor error (calculated as the mean error of the 10 trained networks) was below 4°, the typical performance error threshold adopted while training monkeys in neurophysiological investigations of intraparietal neurons.

The investigation of the hidden layer revealed a small number of neurons (about 10%) characterized by close-to-nil activations. Most of the remaining hidden neurons exhibited clear gain modulation. The distribution of GMI values across hidden neurons is shown in Fig. 3: a different GMI distribution can be observed for each postural variable.

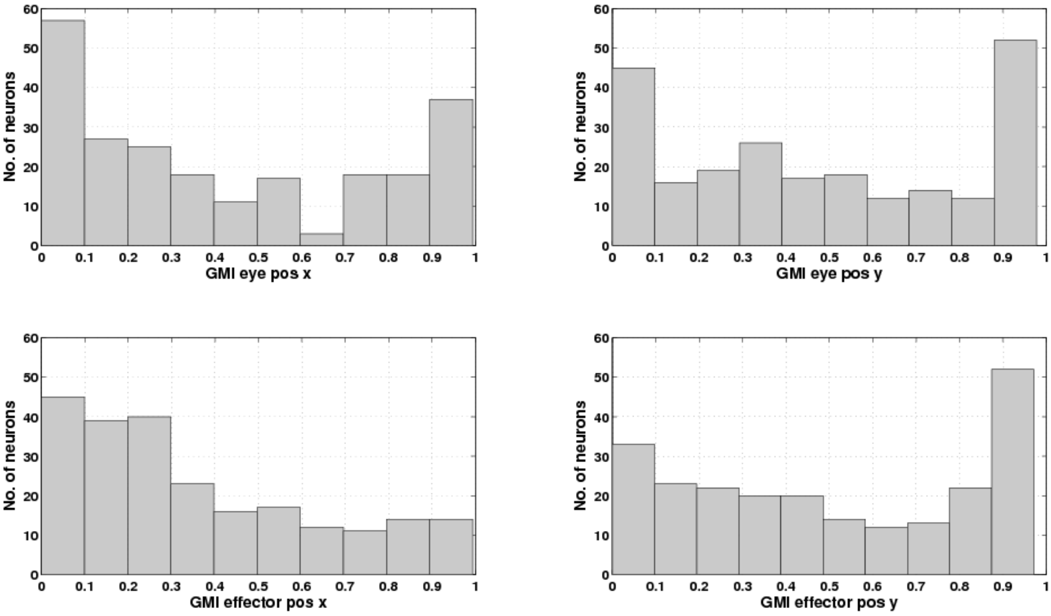

Figure 3 Distribution of GMI values of hidden neurons in one exemplar network as a function of postural position

The GMI scores are distributed along the range [0,1], where zero means that the receptive field of a neuron is retinotopic, hence varying postural positions does not generate any modulation, while high GMI scores indicate that the receptive field of a neuron is strongly modulated by a postural variable. As illustrated in the figure, all postural variables exhibited GMI values encompassing the entire range. Then, we classified all hidden neurons of the 10 trained networks in terms of gain modulation effect in each postural position. We used a GMI of 0.5 as an arbitrary threshold to calculate the percentages of neurons falling in different categories according to modulation type (see Fig. 4).

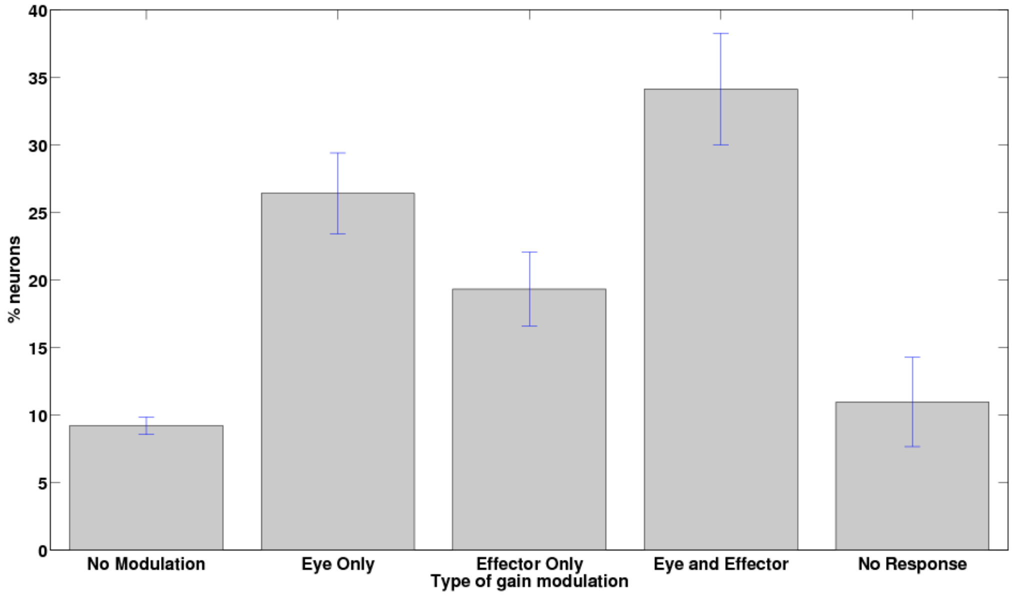

Figure 4 Percentage of the hidden neurons showing a specific type of postural modulation

Only about 9% of the neurons responded to the visual stimuli but were not modulated by postural information. Indeed, activity of most neurons was modulated by the position of the eye (26%), the effector (19%), or both (34%). We investigated the neurons' receptive fields to verify the gain modulation effect and to understand which reference frame was used to compute the motor program. Notably, all receptive fields of the hidden neurons turned out to be strictly retinotopic. Fig. 5 in top row, shows the receptive field of Neuron 11 in the hidden layer of Network 1 as a function of different horizontal eye positions (-18°, 0° and 18°). Although the neuron's receptive field is fixed on the retina, its activity is modulated by eye position: its largest response is observed when the eye is positioned at -18°. Fig. 5 in bottom row shows the receptive fields of Neuron 145 of Network 1 as a function of different horizontal effector positions: here the largest response is observed when the effector is positioned at 18°.

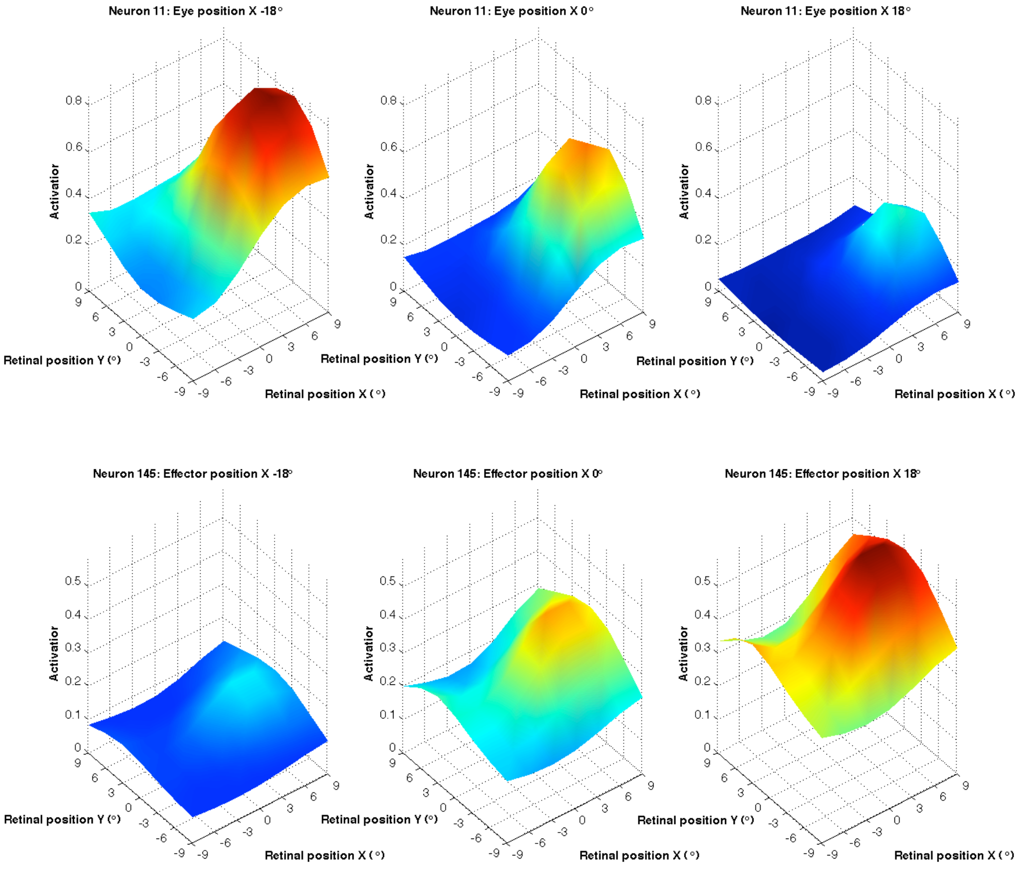

Figure 5 Analysis of hidden layer neurons: top row, receptive field of Neuron 11 (Network 1) as a function of eye position and bottom row, receptive field of Neuron 145 (Network 1) as a function of effector position

Finally, Fig. 6 shows the receptive field activity of Neuron 249 of Network 1 as a function of different horizontal eye and effector positions. These examples show that there are complex selectivity patterns for different combinations of eye and effector positions. In this neuron, the largest response is observed for horizontal eye position of 18° and horizontal effector position of -18°.

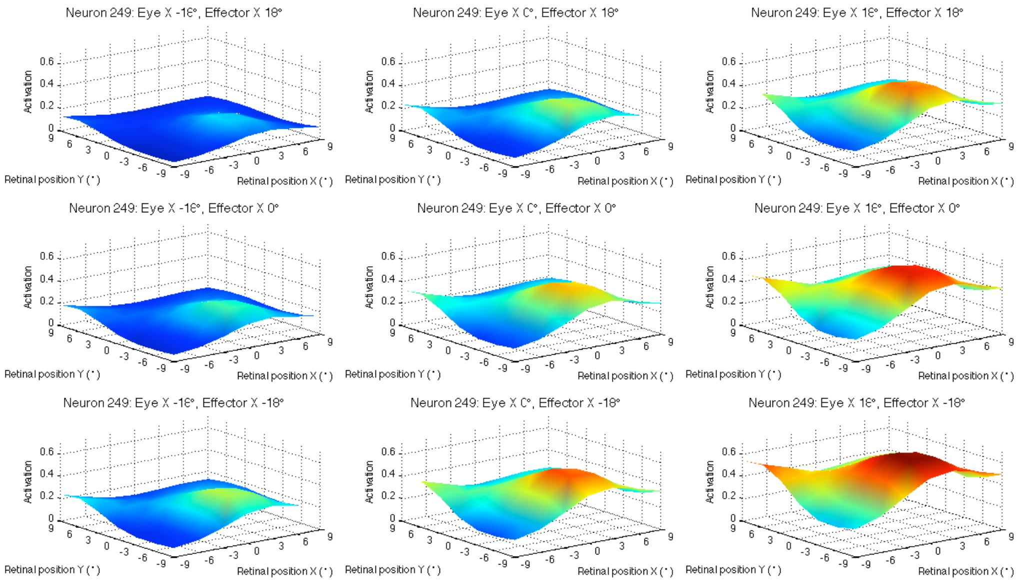

Fig. 6 Analysis of hidden neurons: a more complex receptive field of Neuron 249 (Network 1) modulated by both eye and effector position

3.4 DISCUSSION

Our results show that spatial representations for visually guided movements can emerge through unsupervised learning in a generative model that predicts the sensory input via top-down activation. Generative models are extremely appealing because they represent plausible models of cortical learning and are consistent with neurobiological theories that emphasize the mixing of bottom-up and top-down interactions in the brain (Hinton, 2007). Indeed, a recent study used a hierarchical generative model to model data at both behavioral and neurophysiological level (Stoianov and Zorzi, 2012). Our study sheds light on the integrative mechanisms involved in sensorimotor transformations. The interaction between visual and postural signals observed in the present computational model is in line with neurophysiological data recorded in PPC. All the receptive fields of the hidden neurons were fixed on the retina, showing that their reference frame is based on retinotopic coordinates; nevertheless, their activity was markedly modulated by postural variables: both these properties are strikingly similar to the neural properties observed in the sub-regions of PPC (Brotchie et al., 1995). Most importantly, these properties spontaneously emerged in the hidden layer even though learning did not involve any coordinate transformations (cf. Zipser and Andersen, 1988; Mazzoni and Andersen, 1991).

In conclusion, our results confirm that gain modulation is an efficient coding strategy to integrate visual and postural information towards the generation of motor command. Importantly, gain-fields have been also described in cortical and subcortical areas that are not specifically involved in coordinate transformation (Salinas and Sejnowski, 2001), thereby suggesting that gain modulation can be considered a more general brain mechanism supporting a broader class of non-linear transformations.

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4 SPATIAL CONSTANCY OF ATTENTION: ATTENTION ONLY REMAINS AT OBJECT'S LOCATION ACROSS EYE MOVEMENTS IF THE OBJECT IS PRESENT

4.1 INTRODUCTION

We live in a complex visual environment and our limited processing capacity does not allow us to process all the available visual information to the same degree. In order to deal with such complexity is essential to select among inputs to allocate limited resources to the behaviorally relevant information. The selection can operate overtly, by moving gaze and bringing relevant locations into high acuity foveal vision, or covertly, without eye movements by shifting attention (Posner, Snyder, & Davidson, 1980).

Covert orienting of visual attention can be defined as a set of processes that select relevant location of the environment when the eyes are held stationary. The result of these process is often conceptualized as a priority map of the visual environment, conveying both top-down and bottom-up signals (Fecteau & Munoz, 2006). What is the coordinate system of this representation? A retinotopic, or eye centered, representation would have to face the problem of eye movements because the retinal coordinates of the attended location change dramatically with each saccade. Conversely, a representation organized in spatiotopic coordinates would be unaffected by eye movements.

Recent studies directly addressed this issue: Golomb and colleagues developed a gaze-contingent paradigm in which participants performed an eye movement while keeping in memory the location of a spatial cue (Golomb, Chun, & Mazer, 2008; Golomb, Marino, Chun, & Mazer, 2011; Golomb, Pulido, Albrecht, Chun, & Mazer, 2010). Maintaining a location in memory indeed is equivalent to voluntarily deploying attention to the memorized locations (Awh & Jonides, 2001).

Results have shown a persisting attentional benefit at the retinotopic coordinates of the cued location (even if task irrelevant) for 100 – 200 ms after an eye movement (*retinotopic attentional trace*), and a growing facilitation at the spatiotopic location spatiotopic location that peaks around 400 ms after saccade completion. The authors concluded that the native coordinate system of spatial attention is retinotopic, and that the spatiotopic facilitation depends on the gradual updating of a retinotopic map (*remapping*), which is neither automatic or instantaneous.

Observation of everyday life suggests that humans easily accomplish tasks that require both frequent eye movements and dissociations between gaze and attentional focus (e.g., team sports like basketball) where attention appears to remain on relevant objects even as the eye move. However the finding that attention lingers in retinal coordinates after a saccade challenges this observation, and it raises the question of how it is possible to achieve *attentional constancy*, namely the ability to maintain attention on a spatial location across eye movements.

In a recent experiment Howe and colleagues investigated the effect of saccadic eye movements on a multiple object tracking task (Howe, Drew, Pinto, & Horowitz, 2011). Results showed that tracking performance was disrupted if during a saccade the display was modified to preserve the same retinal image (i.e. preserving the retinotopic coordinate system). In contrast performance was best when the spatiotopic or scene-centered coordinate system was preserved. This finding apparently conflicts with those of Golomb and colleagues results and suggests that the visual system automatically tracks moving objects in spatiotopic coordinates. Another recent studies has shown that before a saccade attentional topography is modified predictively (before the actual execution of the saccade) in order to anticipate the consequences of the upcoming eye movement and shift the retinotopic foci of attention to keep them aligned with the world coordinates of corresponding targets (Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011). This result was recently replicated with exogenous orienting of covert attention (Jonikaitis, Szinte, Rolfs, & Cavanagh, 2012).

