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What underlies the ability to guide action with spatial information that is no longer present in the environment?

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In early evolutionary history, as organisms developed the ability to move through and act on their environment, and to use perception to guide these actions, advantage was surely conferred on those that could, when appropriate, delay their actions relative to the perceived events that prompted them. For example, in some instances the optimal response to perceiving a source of food may not be to instantaneously pounce, but, rather, to withhold that action until the prey reemerges from the hole into which it has disappeared. Thus, the ability to control actions, including the ability to guide actions with information no longer accessible to sensory receptors, likely evolved as a core function of perception-action systems. This perspective highlights the fact that such terms as *attention*, *response inhibition*, and the topic of this volume, *working memory*, are constructs have been developed by scientists trying to reverse engineer a highly evolved neurocognitive system. Although unquestionably useful for the categorization and description of certain types of behavior and/or neurophysiology, they need not correspond to discrete systems that can be meaningfully understood in isolation from the larger system within which they are observed. Rather, they may be better construed as properties or functions of an integrated perception-action system. The focus of this chapter will be on the short-term retention (STR) of spatial information that temporally bridges the offset of the sensory stimulus and the onset of the action that is guided by that sensory information. This is typically operationalized experimentally by studying the delay period of tests of delayed recognition and delayed response.

A perception-action framework

A framework that situates spatial working memory in a perception-action perspective holds that incoming visual information that captures attention, whether endogenously or exogenously, automatically, concurrently, activates several brain systems: parietal and frontal systems involved in the control of attention, the eye movement control system in the superior colliculus, and frontal systems that implement inhibitory control (Theeuwes et al. 2009). An anatomical substrate for the putative simultaneous engagement of what we will refer to as the *perception-action network* exists in the form of extensive bidirectional connections between striate and extrastriate visual regions and the parietal cortex and between these occipital regions and the superior colliculus (e.g., Schiller 1986), between superior colliculus and parietal cortex (e.g., Pare and Wurtz 1997) and superior colliculus and the frontal eye fields (FEF, e.g., Sommer and Wurtz 2000), and between frontal and parietal cortex (e.g., Selemon and Goldman-Rakic 1988). The simultaneous, reverberatory activation (or inhibition) of the representation of one or more retinotopically encoded locations at multiple stations of this network produces a state that, depending on behavioral contingencies, can produce an eye movement, covert attention to a location (or an object at a location), or the STR of spatial information, with the relative balance of excitation and inhibition at each level of the system determining which of these behaviors is expressed. The utility of this framework for understanding the STR of spatial information will underpin much of this review.

The frontal eye fields as a source of attentional control

Visual attention is generally assumed to reflect the top-down prioritization of the perceptual processing of one (or more) region(s) of the visual field over others (Posner

1980). One computational account holds the deployment of attention to emerge from recurrent interactions between posterior perceptual systems and neurons in the frontal eye fields (Hamker 2005). In brief, attentional bias in perceptual regions arises from the interaction of feedforward spatial information encoded in the receptive fields of feature-selective neurons (e.g., in area V4), and the resultant activation of neurons in the frontal eye fields (FEF). The build-up of activity in the FEF generates spatially selective feedback to visual areas – the attentional bias that has been observed in many electrophysiological studies of visual cognition (e.g., Chelazzi et al. 1993; Luck et al. 1997; Treue 1999; Chelazzi et al. 2001). Consistent with this theoretical account are the neurophysiological findings that subthreshold stimulation to a region of the FEF with a known motor field produces a covert shift of spatial attention to the very same region of space represented by the motor field (Moore and Fallah 2001; Moore and