Taken together these results are in conflict: on the one hand, visual objects are automatically tracked in spatiotopic coordinates and attention is predictively remapped in advance of saccades; on the other hand, after an eye movement, relevant (if not predominant) performance benefits are found at the retinotopic coordinates of the cued position. Critically, however, in all the studies that showed attention lingering in retinal coordinates, participants were asked to maintain attention on a blank location of the screen, not on a defined visual object (Golomb et al., 2008, 2011, 2010; Mathôt & Theeuwes, 2010). Conversely, studies showing predictive updating or spatiotopic maintenance of attention had participants attending to visual objects (Howe et al., 2011; Jonikaitis et al., 2012; Rolfs et al., 2011).

Objects constitutes a category of primary importance in the organization of our perception (Feldman, 2003; Spelke, 1990), and it is known that visual objects can play a role in the deployment of spatial attention (Egly, Driver, & Rafal, 1994; Hollingworth, Maxcey-Richard, & Vecera, 2012). We propose that the presence of a visual object at the attended location is a critical factor for the maintenance of attentional stability. When attention is directed toward a visual object and the eyes move, the locus of attention is shifted automatically as the object is remapped (Cavanagh, Hunt, Afraz, & Rolfs, 2010). In this case predictive remapping should allow object tracking in spatiotopic coordinates, with the corollary effect of presaccadic attentional benefits at the future retinal position of the tracked object (Jonikaitis et al., 2012; Rolfs et al., 2011). The aim of the present study is to investigate how saccades affect spatial attention when it is directed to a visual object, in order to clarify what factors allow the maintenance of attentional constancy across eye movements, and hopefully reconcile the conflicting findings on this much debated topic.

4.2 EXPERIMENT 1

In the first experiment, we developed a simple trans-saccadic spatial cueing paradigm to investigate how saccades affect covert orienting to a visual object. Participants were asked to orient attention to one of four squared black frames, delimiting the four relevant location in which probe stimulus could appear, and then made a guided saccade. Probe stimulus could be presented immediately after the saccade or 400 ms later; according to previous results (Golomb et al., 2008, 2011), this longer delay is sufficient for the build up of a significant spatiotopic facilitation. Our hypothesis, however, is that the continuous presence of a visual object at the attended location of the factor required to maintain a spatiotopic benefit, even at the earliest delay after the saccade.

4.2.1 *METHOD*

Participants. Ten volunteers participated in experiment I (including one author and 4 female; mean age was 28.7). All had normal or corrected to normal vision, and gave their informed consent.

Materials and Procedure. Participants were seated in a silent and dimly lighted room, with head positioned on a chin rest at 60 cm in front of the computer screen. The experiment was run on a PC, using E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA). Eye movements were recorded with a Tobii T120 screen-based eyetracker (Tobii Technology, Sweeden), which was used also to present stimuli through its embedded 17-inch TFT monitor.

The experiment consisted in a trans-saccadic cueing paradigm: first, one of four locations was cued, then when the fixation cross was displaced, the participant made a saccade to refixate its new location (see fig. 1 panel A). After the saccade, a probe was presented in one of the four locations and he or she made a speeded discrimination its orientation (horizontal vs. vertical). Each trial started with a black fixation cross appearing on a gray background, horizontally centered but displaced 4° above or below the center of the screen. As soon as the participant fixated the cross, the trial started and 4 black squared frame (squares were 2.5° wide, and the black delimiting line was 0.1° wide) appeared. After a delay (500 ms) the cue was presented. The cue consisted in one of the sector of the cross changing color to black, pointing thus to the squares in the corresponding quadrant of the screen. The cue was presented for a period of 1000 ms, and then the fixation cross returned to its initial shape. After 400 ms the cross was displaced up or down (depending on its initial position) of 8°, and this jump indicated to the participants to make a vertical saccade to the new fixation position. Participants were instructed to maintain attention focused on the spatial location of the cued square but the cue was not predictive as it was spatially congruent with the probe on half of the trials (validly cued spatiotopic trials); the other half of trials was composed by an equal proportion of retinotopic trials (probe appearing at the retinotopic cued position) and control trials (see fig. 1, panel C). In control trials the probe appeared always on the same side of the cue (left or right), to avoid additional costs of crossing the vertical meridian (Rizzolatti, Riggio, Dascola, & Umiltá, 1987).

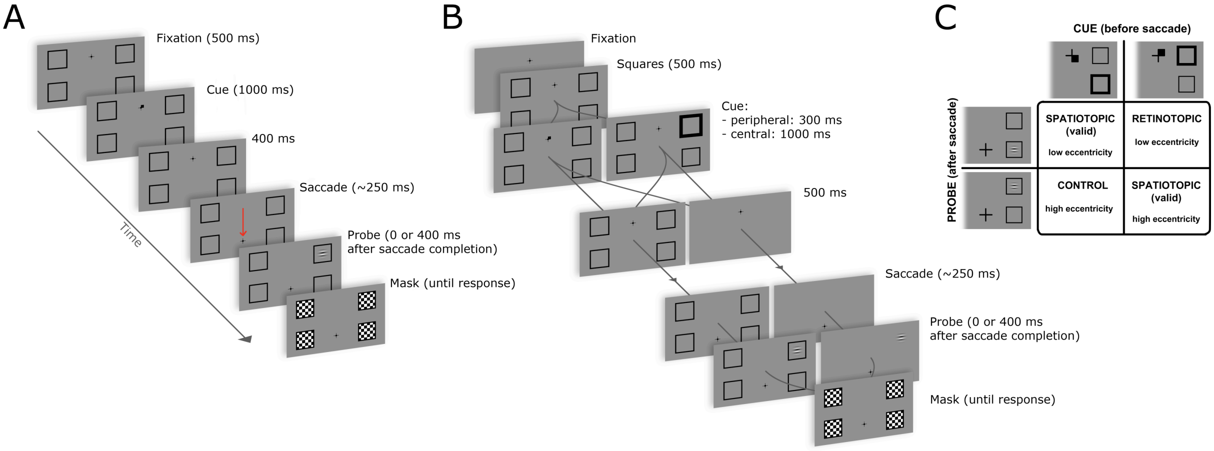

Figure 1 Experimental paradigms. (**A**) The experimental paradigm used in experiment I. One of four locations was cued (centrally with a small black square) then when the fixation cross moved, participants executed a saccade to its new location and then were asked to make a speeded discrimination of probe orientation (horizontal or vertical). The probe stimulus was a Gabor patch with 100% contrast. (**B**) The experimental paradigm used in experiment II. Similar to the previous one, except that the cue could be central or peripheral and that the square frames delimiting the relevant locations disappeared after the cue on half of the trials (randomly interleaved within blocks). (**C**) Cueing conditions and eccentricities. Only the one side of the display is represented since probe stimulus was always presented on the same side of the cue to avoid additional costs of reorienting attention across the vertical meridian. Note that in this display eccentricity should favor performance in retinotopic trials over spatiotopic, since in the former condition probes appear always closer to the fovea, while in the latter probes appear in half of the trials closer and half further from the fovea.

The probe stimulus was a Gabor patch (2.5 cycles/degree, contrast 100%) presented at different delays after saccade completion (0 and 400 ms) either inside the cued square (spatiotopic trials), or inside the square in the retinotopic location of the originally attended square, or in the control position. In order to equate the task difficulty for each participant, the duration of probe presentation was adaptively adjusted online. The goal of the adaptive procedure was to keep the accuracy in the spatiotopic condition approximately within the range 65% - 85%: if after a spatiotopic trial the global spatiotopic accuracy exceeded 85% or was below 65% probe duration was respectively increased or decreased by one monitor refresh cycle (~16 ms).

Eye movements were monitored with a sampling frequency of 120 hz; trials in which subjects did not made the correct saccade or in which gaze deviated more than 2° from fixation point were aborted and redone within the same block. Each participant completed a minimum of 384 trials, 192 trials for the spatiotopic condition, and 96 for each of the other conditions, in 2 experimental sessions on different days; each session was divided in 4 blocks. Before each session, participants completed 40 pre-test trials, consisting of only spatiotopic trials, in which the duration of the probe presentation was adapted according to a *weighted up-down* staircase procedures (Kaernbach, 1991) with targeted performance of 75% correct responses. This quickly adjusted probe duration to individual sensitivity in order to move closer to the desired level of performance before the beginning of experimental trials.

4.2.2 RESULTS

Trials in which the reaction time was 2 standard deviations above or below the mean calculated for each participant and condition were excluded from subsequent analysis (4.5% of total trials). Probe duration was continuously adjusted online, according to accuracy in the spatiotopic condition and after each spatiotopic trial, but since trials from different conditions were presented in random order, this could have produced some unbalance. To check for this potential confound, we carried out a repeated-measures analysis of variance (ANOVA) on probe duration with probe position (spatiotopic, retinotopic, control) as within-subjects factor, to assess whether the average duration was similar across conditions (fig. 2, panel C). No significant differences emerged [$F(2, 18) = 0.2$, $p = 0.8$].

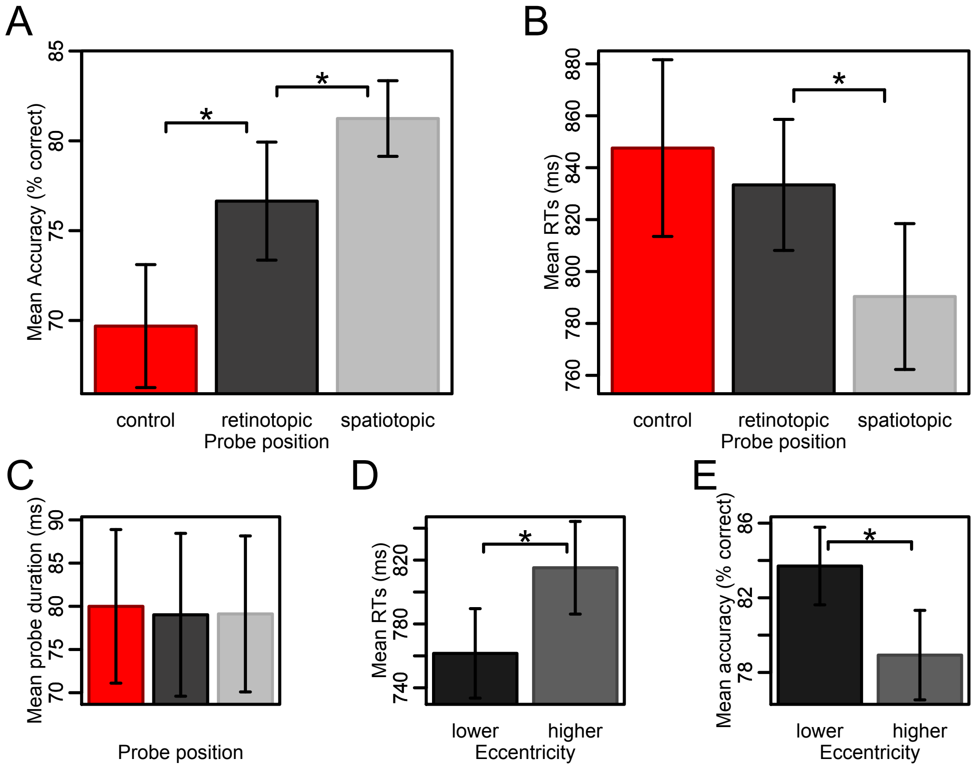

Figure 2 Results of Experiment I. Mean accuracies (**A**) and mean reaction times (**B**) are represented as a function of condition. The duration of target presentation (**C**) did not differ across conditions. Panel **D** and **E** shows the effect of probe eccentricity on performance in the spatiotopic condition. The spatiotopic condition was the only that included both trials with lower and higher probe eccentricity. Performance improved with decreasing eccentricity, both for reaction times (**D**) and accuracy (**E**). Error bars represent within-subjects SEM (Cousineau, 2005).

We conducted a repeated-measures analysis of variance (ANOVA) with mean response accuracy as dependent variable and probe position (spatiotopic, retinotopic, control), Delay (0, 400 ms), probe eccentricity (lower, higher) as within-subject factors (see fig. 2, panel A). This analysis revealed a main effect of probe position [$F(2, 18) = 16.51$, $p < 0.0001$] and eccentricity [$F(1, 9) = 9.21$, $p < 0.05$]; no other effects or interactions were significant. Planned comparisons revealed significant differences between spatiotopic and retinotopic trials [$t(9) = 1.95$, $p < 0.05$], as well as between retinotopic and control trials [$t(9) = 3.91$, $p < 0.01$].

We then conducted another repeated-measures ANOVA with mean reaction times for correct responses as dependent variable. We found a significant main effect of probe position [$F(2, 18) = 5.96$, $p < 0.05$] and probe eccentricity [$F(1,9) = 13.41$, $p < 0.001$]. Neither the effect of Delay or any interactions were significant. Planned comparisons revealed that spatiotopic trials were significantly faster than retinotopic trials [$t(9) = 2.73$, $p < 0.05$], while retinotopic trials were not significantly different from control trials [$t(9) = 0.88$, $p = 0.2$].

The effect of probe eccentricity indicates that performance was better at the lower eccentricity (fig. 2, panel D and E) with respect to both reaction times and accuracy. Eccentricity thus probably produced an additional cost in control trials, but this cannot account for the advantage of spatiotopic over retinotopic trials because probes in retinotopic trials appeared always at the lower eccentricity (see fig. 1, panel C). Therefore the effect of eccentricity should have favored retinotopic trials, while results (fig. 2) show exactly the opposite pattern. Experiment 1 provides evidence of a predominant and stable attentional facilitation at the cued spatiotopic location immediately after an eye movement. These results are markedly different from those of Golomb and colleagues (Golomb et al., 2008, 2011) as they found stronger effects of cueing at the retinotopic location compared to the spatiotopic location. We propose that the difference between the two sets of results is due to the continuous presence of a visual object at the attended location in our experiments. We suggest that the continued presence of the cued object after the saccade serves to anchor attention at the spatial location of the cued object. This interpretation suggests that if the cued object is removed before the eye movement lands (as was the case in Golomb and colleagues' paradigm, 2010), there will be nothing to anchor attention and it should then remain at its retinotopic locus (*retinotopic attentional trace*). This hypothesis was tested in Experiment 2.

4.3 EXPERIMENT 2

In order to investigate whether the presence of a perceptual object is a critical factor in maintaining attentional stability in space, we modified the paradigm used in experiment 1 so that the squared frames delimiting the relevant positions could either disappear after cue presentation or remain visible throughout the trial. These two conditions were randomly interleaved within block. If our hypothesis is correct, the presence or absence of a visual object at the attended location before and during the saccade should determine where attentional benefits will be found after saccade completion. We also used two types of cue, a central, symbolic cue identical to the one used in experiment 1, and a peripheral cue, similar to the one used in previous studies (e.g., Golomb et al., 2008) to control for possible confounding effects related to the type of attentional orienting (pure endogenous versus exogenous but endogenously sustained).

4.3.1 METHOD

Participants. Twelve volunteers participated in experiment 2 (including one author and 5 female participants; mean age was 29.2). All had normal or corrected to normal vision, and gave their informed consent.

Materials and Procedure. Participants were seated in a silent and dimly lighted room, with the head positioned on a chin rest at 60 cm in front of the computer screen. The experiment was run on a Apple MacPro Dual Intel-Core Xeon computer and stimuli were displayed on a 22-inch Formac ProNitron 22800 screen with a spatial resolution of 1440 by 1050 pixels (36.7° by 27.6°) and a vertical refresh rate of 120 Hz. The experimental software controlling stimulus display and response collection was implemented in Matlab (MathWorks, Natick, MA) using the Psychopshysics Toolbox (Brainard, 1997; Pelli, 1997). Eye movements were recorded with an Eyelink 1000 Desktop Mount (SR Research, Osgoode, Ontario, Canada) with a sampling rate of 1kHz.

The procedure was similar to the one adopted in experiment 1 (figure 1). We used two types of cue: in half of the trials we presented a central cue identical to the one used in experiment 1; in the other half of the trials we presented a peripheral cue consisting in the frame of the relevant square increasing its thickness up to 3 times the original value (the internal area of the square remained constant during the increase); the two types of cue were randomly interleaved within blocks. Peripheral cues are faster in orienting attention, and so we used a shorter duration (300 ms), similar to the duration of peripheral cues used in other trans-saccadic cueing experiments (e.g., Golomb et al., 2008).

After cue presentation, the four squares delimiting the relevant positions could either disappear or remain on the screen. Participants were instructed to ignore the disappearance of the squares whenever that occurred, and to maintain attention focused on the spatial location of the cued square whether or not it was still present. After 500 ms the cross was displaced up or down, depending on its initial position, of 10°, and this jump indicated to the participants to make a saccade to the new fixation position. Probe stimulus was a Gabor patch (contrast 100%, spatial frequency 2 cycles/degree) presented at different delays after saccade completion (0 and 400 ms).

The duration of probe presentation was regulated adaptively online by a standard staircase procedure with criterion performance of 75% correct responses in spatiotopic trials and step of one monitor refresh cycle (~8 ms). We used a different procedure with respect to the previous experiment because of the higher monitor vertical refresh rate (120Hz), which allowed a finer modulation of probe duration.

Eye movements were recorded at 1000 Hz and also monitored online: trials in which participants did not make the correct saccade or in which gaze deviated more than 2° from the correct fixation point for more than 50 ms were aborted and redone within the same block. Each participant made a minimum of 512 trials, 256 trials for the spatiotopic condition, and 128 for each of the other conditions, in 2 experimental sessions on different days; each session was divided into 4 blocks. Trials with different cueing conditions (spatiotopic, retinotopic and control), type of cue (central or peripheral) and presence/absence of landmark squares were randomly interleaved within blocks. Before each session, participants completed 40 pre-test trials, consisting of only spatiotopic trials, in which the duration of the probe presentation was adapted according to a *weighted up-down* staircase procedures (Kaernbach, 1991) with criterion performance of 75% correct responses.

4.3.2 RESULTS

The higher sampling frequency of the eyetracker used in experiment 2 (1000Hz) allowed for a finer analysis, that could not be performed online. We detected saccades with a velocity-based algorithm (Engbert & Mergenthaler, 2006) and defined a response saccade as the first saccade that left a circular fixation region and landed inside a target-centered circular region (radii of 2°). We rejected trials with blinks or saccades larger than 1° before the response saccade, or after the saccade and before probe presentation in trials with the longer delay (400 ms). In all, 89% of trials were included in subsequent analysis.

Trials in which reaction times were 2 standard deviations above or below the mean calculated for each participant and condition were also excluded from subsequent analysis (4.8% of total trials). A repeated measures ANOVA on mean probe duration revealed a significant, although small, difference across cueing conditions [$F(2, 22) = 5.55$, $p < 0.05$], in particular the mean probe duration was slightly longer (mean difference 1.94 ms, see fig. 3 panel G) for the control condition with respect to spatiotopic and retinotopic [$t(11) = 2.66$, $p < .05$]; while this could have improved performance in control trials, importantly there was no differences between mean probe durations in spatiotopic and retinotopic conditions [$t(11) = 1.05$, $p = 0.31$].

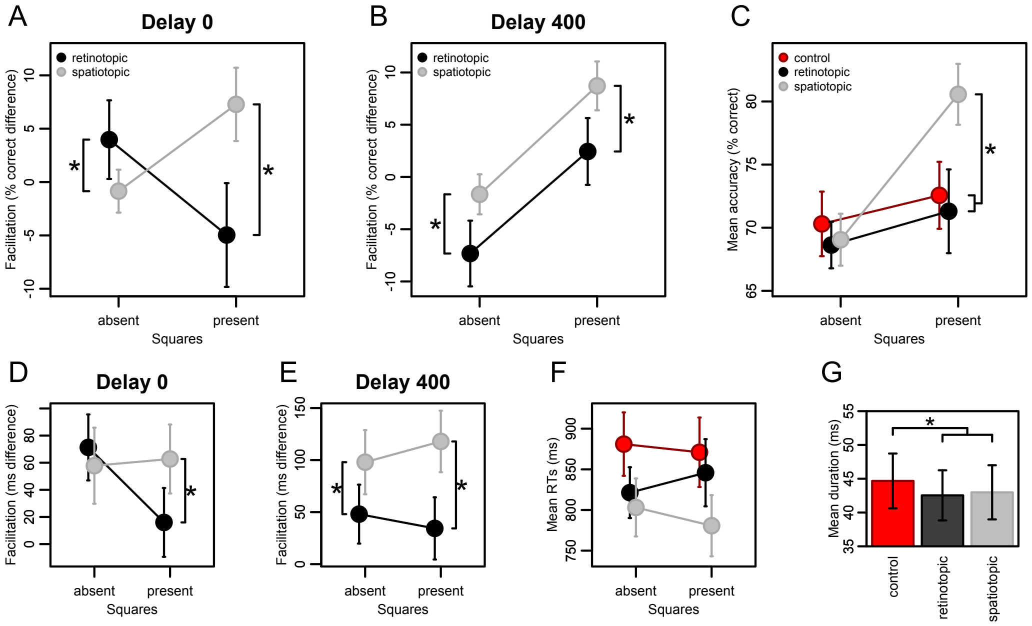

Fig. 3 Results of Experiment 2. (**A**) Mean accuracy differences (with respect to control condition) at immediately after saccade completion and (**B**) at 400 ms delay. Notably retinotopic performance was better than spatiotopic only in the squares-absent condition, at the shortest delay after the saccade. Conversely in the squares-present condition, the results of experiment I are replicated (stable spatiotopic facilitation). Overall (**C**), collapsing across the two delays, it can be seen that squares presence selectively increased discrimination accuracy mainly at the spatiotopic location. Reaction times show the same trend, although the three-way interaction (probe position X delay X squares) was not significant (**D** and **E**). Overall effect of squares presence on reaction times (**F**). Duration of probe presentation (**G**). Mean probe duration resulted slightly longer, 1.94 ms, in control conditions respect to spatiotopic and retinotopic, but there were no differences between spatiotopic and retinotopic (B). Error bars represent SEM after correction for within-subject design (Cousineau, 2005).

We then conducted a repeated-measures analysis of variance (ANOVA) with mean accuracy as dependent variable and probe position (spatiotopic, retinotopic, control), delay (0, 400 ms), eccentricity (lower, higher), cue type (central, peripheral) and squares presence (present, absent) as within-subject factors (figure 3). This analysis revealed a significant main effect of probe position [$F(2,22)=5.53$, $p < .05$], delay [$F(1,11)=110.6$, $p < .001$], squares presence [$F(1,11)=20.12$, $p < .001$] and eccentricity [$F(1,11)=7.29$, $p < .05$]. Eccentricity had a similar effect as in the previous experiment, but it did not interact with any of the other factors. We found also a significant interaction between probe position and squares presence [*F*(2,22)=5.96, $p < .01$], showing that the presence of the squares selectively increased accuracy at the spatiotopic location (figure 3, panel A) [*t*(11) = 4.64, $p < .001$]. However, this was qualified by a significant three-way interaction between probe position, squares presence and delay [*F*(2,22)=6.36, $p < .01$]. Planned comparisons between retinotopic and spatiotopic trials separately for each level of delay and squares presence (all t-tests paired and bidirectional) showed that accuracy was higher for retinotopic over spatiotopic trials only at the shortest delay after saccade completion (figure 3, panel B) in the squares absent condition [*t*(11)=1.98, $p < .05$], while in all the other conditions performance was better at the spatiotopic location (all $p < .05$).

We performed the same analysis on reaction times, and we obtained a significant main effect of delay [*F*(1,11)=59.2, $p < .001$], probe position [*F*(2,22)=30.25, $p < .001$], eccentricity [*F*(1,11)= 10.91, $p < .01$] and cue type [*F*(1,11)=11.26, $p < .01$]. No interactions were significant. When plotting the data for separate delays (figure 3, panel D and E), reaction times show a trend similar to that of the accuracy data, although there were no significant interactions between probe position and squares presence/absence. The type of cue had a significant effect, namely faster reaction times in trials with a peripheral cue [mean difference 32 ms; *t*(11)=3.35, $p < .01$], which however did not interact with the other factors.

In this second experiment we confirmed our hypothesis. The continuous presence of the squares produced a stable benefit at the spatiotopic location even at the shortest delay after saccade completion, thus replicating the results of the first experiment in a different group of participants and with a different experimental setup. Conversely, in trials in which squares were removed before the saccade, we report a significant facilitation at cued retinotopic location immediately after the saccade. That is, in the condition without a visual object present at the attended location, we replicated the finding of attention lingering in retinal coordinates after a saccade (Golomb et al., 2008, 2011, 2010).

4.4 DISCUSSION

The findings reveal that the presence of a visual object at the attended location is a critical factor in the maintenance of the spatial constancy of attention –

the ability to sustain attention in spatial coordinates across eye movements. We showed that when visual attention is directed to an object, it remains steadily anchored to the correct spatial location, despite intervening eye movements. On the other hand, when attention is cued to an empty location it is not maintained at that location in space: the attentional focus moves together with the eyes, leading to stronger attentional benefits at the retinotopic coordinates of the originally attended location immediately after the saccade(i.e., the *retinotopic attentional trace*).

In one of their trans-saccadic cueing experiments, Golomb and colleagues (Golomb et al., 2010) added a background grid to the display, in order to enhance the spatiotopic reference frame. With this manipulation, the spatiotopic facilitation exceeded the retinotopic, even at the earliest delay after saccade completion. However, since the earliest delay of probe presentation in their study was 75 ms after saccade completion and the retinotopic focus remained significant even at the 400 ms delay, it was not clear from those results what happens immediately after saccade landing with the grid present.

Visual attention shares spatial maps with eye movements structures, such as the frontal eye field (FEF) and the lateral intraparietal area (LIP) (Corbetta & Shulman, 2002). It is known that attention modulates the gain of visual responses in oculomotor maps (Colby & Goldberg, 1999), and that neurons in this area update their representation in order to compensate the consequences of eye movements (Duhamel, Colby, & Goldberg, 1992). However, in contrast with Golomb and colleagues results (Golomb et al., 2008, 2011, 2010) neurophysiology would suggest that this updating process occurs on a much faster timescale, being completed by the time the saccade lands and in some cases even before the saccade is started (Kusunoki & Goldberg, 2003). Notably, in Golomb and colleagues' results, the spatiotopic benefit require a large amount of time, in neural terms, to fully develop: the attentional benefit at the correct location exceed the retinotopic facilitation only around 300-400 ms after saccade completion. This is more than the normal saccadic latency (200-300 ms), and probably reflects other mechanisms, e.g. a new covert orienting to the original location, perhaps recovered on the basis of other landmarks present in the visual field.

In contrast, the behavioral correlates of the remapping of neural activity in saccade related areas have been recently highlighted in the study of Rolfs and colleagues (Rolfs et al., 2011). In their study attentional benefits, as indicated by discrimination performance, were measured at several locations while participants performed a double-step saccade task. Before the onset of the first saccade they found a growing benefits not only at the saccadic targets but also at the "remapped" location, that is at the future retinotopic coordinates of the second saccadic target. This predictive mechanism could allows to shift attentional foci in advance of a saccade in order to remain continuously aligned with the corresponding targets in the external world, thereby providing a working spatiotopy for spatial attention and a neural basis for the maintenance of attentional stability.

Spatial remapping updates an internal map of visual space in conjunction with eye movements. But what kind of information get remapped? It is unlikely that a detailed representation of the visual world is retained across eye movements. Change blindness studies show that we are unable to detect scene-changes occurring during saccades unless they affect attended objects (Grimes, 1996; Henderson & Hollingworth, 1999, 2003), suggesting that the visual representation retained across saccades is very sparse. Neurophysiological studies show that visual responses in saccade control maps involved in remapping depend on the temporal and spatial dynamics of attention (Bisley & Goldberg, 2003; Fecteau, Bell, & Munoz, 2004) such that non salient object are not represented or remapped (Gottlieb, Kusunoki, & Goldberg, 1998). Because they represent only relevant objects, these areas have been often characterized as sparse saliency maps of the visual environment (Fecteau & Munoz, 2006; Kusunoki, Gottlieb, & Goldberg, 2000) and we suggest that they can be best described as representing the location of attended objects rather than simply space. Accordingly, neurons in these maps are spatially selective, but otherwise represent visual objects in a featureless manner (Fecteau & Munoz, 2006). Finally, they are also widely connected with the ventral visual pathway (Felleman & Van Essen, 1991) and might thus index the location of object's feature information across multiple representation and modalities (Cavanagh et al., 2010).

Perceptual objects plays a central role in the organization of our perception (Feldman, 2003; Spelke, 1990). Even though the mechanism of object-based attention are still not well understood there is clear evidence that attention can in some cases directly select discrete objects (see Scholl, 2001 for a review), and that visual objects modulate the deployment of attention in space (Egly et al., 1994; Hollingworth et al., 2012). Here we showed that object-defined spatial locations are correctly attended and updated across saccades, while blank locations are not. These results indicate that object-based properties modulate activity in salience maps involved in attention and spatial remapping, coherently with neuroimaging studies showing how posterior parietal cortex in humans is sensitive to object-based properties at attended locations (Shomstein & Behrmann, 2006). It remains a challenge for future studies to determine how this modulation takes place: one hypothesis is that visual representation in these maps depends mostly on putative grouping cells in earlier visual cortices, that operates some pre-attentive figure-ground segmentation (Qiu, Sugihara, & Von der Heydt, 2007).

The present results apparently conflict with the computational model of spatial attention presented in the Chapter 2. However, at least two points must be considered: first, the model does not implement any mechanism aimed to account for contextual influences (e.g., the presence of visual objects) in the deployment of visual spatial attention. Indeed, a recent model proposed to account for these types of effects (Mihalas, Dong, Von der Heydt, & Niebur, 2011) is based on the assumption that attentional signals modulate activity in neuronal populations that mediate perceptual organization. If that is the case, remapping should operate on a structured representation of the visual input (organized in terms of perceptual objects), thereby updating automatically only the locations of visual objects. Second, the time course of the remapping process in the model was scaled on the basis of the previously available empirical data (Golomb et al., 2008, 2011, 2010) but the timing of remapping onset was not linked to a proprioceptive signal generated by movement execution. Instead, it was triggered by movement planning (i.e., a corollary discharge of the motor command). This implies that the same remapping process could have a predictive nature and start well in advance of a saccade, in agreement with the presaccadic remapping described by Rolfs and colleagues (Rolfs et al., 2011). Overall, even if the model lacks a mechanism that could account for interactions between attention and image structure, it still provides a biologically plausible hypothesis of how a retinotopic map is updated on the basis of a corollary discharge of the motor command.

We also showed that when the attended object disappears before the saccade, the locus of attention remains in retinal coordinates, temporarily losing its alignment with the relevant spatial location. It is important to note that participants were explicitly told to concentrate and focus on the cued spatial location, irrespective of whether it was defined or not by the square. Nevertheless, we found an improvement in performance at the retinotopic task-irrelevant location immediately after the saccade. This suggests that an empty locations, even if task relevant, are weakly represented in maps on which remapping operates, and consequently weakly, or not at all updated to compensate for eye movements. Accordingly, LIP neurons that respond to stable objects when these are selected as saccade targets, respond much less in the case of the same saccades without target objects (Kusunoki et al., 2000).

In conclusion, our findings help resolve existing conflicts in the literature about the allocation of attention across saccades. We showed that a critical factor for the maintenance of spatial constancy of attention is the continued presence of a visual object at the to-be-attended location. In a nutshell, sustaining attention at a spatial location across an eye movement is efficient and automatic when there is an object present at that location. If attention is directed to an empty location and the eyes move, attentional constancy is broken and other strategies are required to redicover the spatial location of the original cue.

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5 COVERT SHIFTS OF SPATIAL ATTENTION IN THE ABSENCE OF DIRECTIONAL AND PREDICTIVE SYMBOLIC CUES

5.1 INTRODUCTION

The commonsense intuition suggests the existence of specific cognitive mechanisms allowing the rapid and efficient exploration of the environment. Nowadays, the standard method to isolate voluntary (endogenous) components characterizing the orienting of spatial attention consists in the Posner’s (1980) cuing paradigm, where leftward vs. rightward oriented arrow cues with a predictive value are centrally presented, prior to the occurrence of a (spatially) valid or invalid unilateral target stimulus. Since the landmark work of Jonides (1981), it has been assumed and demonstrated that the orienting of spatial attention arising from central arrows, thought to be a pure voluntary cognitive mechanism, takes place only if these arrows are predictive regarding the spatial position of the subsequent target stimulus (e.g. Muller & Rabbit, 1989; Posner, Walker, Friedrich, & Rafal, 1984). These findings are consistent with Jonides (1981)’s original statement postulating that the endogenous orienting of spatial attention is primarily sensitive to the expectations of the participants. Given the attribution of this specific property, in subsequent studies, participants usually were not only instructed to orient spatial attention according to the cue direction, but also informed that the target stimulus was more likely to appear at the cued position.

Nonetheless, several subsequent studies reported results at odds with the dominant view although without challenge the assumption that predictive cueing is necessary to induce endogenous orienting of spatial attention. For instance, Koshino, Warner, and Juola (1992) found that a predictive central arrow can actually produce stronger spatial orienting effects than peripheral non-predictive cues. Tassinari, Aglioti, Chelazzi, Marzi and Berlucchi (1987) showed that attention can be voluntarily allocated, without the need to resort to predictive cues. Several other studies (Eimer, 1997; Hommel et al., 2001; Tipples, 2002; Ristic & Kingstone, 2006; see Bonato et al., 2009 for a clinical study) showed that centrally-presented arrows, although non-informative regarding the spatial position of the subsequent target stimulus (i.e. non-predictive), can induce an effective orienting of spatial attention, called "reflexive" in the present case. However, these studies only questioned the appropriateness of using of an asymmetric overlearned cue as arrows to induce endogenous orienting (Lambert, Roser, Wells, & Heffer, 2006) without extending the criticism to cue predictivity itself. Nevertheless, cueing effect produced by a predictive (central) arrow are much larger than the sum of the so-called reflexive orienting of spatial attention triggered by non-predictive arrows, and of the "volitional" shift of spatial attention produced by predictive non-directional cues (Ristic & Kingstone, 2006).

In sum, it is nowadays commonly assumed (see Carrasco, 2011, for review) that cue predictivity causally determines the expression and amount of volitional spatial orienting (Prinzmetal & Landau, 2008). The main goal of our study was to test this strong tenet and assess whether endogenous shifts of spatial attention could be evidenced in the absence of both cue directionality and cue predictivity or not. For this purpose, we manipulated cue predictivity in a variant of the Posner paradigm where predictivity was manipulated unbeknown to the participants and tested the prediction that it is not a necessary condition in order to elicit reliable shifts of spatial attention.

5.2 METHOD

The task was based on the well-established Posner paradigm, where lateralized targets are presented after a cue indexing where attention had to be oriented "covertly". In order to obtain both RT and accuracy data we selected a discrimination task, a condition where attention orienting is supposed to arise slower than with a simple detection task (Rafal & Henik 1994). Two specific manipulations, yet never combined together in earlier studies, were implemented. First, non directional (color) cues were used. Second, no information was given to participants beforehand regarding the predictive value of these cues. Participants were asked to attend either to the left or the right side relative to the fixation cross, depending on the color of the cue, without being informed about how this orienting was related to the probability of target appearance in the cued location (validity was 90% in some blocks and 50% validity in other blocks). This way, no confound was introduced between task instructions (i.e. attend left or right depending on the color of the cue) and cue predictivity (present vs. absent, unknown to participants).

Participants. Twenty-four healthy adult participants (mean age 23.6 years, range 19-29 years, 8 males), with normal or corrected-to-normal vision freely took part in the experiment in exchange of thirteen euros.

Materials and procedure. Using E-Prime2 (Schneider, Eschmann, & Zuccolotto, 2002), visual stimuli were presented on a 17 inch screen positioned at a distance of 50 cm in front of the participant; eye movements were continuously monitored using a Tobii Eye-Tracker devise (model T120). Each trial started with a black fixation point (diameter 0.5°), presented against a gray homogenous background (see Figure 1). The sequence continued as soon as participants kept fixation for at least 250 ms. Then, two placeholders (squares, side 3.4°) were presented, one on the right and one on the left relative to the fixation point (distance from the centre ≈ 10°). After 800 ms, the fixation point turned either yellow or blue (e.g. orient to the left when yellow, while to the right when blue; counterbalanced across participants). Either a short (160 ms) or a long SOA (600 ms) was introduced between the cue and the target. The target stimulus consisted of a vertical or horizontal Gabor Patch (contrast 100%; visual angle 3°) appearing in one of two placeholders. Target duration was individually determined according to a calibration procedure (see below). At the offset of the target, the fixation point turned black again and the two placeholders were filled by a mask (a black & white checkerboard) until response or after 2.5 seconds elapsed. Half of the participants were required to press (index finger left hand), the “v” key for “vertical” and (index finger right hand) the “n” key for “horizontal” while the other half received the opposite stimulus-response mapping (e.g. “v”/horizontal vs. “n”/ vertical). Instructions emphasized both speed and accuracy.

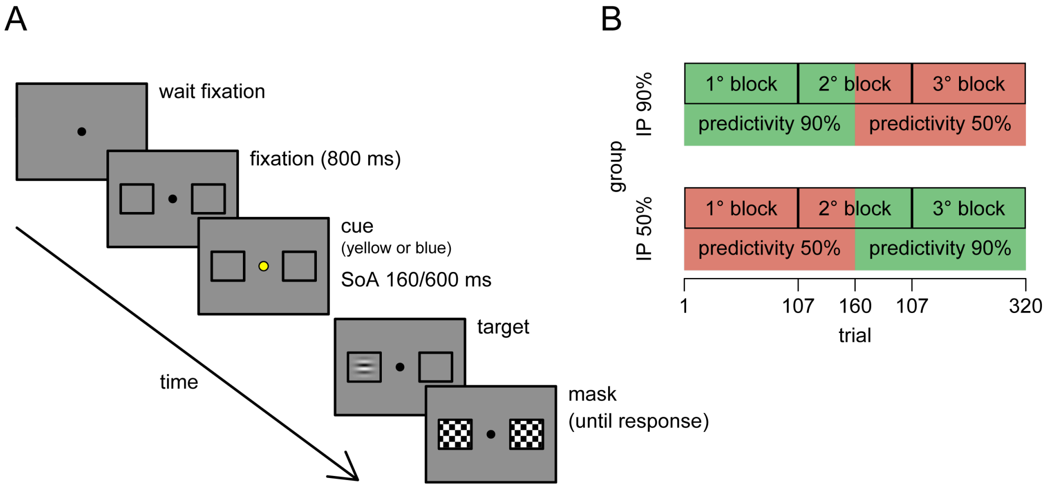

Figure 1 (**A**) Decomposition of a trial. Half of the participants were instructed to orient attention to the right (relative to fixation) following a yellow cue and to the left after a blue cue. Half of the participants received the reverse assignment. Target duration was adjusted individually following a separate calibration procedure. Participants were required to discriminate the orientation of the unilateral Gabor patch (Horizontal vs. Vertical) by means of two pre-defined response keys. (**B**) Experimental design. There were two main trial lists, one with a cue predictivity of 50% (depicted in red) and the other of 90% (depicted in green). For half of the participants initial cue predictivity was set to 50% before changing to 90% after half of the trials (IP 50%), while for the other half of participants, the reverse order (cue predictivity) was used (IP 90%).

The experiment started with sixteen practice trials where the cued placeholder turned yellow/blue synchronously with the cue and then each subject went through two lists of experimental trials, one with a cue predictivity set to 50% and another one with a cue predictivity set to 90%[1]. List order was counterbalanced across participants. There were two short breaks, after 1/3 and 2/3 of the trials. After 160 trials, there was an unexpected and abrupt change of cue predictivity, from 50% to 90% or vice versa depending on the group. Participants were never informed about the initial level of cue predictivity, nor about the change in cue predictivity midway. After the experiment, participants filled out a questionnaire

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[1] Of note, the two levels of cue predictivity used here are only indicative because "true" cue predictivity is probably to be calculated for each trial depending on the immediate trial history. Presumably, for participants who started off the experimental session with the 90% target validity, the putative effect of the cue predictivity could progressively decrease as soon as more invalid trials are encountered (50% cue predictivity condition). However, despite this abrupt (and unforeseen) change in cue predictivity (from 50 to 90%, or vice versa), which might introduce some noise in the results, a strong effect of this variable (cue predictivity) was evidenced (see results).

adapted from Bartolomeo et al. (2006) and Risko and Stolz (2010), assessing their level of awareness regarding the main experimental manipulation introduced (i.e. cue predictivity).

Calibration procedure. Before starting the experiment, participants were administered a calibration procedure (48 trials) aiming to adapt target duration to individual sensitivity and avoid ceiling effects. Trial sequence was similar to experimental trials with the difference that there was no cue (the fixation point remained black). Target duration was set to 133 ms and then adjusted online (within the range 17-266 ms) through a *weighted up-down staircase* procedure (Kaernbach, 1991) with target performance 75% accuracy. Duration values for the last 12 trials were averaged and adopted as individual target duration.

5.3 RESULTS

The data of two participants had to be excluded from subsequent statistical analyses, one due to excessive eye movements (52.8%), and one due to deviant low accuracy (error rate of 28%, 2 standard deviations (SD) above the group average). Trials containing eye movements (8%) were excluded from the statistical analyses.

5.3.1 REACTION TIMES.

RTs above 2500 ms or above/below 2 SD from the mean (for each participant and condition) were discarded (about 5% of trials).

We performed an ANCOVA with Predictivity [50% (P50) vs. 90% (P90)], Validity (Valid vs. Invalid trials) and SOA (160 vs. 600 ms) as within-subject factors, order (50% vs. 90% first) as between-subject factor and target duration as covariate. There was a significant main effect of Validity $F(1,21) = 19.74$, $p < .001$ (valid trials faster than invalid trials; 791 vs. 869 ms) and of SOA $F(1,21) = 65.74$, $p < .001$ (faster RTs at long than short SOA, 787 ms vs. 874 ms), while the main effects of Predictivity and target duration were not significant, *ps* > .05.

Critically, the interaction Predictivity X Validity $F(1,21) = 11.3$, $p < .01$ was significant, showing a larger validity effect for the 90% (about 100 ms) than for the 50% condition (about 50 ms); see Figure 2.

We then performed planned comparisons (using paired t-tests) between valid and invalid trials, separately for the two levels of cue predictivity. The two comparisons were significant: P50 invalid (862 ms) vs. P50 valid (812 ms) $t(21) = 3.47$, $p < .01$; and P90 invalid (876 ms) vs. P90 valid (770 ms) $t(21) = 4.56$, $p < .001$ showing a reliable effect of cueing, also in the 50% condition.

Noteworthy, P90 valid (M = 770 ms) trials were significantly faster than P50 valid trials (M = 812 ms) $t(21) = 2.74$, $p < .05$, unambiguously revealing that higher cue predictivity resulted in faster orienting.

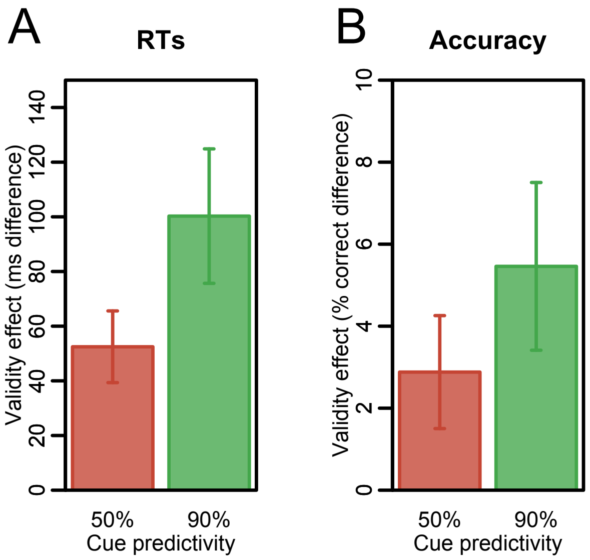

Figure 2 (**A**) Validity effect (invalid minus valid trials) in RT reported separately for the two levels of cue predictivity (see Figure 1, right panel). (**B**) Validity effect (invalid minus valid trials) in accuracy. Error bars represent SEM.

In sum, cue predictivity reliably influenced RT in a predictive direction. The spatial orienting effect triggered by the non-directional cue was larger when cue predictivity was set to 90%, but crucially, this effect was also significant in the 50% condition where the cue-target validity effect was by definition not related to cue predictivity.

5.3.2 CUE PREDICTIVITY AND TRIAL HISTORY

We ran an additional analysis to test whether the effect of cue predictivity on the size of the spatial orienting effect (RTs) could also be backed up when considering the “immediate” trial history. For each trial, we calculated the proportion of valid/invalid trials across the preceding 10 trials. Using the lme4 library (Bates and Sarkar, 2007), we fitted a linear mixed-effects model (Baayen 2005) with Validity, Cue predictivity, Proportion of valid/invalid trials in the previous 10 trials (PVP10) and Target duration as fixed effect predictors, and Subject as random factor. For each predictor, we compared the change in the residual deviance between the full and the reduced model (i.e. without the selected predictor) using a χ^2 test. Results (see Figure 3) showed a significant effect of Validity, $\chi^2(1) = 83.02$, $p < 0.001$, SOA, $\chi^2(1) = 215.68$, $p < 0.001$ and PVP10, $\chi^2(1) = 21.81$, $p < 0.001$. In addition, the interaction effect between Validity and PVP10 was significant, $\chi^2(1) = 14.65$, $p < 0.001$, indicating a strong modulation of the validity effect driven by the "immediate" trial history (see fig. 3). Hence, this single trial analysis corroborated the conclusion of the main statistical analysis, but also refined it showing that the effect of cue predictivity extends to the short-term history of each trial.

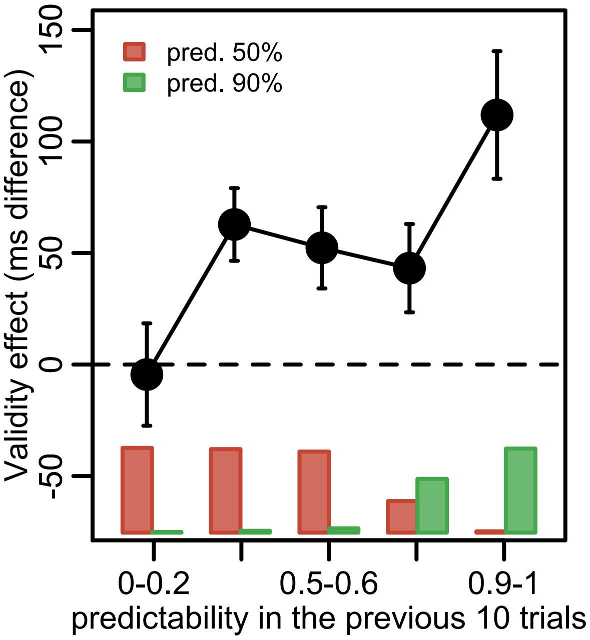

Figure 3 Single trial analysis of the cue-predictivity effect on spatial orienting. Black Dots represent mean validity effects (left scale: invalid minus valid RT) reported as a function of the cue predictivity encountered during the last ten trials, PVP10 (calculated including practice trials and trials affected by eye movements). The interaction between Validity and PVP10 resulted significant, with an estimated coefficient of -125.04 (with invalid as baseline condition). The model thus predict a strong increase in the validity effect for an unitary increment in the predictor (more than 100 ms larger when preceded by 10 valid trials vs. those preceded by 10 invalid trials). Error bars represent SEM. Histograms represent, for each of the 5 individual bins, the respective proportions of experimental trials from the different cue predictivity lists.

5.3.3 Error rate

The ANCOVA performed on mean accuracy scores showed a significant main effect of Validity *F*(1,21) = 11.25, *p* < .01 (invalid 14.5% vs. valid 10.3 %) and of SOA *F*(1,21) = 8.9, *p* < .01 (short 14.1% vs long 10.6%). The interaction between Validity and Order was significant, F(1,21) = 5.06, p < .05, showing that IP90 participants had a larger validity effect (in accuracy) across IP50 participants.

5.3.4 Awareness of cue predictivity and influence on validity effect

Finally, we resorted to post-experiment ratings to assess whether there was any relation between awareness of predictivity and spatial orienting effect. For this purpose, we calculated exploratory correlations between the individual cueing effects (RT or accuracy) and the individual cue predictivity's awareness (see Risko & Stolz, 2010 for a similar procedure).

We performed these correlations separately for the two levels of predictivity, cue colors (for which a separate estimate of predictivity was provided) and SOAs, taking into account the degree of confidence on the estimate of valid trials [reported on a Likert scale, from 1 (totally unsure) to 6 (absolutely sure)]. Across all these variables, the two measures were not significantly related to each other (all *ps* > .05) (Figure 4).

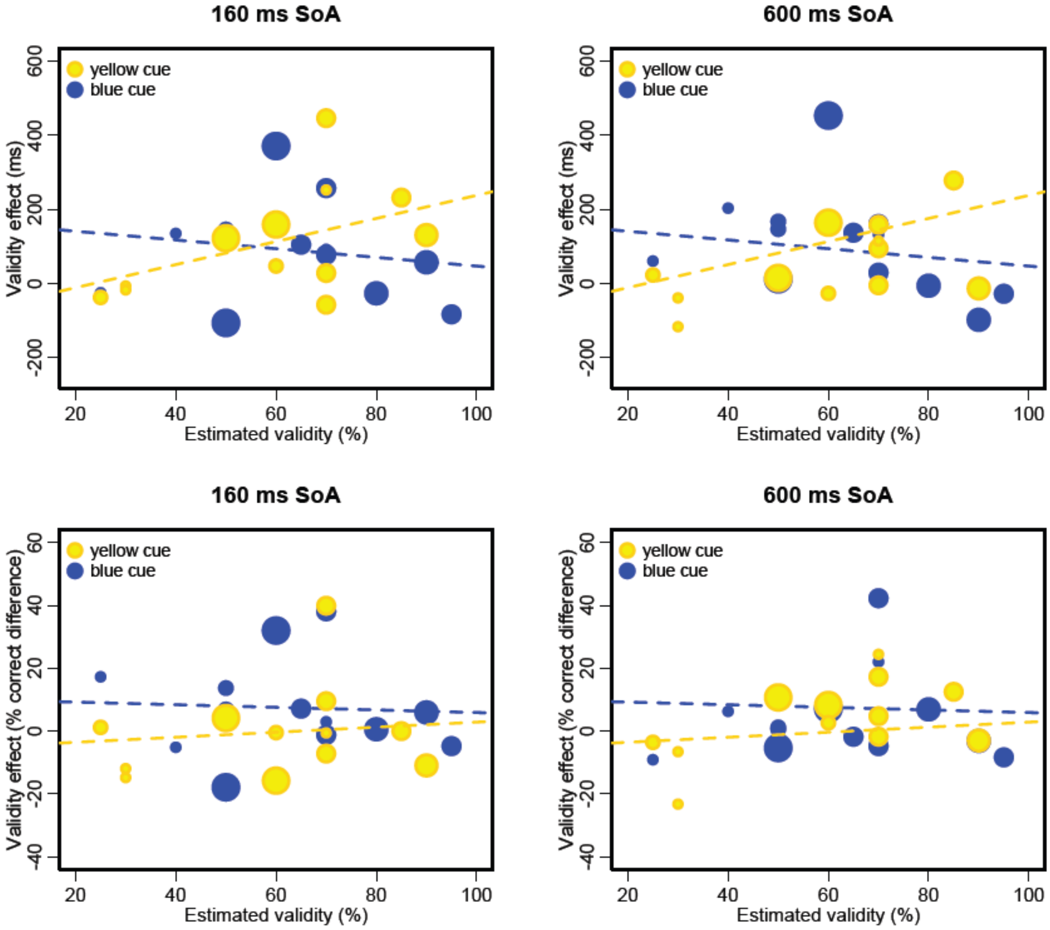

Figure 4 For each subject individually, mean validity effect plotted against the estimated cue validity, separately for the two SOAs (left: 160 ms vs. right: 600 ms), and for RTs (upper panels) vs. Errors (lower panels) . The size of the dot represents subject confidence rating over his/her cue validity estimate (larger dots correspond to higher confidence). Dashed lines represent linear fit, weighted by confidence ratings (all ps are ns).

5.4 DISCUSSION

In this study we instructed participants to orient attention according to the colour of a central non-directional cue that, unbeknown to them, was predictive (90% validity) or not (50% validity) of target position. We show that although non-directional and non-predictive, the cue reliably led to faster and more accurate target discrimination when its location was “primed” by the symbolic cue, that was amplified however when the cue had an higher predictive value. Accordingly, the present results cast doubt on the assumption that predictive cueing results in “pure” voluntary orienting of spatial attention. Then, it seems logical to conclude that several earlier studies that attributed shifts of spatial attention to a voluntary control mechanism could actually be explained by effects of target predictability or cue predictivity per se, in the absence of voluntary control (Prinzmetal, McCool & Park, 2005). As a matter of fact, predictive cueing is still the current gold standard in research on attention including neuroimaging or clinical evidence (Corbetta & Shulman, 2011) in order to distinguish endogenous from exogenous mechanisms (Awh, Belopolsky & Theeuwes, 2012). The present results suggest that such a dissociation may actually be inflated by differences in levels of cue predictivity, rather than core attentional components (see Doricchi et al., 2010, for a similar view). More generally, our new results somehow question the appropriateness of predictive cueing to induce pure voluntary orienting.

Mounting empirical evidence lends support to the notion that cue predictivity plays a central role in spatial orienting effects, including the so-called “proportion cued” or “proportion valid” effect, whereby increased proportion of valid/cued trials results in increased orienting effects (Eriksen & Yeh, 1985; Johnson & Yantis, 1985). There is growing consensus that arbitrary (spatial) associations between cue and target emerge more likely when predictive cueing is used. Paradoxically this has not resulted in concluding that it might be sufficient, possibly more appropriate, and surely more straightforward, to merely tell participants where to orient spatial attention (either left or right) without the need to subsume to predictive cueing.

An unsolved question is whether these involuntary cue-target (spatial) associations are the only mechanism through which the proportion valid effect emerges, or alternatively, whether genuine voluntary mechanisms or components are also involved. In a seminal study, Lambert, Naikar, McLachlan, and Aitken, (1999) reported an implicit cuing effect (peripheral symbolic cues and peripheral targets) that was unrelated to participants' awareness of the cue-target relationship and perceptual awareness of the cue itself, corroborating the notion that spatial shifts of attention could be triggered by implicit cue-target associations.

Likewise, in another seminal study, Bartolomeo et al. (2006) manipulated the proportion of valid trials to assess the role of different levels of predictivity in a cued detection task (central arrow or peripheral cue). Results showed that those participants who were aware of the predictivity levels (according to a questionnaire) presented larger validity effects in the case of central cueing. The link between awareness of predictivity and validity effects led Bartolomeo and colleagues to conclude that spatial validity effects may be due to a voluntary component, as spatial orienting occurred only when cue predictivity level accessed awareness.

Risko and Stolz (2010a) proposed implicit learning as an alternative, more viable, explanation for the proportion valid effect. They manipulated the predictivity (e.g. 50% vs. 75%) of either a peripheral or a central arrow cue. In both conditions validity effects increased with increase in predictivity. A questionnaire showed that following peripheral but not central cueing participants correctly identified two different levels of predictivity. Crucially, the estimated levels of predictivity were unrelated to the actual cueing effects on both response times and accuracy. Given that, despite the short SOA (150 ms), participants presented a robust validity effect, the authors suggested that endogenous orienting is too slow to modulate the proportion valid effect (which extended to participants unaware of cue predictivity level). They concluded that the proportion valid effect cannot be ascribed to endogenous orienting but rather to involuntary attentional capture and implicit learning (see also Peterson & Gibson, 2011 for similar findings and interpretation). Chica and Bartolomeo (2010) argued that, although implicit learning might play a role in this phenomenon, strategic control might also be important (see Risko & Stolz, 2010b, for a re-reply). Interestingly, our mixed-models analysis of the single trial data show that these effects likely survive even when only the “immediate” trial history (i.e. the last ten trials in the present case) is taken into account. Earlier findings (Risko, Blais, Stolz, & Besner, 2008a,b) suggest a modulation of spatial orienting performance due to frequency differences, whereby the more frequent condition would give rise to a more efficient processing than the less frequent condition (see Cutini et al., 2008 for converging evidence in task-switching).

The lack of systematic association between the awareness of cue predictivity and the observed validity effects during the task further suggests that spatial orienting based on predictive cues cannot be qualified as purely “voluntary”

(Peterson & Gibson 2011; Risko et al., 2008; Risko & Stolz, 2010a). The absence of this correlation in our data held for both RT and accuracy scores, regardless of the SOA (either short or long). Accordingly, even if one assumes that voluntary orienting is by definition a slow process (an assumption which appears overall overstated in paradigms like these), the lack of association between awareness of cue predictivity and observed validity effects even at the long SOA reinforces the notion that cue predictivity is not a necessary condition for the voluntary orienting of spatial attention.

In sum, the present results show for the first time that (i) central non-directional and non-predictive cues can effectively trigger shifts of spatial attention; (ii) cue predictivity clearly bolsters spatial validity effects; and (iii) under these conditions (i.e., non-directional and non-predictive cues) spatial validity effects happen to be fast and automatic (possibly reflecting an implicit learning effect), and they take place irrespective of participant's awareness of the cue predictivity.

Although there are almost no alternatives, it seems already questionable to study voluntary mechanisms of spatial attention in experimental contexts or situations where orienting is promoted again and again uniformly using the same task, and thus volition can rapidly turn into automatic processes. Crucially, we can add that cue predictivity of target location add unwarranted and unnecessary components to brain mechanisms of attentional orienting, whose nature is complex and labile, but not merely voluntary

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6 PUPIL DILATION REVEALS TOP-DOWN ATTENTIONAL LOAD ON SPATIAL AWARENESS

6.1 INTRODUCTION

The measurement of pupil diameter (i.e., ‘pupillometry’) has been used in psychology for more than 50 years as a general measure of cognitive effort (Hess & Polt, 1960; Hess & Polt, 1964; Kahneman & Beatty, 1966). Since the sixties it has been profitably used to provide an estimate of the intensity of cognitive activity. Kahneman (Kahneman, 1973) used the pupil diameter as the primary measure of processing load in his *effort theory of attention*, suggesting that it could provide a window on the “intensive” aspects of attention, intended as distinct from the more often studied “selective” aspects.

The size of the pupil is determined primarily by light and accommodation reflex. Changes in illumination can elicit pupil dilation up to a maximum of more then the double of its typical size (about 120% over an average size of about 3mm, MacLachlan & Howland, 2002). Instead, changes in pupil size reflecting cognitive processes are much more modest (typically less that 0.5 mm). These changes are extracted by performing time-locked averaging with respect to the event of interest, and are often normalized with respect to the pupil size at baseline (measured before the onset of the event Beatty & Lucero-Wagoner, 2000; Beatty, 1982).

It has been shown that cognitively-related pupil dilation is closely related to a neurotransmitter system, namely the locus coeruleus–noradrenergic (LC-NE) neuromodulatory system (Aston-Jones & Cohen, 2005). Specifically, it has been shown that tonic activity of locus coeruleus (LC) has a direct relationship with pupil size, and it has been suggested that cognitively related pupil dilation probably occurs as the result of an inhibitory mechanism on the parasympathetic oculomotor complex or Edinger–Westphal nucleus (Wilhelm, Wilhelm, & Lűdtke, 1999). The LC is likely a key node within the neural circuit that control the muscles of the iris

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(Samuels & Szabadi, 2008), and being also the sole source of the neurotransmitter norepinephrine (NE) in the brain, activity within the NE system gets reflected in the dilation of the eye's pupil (see fig. 1) offering a unique window on the NE system activity (Laeng, Sirois, & Gredeback, 2012).

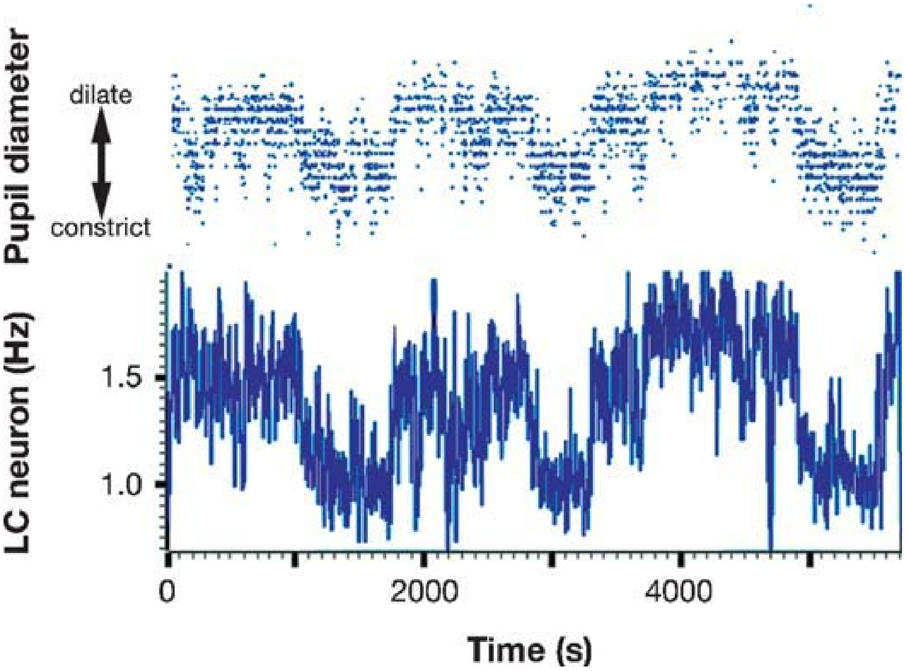

Figure 1 Association between firing rate of an LC neuron in monkey and pupil diameter during a signal detection task (Aston-Jones & Cohen, 2005)

The LC-NE system has widespread connections and is though to be involved in many cognitive functions, including attention and alertness (Petersen & Posner, 2012; Posner & Petersen, 1990). One recent hypothesis is that it plays a central role in the functional integration of the entire attentional system (Corbetta, Patel, & Shulman, 2008). Coherently with this view the adaptive gain theory (Gary Aston-Jones & Cohen, 2005) proposes for the LC-NE system two modes of activity, phasic and tonic (or perhaps a continuum between these two modes). In the phasic mode, LC cells exhibit activation related to the processing of task-relevant stimuli. This mode of function is usually associated with higher levels of task engagement and performance (Aston-Jones, Rajkowski, & Cohen, 1999; Aston-jones, Rajkowski, Kubiak, & Alexinsky, 1994; Gabay, Pertzov, & Henik, 2011; Murphy, Robertson, Balsters, & O'connell, 2011; Usher, 1999). Conversely, in the tonic mode, LC cells show less phasic responses to task event. This is associated with increased distractibility and poorer performance on tasks that require focused attention. However, also the tonic mode could be advantageous in certain situations, for example during exploration for new rewards since it is associated with increased sensitivity in detecting novel stimuli. Indeed, the theory propose a crucial role for the LC-NE system in regulating task engagement and behavioral flexibility according to environmental contingencies and task utility (Aston-Jones & Cohen, 2005). In particular when performing an attentional demanding task, phasic LC activation is thought to function as an ‘interrupt’ or ‘system reset’ signal (Bouret & Sara, 2005; Dayan & Yu, 2006) allowing the engagement of the ventral attention system, which is responsible for reorienting attention to important novel stimuli (Corbetta et al., 2008). However the phasic mode of the LC-NE system correspond also to reduced LC tonic activity, and has been associated to the deactivation, relative to rest, of the temporoparietal junction (TPJ), a key region of the ventral stimulus-driven attentional system (Corbetta et al., 2008; Shulman et al., 2003; Todd, Fougnie, & Marois, 2005). Thus large phasic response in LC indicates the occurrence of relevant events, when subjects engage in a demanding task, and are accompanied by larger pupil dilations (Gabay et al., 2011). In the present study we investigated whether pupil dilation could reflect ‘pure’ top-down attentional load, as opposed to those experimental manipulations where task difficulty increase with increasing number of stimuli presented (Ahern & Beatty, 1979; Beatty, 1982; Kahneman & Beatty, 1966).

For this purpose, we modeled our experimental paradigm on the dual-task method developed by Bonato and colleagues (Bonato et al., 2010). This method has proven very effective in reducing the attentional resources deployed for spatial monitoring by brain-damaged patients, yielding severe awareness deficits for the contralesional hemispace (Bonato et al., 2010, 2012). While top-down attentional load was manipulated by varying task demands, the stimuli were kept identical across conditions. In our paradigm the primary task consisted in verbally reporting the position of lateralized, briefly-presented, masked targets that could appear either on the left, right or on both sides of central fixation. By including trials with bilateral masked targets we aimed to increase any ‘sensory competition’ between hemifields (Kinsbourne, 1977; Miller, 1989) and examine asymmetries in visuospatial awareness together with their possible modulation by attentional load.

Increasing task demands impair visuospatial awareness not only in patients with unilateral brain damage (Bonato, Priftis, Umiltà, & Zorzi, 2012; Bonato et al., 2010; Bonato, Priftis, Marenzi, Umiltà, & Zorzi, 2012; Bonato, 2012) but also also in healthy subjects (Dodds et al., 2008; O’Connell, Schneider, Hester, Mattingley, & Bellgrove, 2011; Peers, Cusack, & Duncan, 2006; Pérez et al., 2009). Therefore, the aims of our study are twofold: first to investigate whether pupil dilation could provide useful information of the engagement of 'pure' top-down attentional load and, second, to assess whether increasing top-down attentional load affects asymmetries in visuospatial awareness. The recording, after increased attentional load, of both pupil dilation changes and spatial monitoring failures (omissions) will also allow to investigate the correlation between psychophysiological and perceptual correlates of increased task demands.

6.2 METHOD

Participants. Twenty-four participants (mean age 23.3 years, range 19-29 years, 15 females) participated in the study. All participants provided written informed consent and had normal or corrected to normal visual acuity.

Apparatus. The experiment was conducted in a quiet and dimly lit room. Participants were seated with the head positioned on a chin rest at 60 cm in front of the computer screen. The experiment was run on a PC, using E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA). Eye movements were recorded with a sampling frequency of 60 Hz through a Tobii T120 screen-based eyetracker (Tobii Technology, Sweeden), which was used also to present stimuli through its embedded 17-inch TFT monitor.

Procedure. The experiment consisted in 4 experimental blocks (81 trials each) plus a pre-test block, to be completed in one session, lasting approximately one hour. Each trial (Fig. 2, panel A) started with the presentation of a black fixation cross (0.7° wide) in the center of the screen. Stimuli were then presented 800 ms after fixation was kept within an area of 2° around the center of the screen. Stimuli (presented simultaneously) consisted in *lateralized targets* (black dots, 0.75° diameter) appearing either on left, right or both side of the screen at 14° eccentricity *a colored shape* appearing at fixation (3 shapes: square, rhombus and circle, with the same area; 3 colors, orange, green and blue; this yielded a total 9 different color-shape combination; see fig. 2, panel B) and *a 100 ms tone* presented through headphones (3 tones with different pitch were used: high, 796 Hz, medium, 450.53 Hz and low pitch, 250 Hz). After the presentation the lateralized targets were masked by four black dots, arranged as the corners of a square, centered on target position and measuring 1.8° in width. The mask always appeared on both sides, independently from target appearance position, and simultaneously the fixation cross replaced the central shape. One second later, a question mark appeared in the middle of the screen to prompt the participant to vocally report the target stimuli according to task instructions.

While the stimuli were always identical, the instructions changed across four experimental blocks. Each participants performed a *single task* (position), where only the position of the targets had to be reported (left, right, both sides) a *visual dual-task* (position-color) in which also the color of the central shape (green, blue or orange) had to be reported, an *auditory dual-task* (position-sound) in the position of the targets and the pitch (high, medium or low pitch) had to be reported, and a *visual triple-task* (position-shape-color) in which targets position and both the color and the type of the central shape (square, rhombus or circle) had to be reported. The order of the four blocks was counterbalanced across participants.

The duration of visual stimuli presentation was adapted to individual sensitivity in the pre-test block, which had instructions identical to the single-task (position), through a weighted up-down staircase procedure (Kaernbach, 1991) with a target performance of 75% correct responses.

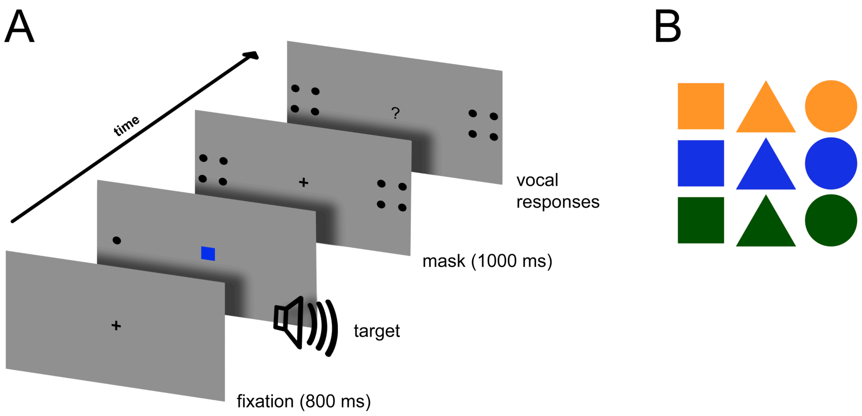

Fig. 2 (**A**) The experimental paradigm. A trial with a left target is represented. (**B**) Central shape stimulus, representing the nine possible combinations of color and shape. The three shapes were constructed in order to subtend a similar area on the display.

6.3 RESULTS

6.3.1 BEHAVIORAL DATA

Gaze position recordings were analyzed offline according to the following criteria: trials in which the recorded gaze position in the fixation-mask interval diverged from fixation cross for more than 2°, and for more than 100 ms consecutively, were excluded from subsequent analysis. Gaps in the recordings shorter than 75 ms were linearly interpolated, while trials with gaps longer than 100 ms were also excluded. This procedure resulted in the exclusion of 6% of the total trials from subsequent analysis. Mean accuracies to the additional tasks (i.e., other than the primary task of reporting the position of the lateralized targets) were 99% correct for the position-color task, 94% for the position-color-shape task and 92% for the position-sound task respectively (see fig. 3). We fitted a logistic mixed-effect model to the dual-tasks accuracies, with participant as random-effect predictor and the type of task as fixed-effect predictor, which revealed a significant effect of the type of task on the accuracy to the dual tasks [$\chi^2(2) = 68.36$, $p < 0.001$]. Specifically, accuracy in the 'color' dual-task was higher than in the 'sound' dual-task [$\beta = -2.52$, $z = -8.24$, $p < .0001$] and in the 'shape-color' dual-task [$\beta = -2.21$, $z = -7.16$, $p < .0001$]. A significant, although much smaller, difference was observed also between the 'sound' and 'shape-color' dual tasks [$\beta = 0.3$, $z = 2.22$, $p < .05$].

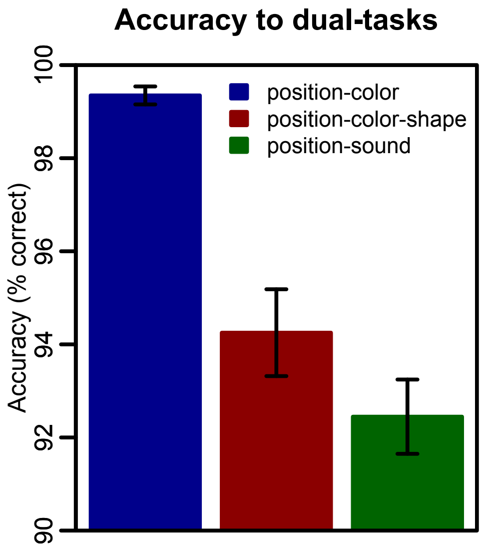

Fig. 3 Accuracy to secondary tasks. Although accuracy was generally high (>90%), the three types of secondary tasks yielded significantly different proportion of correct responses. Note that in the 'color-shape' dual-task a correct response consisted of two correctly reported information. Error bars represent within-subjects SEM (Cousineau, 2005).

We then analyzed response accuracy in the primary task including only trials with correct responses to the dual-tasks. Using the library *lme4* (Bates, 2005) we fitted a generalized mixed-effect model (Baayen, Davidson, & Bates, 2008) with the logistic function as link function and the frequency of success and failures of participants response to the lateralized targets as dependent variable. The model included task type (position, position-color, position-color-shape, position-sound) and target position (left, right or both) as fixed-effect predictors and participant as random-effect factor. To test the statistical significance of each fixed-effect predictor, we compared the change in the residual deviance between the full and the reduced model (i.e., without the selected predictor) using a χ^2 test. Results showed both a significant effect of task type [χ^2 (3) = 17.93, p < 0.001] and target position [χ^2 (2) = 253.69, p < 0.001]. By using a logistic model we estimated the differences between conditions. The condition with targets appearing in both hemifields ('bilateral') yielded a significantly lower accuracy with respect to the condition with target appearing only on the left side, as indexed by the parameter of the correspondent contrast in the model [β = -1.42, z = -7.89, p < .0001], while there were no differences between trials with 'left' and 'right' targets [β = -0.4, z = -0.2, p = 0.83]. We can quantify more precisely these differences, recalling the basic equation of the logistic regression model (in the logit form):

$$\log\left(\frac{\mu}{1-\mu}\right)=\beta_0+\beta_1 x_1+\beta_2 x_2$$

where $\frac{\mu}{1-\mu}$ refers to the odds of 'correct response'. By solving the equation, assuming that all other covariates (only x_2 in the example) are constant, and comparing the odds in x_1 and x_2+1 we obtain:

$$\frac{\exp\left(\beta_1\left(x_1+1\right)+\beta_2 x_2\right)}{\exp\left(\beta_1 x_1+\beta_2 x_2\right)}=\exp\left(\beta_1\right)$$

Thus an increase in x_1 of one unit corresponds to an increase in the odds of correct response multiplicatively by $\exp(\beta_1)$. For a categorical predictor, $\exp(\beta_1)$ can be directly interpreted as odds ratios between groups. The significance of the contrast thus indicates a decrease in the odds of 'success' from the 'left' target condition to the 'bilateral' targets condition, multiplicatively by the factor of $\exp(\beta_1)$= exp(-1.42)=0.24. The model indicates a log-odds ratio of 2.65 for the 'left' target condition, which correspond to an odds ratio of 14.22, which in turn correspond to a probability of a correct answer of 93% (in the single task condition). Accordingly, the odds of a correct answer (keeping fixed the 'task type' factor to 'single') drop to $\exp(\beta_{0+}\beta_1)$= exp(2.64-1.42)=3.43 in the 'bilateral' targets condition, which correspond to a probability of 77%.

As expected, also the 'task type' yielded a significant effect, whereby mean accuracies decreased with the increasing task demands induced by the dual tasks manipulation. All task conditions resulted in a significantly lower accuracy with respect to the reference single task (i.e., 'position' only task) ['color', β = -0.66, z = -3.4, p < .001; 'color-shape', β = -0.75, z = -3.89, p <.001; 'sound', β = -0.83, z = -4.31, p < .001]; considering the 'left' target position this corresponds to a drop in accuracy from 93% to 88% in the 'color' task, to 87% in the 'shape-color' task and to 86% in the 'sound' task. By switching the contrasts for the 'task type' factor we can appreciate no significant differences in accuracy for the 3 dual-tasks conditions (all p > .05). The interaction between 'task type' and 'target position' was not significant [χ^2 (6) = 11.18, p = 0.08], indicating that the decrease in performance (due to the different task demands) similarly affected all the positions of target appearance (left, right or bilateral), although there is a trend for a greater decrease in the 'left' target condition (see fig. 4).

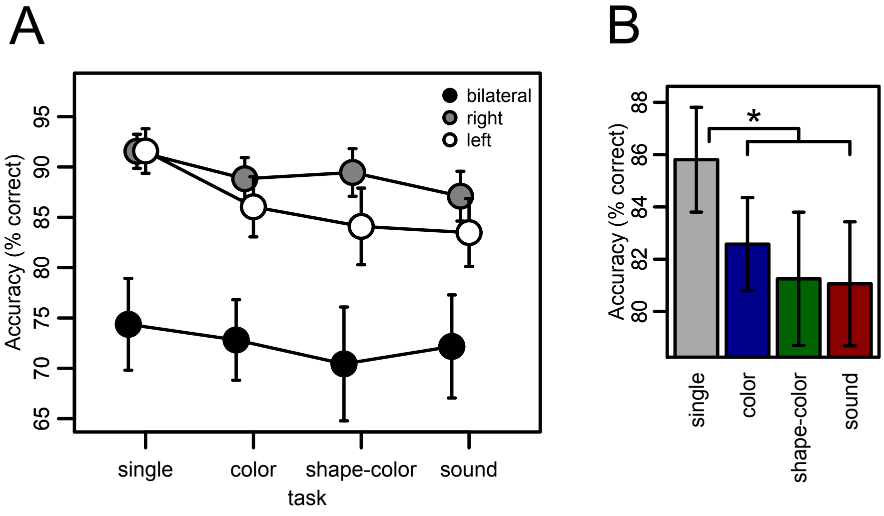

Figure 4 Accuracy results. (**A**) Effect of task and target position. (**B**) Overall task effect. Error bars representing within-subjects SEM (Cousineau, 2005).

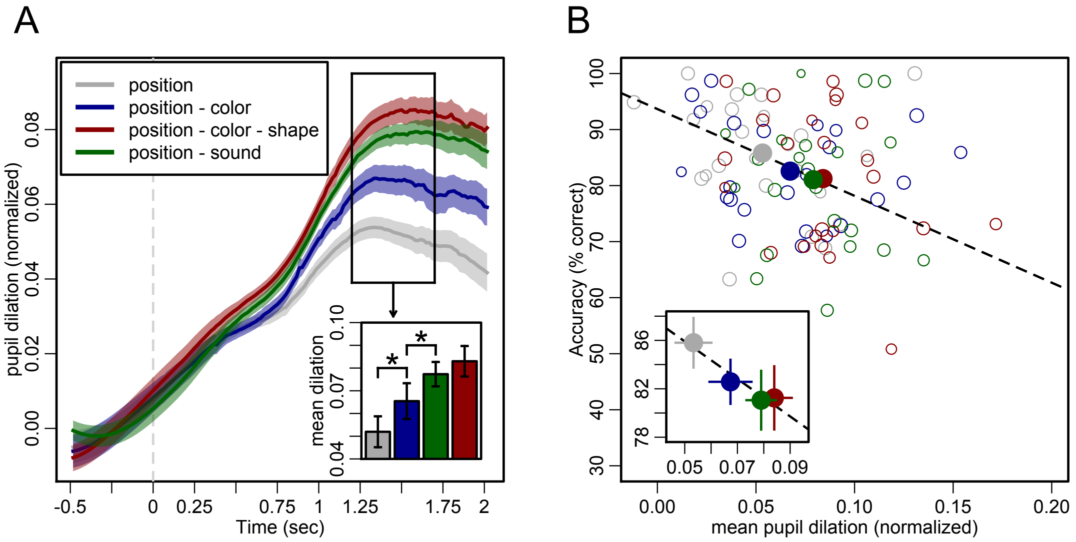

Figure 5 Pupil dilation. (**A**) Dilation patterns and mean dilations in the selected time window (black rectangle). The vertical dashed line represents the stimuli onset. (**B**) Relation between response accuracy to the lateralized targets and pupil dilation across the different tasks. Empty dots represent individual data, and filled dots represent group means. Error bands and bars represent within-subjects SEM (Cousineau, 2005)

6.3.2 EVENT RELATED PUPILLARY RESPONSE

We analyzed the event-related pupillary response, time locked to the onset of target stimuli, for each experimental block (see fig. 5). Pupil size was recorded at 60 Hz together with gaze position, and then analyzed offline with the open-source software R (http://www.r-project.org; see also the appendix for description of custom functions used in the analysis). Data from the left and right pupil were averaged together, and gap in the recordings were linearly interpolated. For each participant and block, pupil data were segmented in epochs aligned to target onset. Each epoch was then low-pass filtered with a central moving average filter of 13 samples (at 60 Hz of sampling frequency it corresponds roughly to an half-power point of 2 Hz), and normalized with respect to a baseline level, namely the average pupil size in the 500 ms before target onset, according to the following equation:

$$P_{norm} = \frac{(P_{raw} - baseline)}{baseline}$$

Only trial with all correct responses (both the primary 'position' task and the dual tasks) were included in the analysis. It is worth reminding that pupil dilation is a relatively slow signal and thus the earlier pupillary changes related to the processing of a given stimulus can be appreciated several hundred milliseconds after its presentation.

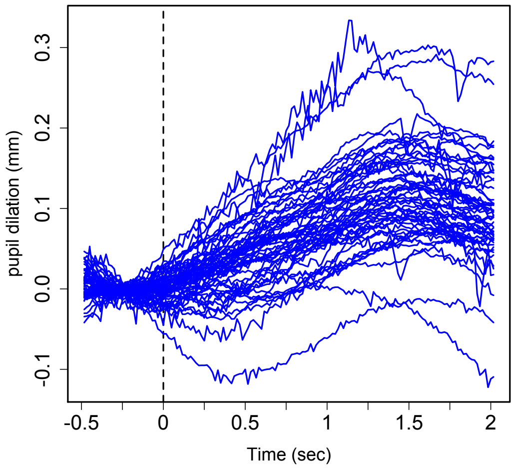

Figure 6 Raw pupil dilations (centered on the pre-stimulus baseline) for a representative subject in the single (position) task.

Peak dilation was defined as the average dilation in the time window from 1.2 to 1.7 seconds after stimuli onset (see fig. 5, panel A), and analyzed as a function of task instructions. A repeated measures ANOVA confirmed that pupil dilation increased according to task difficulty [$F(3, 69) = 14.56$, $p < .0001$]. Planned comparisons revealed that the ‘position-color’ condition elicited a significantly greater dilation than the ‘position’ condition [$t(23) = 2.6$, $p < .05$], and both the ‘position-sound’ and the ‘position-shape-color’ conditions elicited a greater significantly dilation than the ‘position-color’ condition [‘sound’, $t(23) = 2.32$, $p < .05$; ‘shape-color’, $t(23) = 3.04$, $p < .001$], but did not differ between themselves [$t(23) = 1.24$, $p = 0.23$] (all t-test comparisons were paired and two-tailed).

Comparing pupil data to the accuracy on the primary spatial task, it can be seen that the increase in pupil dilation closely mirrors the reduction in response accuracy following increased task demands. The relation between the two variables is not evident at the individual level, likely due to the different task order. Since the order was counterbalanced across participants, the pattern of data could be better appreciated at group level, where carry-over effects were equated. Indeed the average response accuracy and peak pupil dilation showed a strong negative correlation, $r(2)=-.96$, $p = 0.03$ (see fig. 5, panel B).

6.3.3 HEMI-FIELD ASYMMETRIES

Since our primary detection task comprised lateralized targets, we further analyzed error responses to explore the role of increased tasks demands on spatial awareness, including hemispatial differences. Error responses were much more frequent in the bilateral target condition (fig. 3, panel A), indicating that participant extinguished one of the two targets in approximately 25% of the trials. We analyzed the pattern of extinction-errors to determine whether they reflected a specific hemifield bias. Figure 7 shows the pattern of extinguished targets for the different tasks and for the different target durations adopted in the experiment. Extinctions were slightly more frequent for left than right targets and this asymmetry seems to depend on the stimuli duration: that is, participants who had longer stimuli durations (i.e., > 200 ms) did not show any extinction.

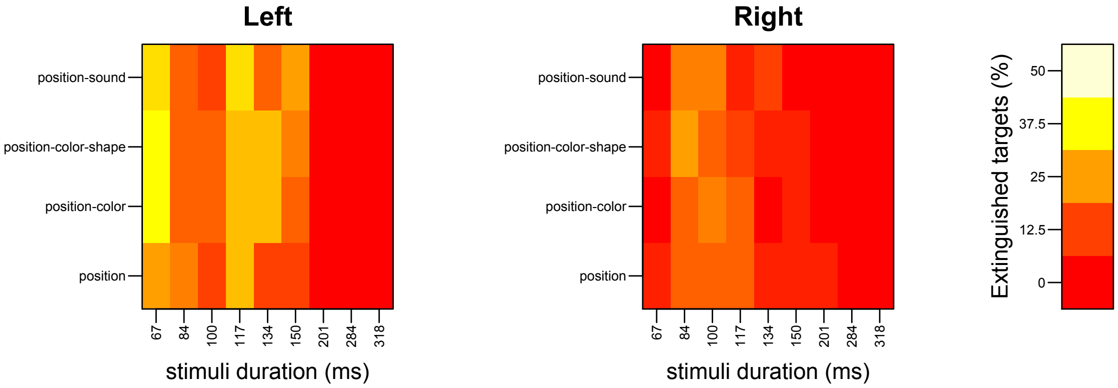

Figure 7 The distribution of extinguished targets (bilateral trials) for the different tasks and the different stimuli durations. Note that while all the participants went through the four tasks, stimuli duration was individually adapted in the pre-test session.

We fitted a logistic mixed-effect model to the proportion of extinguished targets, with duration, side (left, right) and task as fixed effect predictor, and subject as random effect predictor. Results showed a reliable effect of duration [χ^2 (1) = 16.97, *p* < 0.001], side [χ^2 (1) = 41.83, *p* < 0.001], as well as a significant duration X side interaction [χ^2 (1) = 8.88, *p* < 0.01]. The coefficient for duration is a negative value [*β* = -0.024, *SE* = 0.006] which indicates that the probability of missing a target depended on stimuli duration, and specifically decreased with increasing duration. However the coefficient for the left-side and for the interaction duration X left-side are positive [left-side: *β* = -0.272, *SE* = 0.712; duration X left-side: *β* = -0.002, *SE* = 0.006], which indicates that the probability of missing a left target was always higher than the probability to miss a right target, and that this difference was even more evident at medium-high stimuli durations. As can be seen in fig 8, which represents the left minus right difference in the proportion of extinguished targets (thus a positive value indicates more missed targets on the left side and a rightward bias), there is a consistent although small asymmetry, indicating a rightward bias, which is neither affected by the type of concurrent dual task (fig. 8, panel B) nor by the individual block order (i.e., time-on-task, fig.7 panel A).

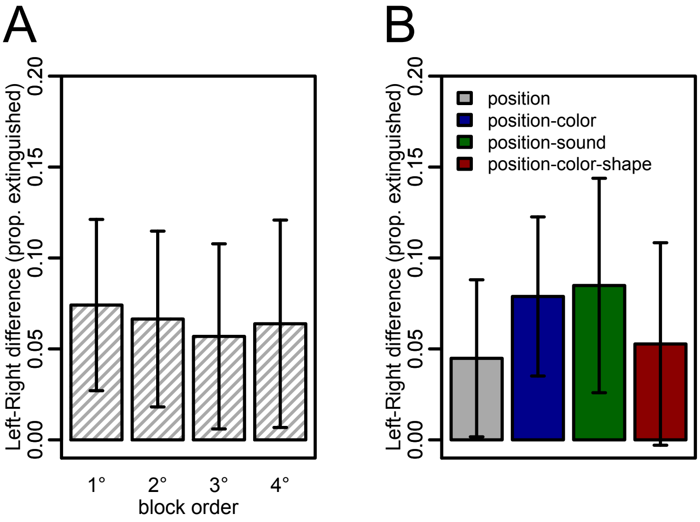

Figure 7 Hemifield asymmetries in the detection of lateralized targets as a function of task (**B**) and block order (**A**).

6.4 DISCUSSION

We examined whether event related pupillary responses could reflect a 'pure' top down attentional load. In our paradigm attentional load was manipulated by adding a concurrent dual tasks to the primary spatial task (detection of lateralized spatial targets). Importantly, across all single and dual tasks conditions the stimulation was kept constant: this was necessary in order to measure the effect of pure top-down attention load, because it is known that any stimulus that have some relevance for the observer is likely to elicit a pupil dilation response (e.g., Hess & Polt, 1960; Laeng et al., 2012; Laeng & Falkenberg, 2007; Partala & Surakka, 2003) this was necessary in order to measure the effect of pure top-down attention load. Results have shown that that event-related pupil dilation, time locked to stimulus onset, was modulated by the increasing task demands: as expected, the single task, which showed the highest accuracy, also yielded the smallest pupil dilation. The dual task position-color was performed with an accuracy level lower than the single-task and elicited a greater pupil dilation . The position-color dual task produced a lower dilation with respect to the other dual-tasks conditions (position-sound and position-color-shape), which on the contrary did not differ between themselves. The pattern of results overall indicates that a top-down manipulation of task difficulty not only resulted in increased error rate on the primary spatial task but also committed participant to greater task engagement, as indexed by larger phasic pupil dilation response. Notably, our experimental design allows to disentangle potential confounding effect like the number of stimuli that had to be responded to and/or the number of alternative responses, thereby ruling out that pupil dilation was a function of the working memory (WM) load (Beatty & Lucero-Wagoner, 2000; Kahneman & Beatty, 1966; Kahneman, Peavler, & Onuska, 1968). Moreover, both the temporal window analyzed and the pattern of results found confirm that we were tapping into relatively early-stage effects, where response-selection/preparation mechanisms can be readily excluded on the basis of invariance between the dual and the triple task. Indeed the 'triple-task' (position-color-shape) and the dual task position-sound elicited a similar pupillary response and also yielded a similar error rate, even if the number of target to be discriminated was greater in the 'triple' task. This can be explained only by assuming that the two tasks had similar attentional demands, and thus elicited the same level of task engagement and similar error rates in the concurrent primary spatial task. Overall, this pattern can be readily explained if we assume that color discrimination produced much less load on attentional capacity than the other dual tasks. This fits well with the notion that color is a feature that is processed *pre-attentively* (Treisman & Souther, 1985; note, however, that attention can be critical even for the detection of the so-called pre-attentive features; e.g., Joseph, Chun, & Nakayama, 1997). This hypothesis is confirmed by the fact that the position-color dual task elicited lower error rates and pupil dilation than the position-sound dual-task, which many participants spontaneously categorized as the most difficult. Overall, the pattern of results can be explained only assuming that our measures (pupil dilation, and error rate in the concurring primary spatial task) reflect the true task difficulty not confounded by other factors (e.g., number of attended targets). In particular our results confirm and extend the view of pupil size as a robust and informative index of task difficulty. It has been shown previously that more complicated task, such as discrimination, elicit larger phasic dilation than easier tasks like simple detection (Gabay et al., 2011), coherently with the notion that the LC-NE system has two modes of activity and that the one engaged during more demanding tasks is characterized by larger phasic dilation (Aston-Jones et al., 1999; Corbetta et al., 2008). Our results extend this finding by showing that phasic pupil dilations precisely mirrors increasing levels of top-down attentional load in a discrimination task, and suggest that the phasic mode of the LC-NE system can be activated at different levels in a flexible way according to task demands.

The second aim of the present study was to explore the consequences of increased attentional load upon spatial monitoring and visuospatial awareness.

Trials with bilateral spatial targets resulted in an higher error rate than trials with unilateral targets, coherently with the idea of between hemifield competition in conditions of double simultaneous stimulation (Driver & Vuilleumier, 2001; Kinsbourne, 1977; Miller, Gochin, & Gross, 1993). We then focused on the proportion of missed targets for both hemifields in the bilateral condition (i.e., extinguished targets). A consistent rightward bias (as indexed by more left target omitted/extinguished) emerged, which was neither affected by task demand nor by time-on-task. The finding of a rightward bias is in line with a widely accepted theory of neglcet and attentional asymmetries (Corbetta, Miezin, Shulman, & Petersen, 1993; Mesulam, 1981), which maintains that attentional functions of the right hemisphere span both hemifields. If the attention to right visual field is controlled bilaterally by areas in both left and right parietal cortices, presumably right stimuli are attended and detected more easily. This is in line with studies showing greater attentional effects for targets in the right hemifield in healthy subjects and split-brain patients (Castro-Barros, Righi, Grechi, & Ribeiro-do-Valle, 2008; Kingstone, Enns, Mangun, & Gazzaniga, 1995; Mangun et al., 1994). However, the asymmetry seems to be strongly dependent on the parameters of stimuli, like spatial frequency (Proverbio, Zani, & Avella, 1997), as well as on the type of spatial task (Roth & Hellige, 1998) and task demands, like visual short-term memory (VSTM) load (Sheremata, Bettencourt, & Somers, 2010). This dependence on task contingencies might be the reason why other studies using a very different paradigm, a dual stream rapid serial visual presentation (RSVP) task, reported the opposite result, a left visual field advantage (Verleger et al., 2009, 2010; Verleger, Śmigasiewicz, & Möller, 2011), which might thus reflect a specific advantage of the right hemisphere for processing fast-paced sequences of stimuli. Other studies have shown that the attentional bias at baseline turns into a rightward bias following increasing cognitive load (Dodds et al., 2008; Peers et al., 2006) or decreasing arousal and alertness (Bellgrove, Dockree, Aimola, & Robertson, 2004; Fimm, Willmes, & Spijkers, 2006; Manly, Dobler, Dodds, & George, 2005; Matthias et al., 2009; Schmitz, Deliens, Mary, Urbain, & Peigneux, 2011). However in our study we had a rightward asymmetry at baseline with no significant modulation due to load. It must be noted that while our dual task manipulations yielded a consistent and significant effect, the drop in accuracy with respect to the single task condition was not dramatic, since the average accuracy remained above 80% of correct responses. Is it thus possible that within this limited range of performance, variations in hemifield asymmetry due to increasing task demands, if any, are small and hardly detectable. Another possibility is that verbal responses, mediated by the left-hemisphere, could have interfered with the processing of visual stimuli in the right-hemifield: according to the ‘functional distance model’ (Kinsbourne & Hicks, 1978) the amount of interference in a dual task is dependent upon the distance between the control centers involved in the two concurrent tasks. This means that tasks that are processed by anatomically close regions are more difficult to perform together, such as speaking and using the right hand (Kinsbourne & Cook, 1971). Our dual tasks required an additional vocal response, recruiting more resources in the left hemisphere and perhaps weakening visual processing of the right stimuli. In turn, this could have prevented the rightward asymmetry to increase in the dual task condition, in contrast to other studies which used manual responses (Peers et al., 2006; Pérez et al., 2009).

In summary, our results show that (1) pupil dilation accurately mirrored variations in top-down attentional load in a task were bottom-up confounds were kept constant across conditions, supporting and extending the use of this valuable and easy-measurable psychophysiological index; (2) the detection of lateralized targets in the primary spatial task indicated a significant rightward bias, which was most evident in the case of double simultaneous stimulation of both hemifield.

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7 CONCLUSIONS

In this thesis I investigated the mechanisms underlying the deployment of top-down attention in space. In a series of experimental studies, both behavioral and computational, I addressed several issues regarding how and to what extent we can voluntarily allocate attention to relevant locations in space in different conditions, e.g. during an eye movement or when the targets to be attended are multiple.

In Chapter 2, I presented a recurrent model of saccadic planning that can account for several attentional effects without requiring additional or specific mechanisms separate from the circuits that perform sensorimotor transformations for eye movements, in agreement with the premotor theory of spatial attention. The model includes a circuit that update the retinotopic visual representation using an ‘internal forward model’ of how visual inputs are modified as a result of saccadic movements. Simulations have shown that the latter circuit is crucial to account for dissociations between attention and eye movements that may be invoked to disprove the premotor theory. Finally the model provides new insights into how spatial remapping may be implemented in parietal cortex.

In Chapter 3 I presented another computational model that mimics the sensorimotor transformations occurring in the posterior parietal cortex (PPC). A recurrent neural network with one layer of hidden neurons (Restricted Boltzmann Machine) learned a stochastic generative model of the sensory data, both visual and postural, without supervision. Importantly, analyses of the hidden neurons revealed gain modulated visual receptive fields, thus showing that space coding for sensorimotor transformations similar to that observed in the PPC can emerge through unsupervised learning. These results suggest that gain modulation is an efficient coding strategy to integrate visual and postural information towards the generation of motor commands, and provide additional support for the computational approach adopted in the model presented in Chapter 1.

In the Chapter 4, I presented a novel object-based effect in the allocation of attention across eye movements. Recent studies have shown that attentional facilitation lingers at the retinotopic coordinates of the previously attended position after an eye movement. Those results are puzzling, because the retinotopic location is behaviorally irrelevant in most ecological situations, and are also in contrast with other studies that showed predictive and efficient remapping of attention across saccades. Critically, in the former studies participants were asked to maintain attention on a blank location of the screen, not on a defined object. In the present study I tested whether the continuing presence of a visual object at the cued location influences the postsaccadic attentional topography. Attention orienting was tested within a trans-saccadic cueing paradigm in which the relevant positions were defined by squared black frames that either remained visible throughout the trial or disappeared after cue presentation. Results have shown that a stable attentional benefit is found at the spatial location of the cue only when a perceptual object is continuously present at that location. This finding helps resolve current controversy regarding the allocation of attention across saccades and suggests that attention operates mostly on a structured representation of the visual input.

In the Chapter 5, I addressed a methodological issue of the spatial cueing paradigm, probably the most used experimental paradigm in studies of covert attention. Traditionally, studies of voluntary covert attention have resorted to the presentation of unilateral visual targets preceded by centrally-presented arrows carrying two distinct functional properties; directionality (i.e., indicating where attention had to be shifted) and predictivity (i.e., informing where the target was more likely to appear). More recently, a wealth of behavioral studies showed that for arrow cueing predictivity is not a necessary condition to obtain reliable shifts of spatial attention. The goal of the present study was to assess whether by removing both directionality and predictivity, covert shifts of spatial attention could nevertheless arise. Participants were asked to judge the orientation of a unilateral Gabor grating that was preceded by a non-directional centrally-presented color cue, informing them about the side (either left or right) to be covertly attended. Unknown to participants, cue predictivity was manipulated across blocks, such that the cue was predictive for half of the experiment, but unpredictive in the other half. Results have shown that reliable shifts of spatial attention can emerge in the absence of both directional and predictive cues. Crucially, predictive cues led to larger spatial orienting effects, which were nonetheless totally unrelated to the subjective estimates made by the participants regarding cue predictivity. Ultimately, these findings deeply question the appropriateness of predictive cueing for delineating ‘pure’ voluntary shifts of spatial attention.

Finally, in Chapter 6 I investigated limitations that arise when two task are performed simultaneously. Under these conditions performance typically degrades in one or both the tasks, an effect interpreted in terms of load on shared attentional resources. In particular, I investigated whether pupil dilation, a measure easily obtainable with modern eyetrackers, could reflect changes in visuospatial awareness induced by a dual-task manipulation that consumed the attentional resources available for spatial monitoring. In the single-task condition, participants had to report only the position of lateralized, briefly-presented, masked visual targets (”right”, “left”, or ”both” sides). In the multitasking conditions, while monitoring for the lateralized targets, they performed also a second task, visual or auditory, to increase the cognitive load, or a second and a third task (central shape and color + target position). Results show that event-related pupil dilation strikingly increased according to task demands. Moreover, the comparison between the auditory dual-task condition and a condition where three visual characteristics had to be responded to revealed no differences, thus confirming that the effect was led by the amount of unspecific attentional resources recruited rather than by the mere number of stimuli to be processed. The paradigm adopted allowed also to investigate load-related effects on attentional and visuospatial asymmetries across hemifields: results have shown a significant rightward bias, not modulated by the increasing task demands. This result was interpreted according to a widely accepted theory of neglect and attentional asymmetries, which maintains that attentional functions of the right hemisphere span both hemifields.

In summary, these studies shed light on the mechanism underlying top-down orienting of visual spatial attention. I have provided a biologically plausible computational framework for the orienting of attention in space and several new experimental results that show, for example, how spatial attention is affected by the structure of the image during eye movements, and by ‘statistical’ regularities in the task (i.e., cue predictivity). Overall, the emerging picture is that of a complex mechanism that even in its volitional aspects is considerably affected by other non-volitional factors, both external and internal to the individual.

8 APPENDIX

8.1 EYER: AN R LIBRARY FOR THE ANALYSIS OF EYETRACKING DATA[1]

The library consist in a set of R (http://www.r-project.org) functions developed for the analysis of eye tracking data (both eye movement and pupil dilation), plus some other general purpose functions This set of functions is suited for eyetrackers with medium or low sampling frequency (e.g., < 300Hz), in particular Tobii eyetrackers.

The library (version 1.0) is composed by the following functions:

`baselineNorm(X, baseLength=30, norm=T)`

Perform baseline correction and/or normalization (usually used in the case of event-related pupil dilation data). `X` is the matrix containing all trials data (one for each row). `baseLength` is the length of the pre-stimulus baseline defined in number of samples. `norm` is a logical flag that determine whether divisive normalization will be performed (if `FALSE` the baseline is only subtracted)

`buildTimeStamp(sec, microsec)`

Build a zero-based timestamp vector defined in ms starting from the seconds (`sec`) and micro-seconds (`microsec`) timestamp vectors used by the Tobii gazedata files

`checkSingle(X,nBefore=30,sp=1/60)`

Plots recursively, and allows to inspect for artifacts, individual trials from the matrix `X` (trials in different rows and a samples in columns). `sp` is the sampling period (default to 1/60, i.e. sampling at 60Hz) and `nBefore` is the number of samples before the onset of the relevant stimulus (default to 30, which corresponds to 500 ms at 60Hz sampling frequency). Trials with artifact can then be manually

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[1] The library is available upon request, free of charge. For more information, please send an email to one of the following email address matteo_lisi@yahoo.it, matteo.lisi@parisdescartes.fr or visit http://ccnl.psy.unipd.it.

excluded, the output of the function will be the same matrix but without the selected rows

`countTrials(event,tag)`

In the Tobii output, the gazedata file, usually one column is used to record which was the event when that sample was recorded (e.g., “cue”, “target”, etc.). Starting from this event-vector (`event`) this function builds a vector of the same length that indicates the number of trials, by counting the occurrence of a particular event (which is supposed to be the first of the trial, e.g., “fixation”) defined by `tag`

`fillGap(x,sp=1/60,max=50,type="linear")`

This function fills gaps in the recordings (defined as NA values) that are shorter than `max` (defined in ms). Two types of interpolation are possible: `“linear”` and `“cubic”`. `sp` indicates the sampling period

`filtCMA(x, n)`

Central moving average, with a symmetrical widows of size `n` samples (note: `n` must be even)

`filtLP(x,fc,sp=1/60)`

Low-pass exponential average filter. This function implements an infinite-impulse-response (IIR) single-pole low pass filter, with cut-off frequency at `fc` Hz. `sp` indicates the sampling period

`filtMM(x, n)`

Central moving median filter, with a symmetrical widows of size `n` samples (note: `n` must be even)

`is.even(x)`

Determines if a number `x` is even or odd (return `TRUE` if even)

`mostrepeated(x)`

Returns the most repeated value in a vector `pasteFactor(data,factornames)`

Given the dataframe `data`, finds the factors named with names corresponding to the character vector `factornames` and merge them in an unique factor (labels for the different factors are pasted together with `“_”` as separator). Allows the easy calculation of post-hoc comparisons for interactions in a factorial design, or the filtering of reaction times data based both on subjects and conditions (see `RTfilter`)

`pix2deg(x,xRes=1400,xWidth=40,sDist=60)`

Converts pixels in degree of visual angle. `x` is the measure in pixel to be converted, `xRes` is the horizontal resolution of the screen, `xWidth` is the width of the screen in centimeters, and `sDist` is the eyes-display distance.

`removeGap(x)`

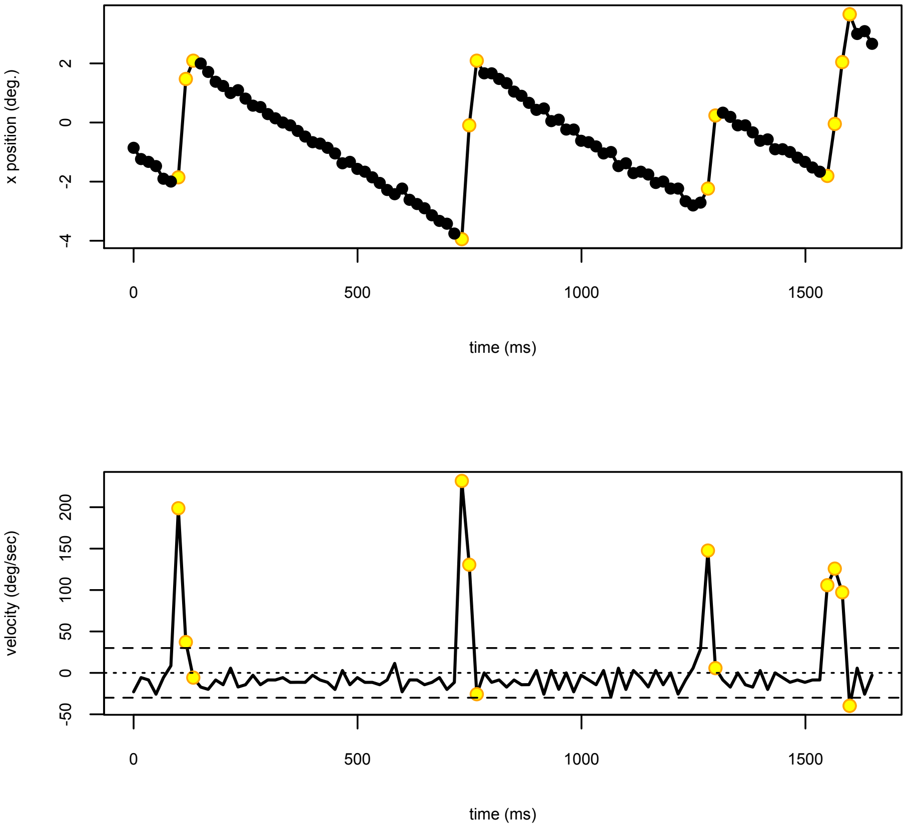
For the Tobii gaze data files: converts gaps in the recordings (vector `x`) from `-1` values to `NA` (necessary for gap interpolation, see `fillGap`)

`RTfilter(x,s,nsd=2)`

Filters reaction times (`x`) based on subject means (`s` is the vector that defines participants ID). Returns the index of trials that exceed `nsd` standard deviations from the average of reaction times that correspond to the same level of factor `s`

`sacDet(v,xy,t,th=30,mvh=0.5)`

Performs automatic velocity-based saccade detection. `v` is the velocity vector, `xy` is a two-column matrix with x and y gaze position respectively (if is one column, then only one dimension will be considered), `t` is the timestamp (in ms), `th` is the velocity threshold for saccades (default 30°/sec) and `mvh` is a movement thresholds: saccades with estimated amplitude lower than this threshold will not be considered. The algorithm is optimized for low sampling frequency recordings and simple two-points velocity calculations: for each saccade considered the algorithm includes also the first sample after the last exceeding the velocity thresholds. This allows the estimation of saccade amplitude even for small saccades at low sampling frequency. See the figure below for an example of the algorithm used to detect fast and slow phases of oculomotor nystagmus during optokinetic stimulation (gaze recorded at 60Hz), samples classified as “`saccade`” by the algorithm are represented in yellow, note that the last value for each saccade does not exceed the velocity thresholds of 30°/sec



Velocity based detection of fast and slow phases of optokinetic nystagmus recorded at 60Hz

The function returns a list with several arguments: `s` is the vector index of saccade data points; `n` is the total number of the saccades detected; `a` provides for each saccade detected an estimate of saccade amplitudes (quite a rough estimates, given that the function is though to be used with eyetrackers with low sampling frequency); `t` indicates the saccade onsets based on the timestamp.

`selectEvent(x,event,flag,trialsDet=NA,maxEpochNa=0)`

Selects and makes a list of recordings associated with a particular event defined by flag. `x` is the data vector, `event` the event vector (factor or character), `flag` indicates a level of event. `trialsDet` (optional) is a matrix with the details for each of the trials (one row for each trial). The output is a list with arguments: `coord`, which is also a list with the corresponding segment of `x` for the event `flag` for each trial, and `tdMat`, which is a matrix with the details included in `trialsDet` (this is useful for practical reasons, in order to keep all information in one single file). `maxEpochNa` indicates the maximum proportion allowed of `NA` values: trials that exceed that proportion will be excluded.

`splitGazeData(x, evento, flag, tw, sp = 1/60, baseLength = 0.5, maxEpochNa = 0.1)`

Select and organize into a matrix all the epochs time locked to the event `flag` (in the corresponding event vector `event`). Each row will contain one trial, and each trial will be aligned to the onset of the event. `tw` indicates the length of the time window of the epochs (in seconds); `sp` is the sampling period, `baseLength` is the duration of the baseline pre-stimulus interval (in seconds); `maxEpochNa` indicates the maximum proportion allowed of NA values: trials that exceed this proportion will be excluded.

`vel2(x,t)`

Basic two-samples velocity calculation

`WScorrect(x,s)`

Corrects a vector of data (`x`) based on a vector `s` that indicates subjects' ID. The correction removes the between-subjects variance, allowing the calculation of within-subjects SEM and confidence interval according to the method of Cousineau (Cousineau, 2005):

$$WScorrect\left(x_{ij}\right) = x_{ij} - \overline{x_j} + \overline{x}$$

where x_{ij} indicates data for the *j*th participant in the *i*th condition, $\overline{x_j}$ represent the participant mean across conditions and $\overline{x}$ is the group mean.

9 ACKNOWLEDGEMENTS

First I would like to thank Marco Zorzi for his supervision, encouragement and the numerous advices he has provided. Next I would like to thank my laboratory and all its members, in particular Marco Casarotti, Mario Bonato, Simone Cutini and Michele De Filippo who gave fundamental contributions to the work presented in this thesis. A special thanks goes also to Carlo Umiltà, who set a shining example of academic excellence and intellectual honesty.

Another very special thanks goes to Patrick Cavanagh and the people from the CavLab and the Laboratoire Psicologie de la Perception, for welcoming me in Paris, I learned a lot and I had a very good time.

Finally, I would like to thanks my parents, for their kind support; and my partner in life Isabella, who accompanied and helped me during the last three years, for tolerating me in the last (chaotic) months, and ultimately for ‘keeping it real’ and changing me for the better. A special thank goes to my friend Pouia, for downplaying all the hard times we have been through together. The last special thanks goes to all my two- and four-legged friends (too many to be listed here) for their friendship and all the precious good times we have had together.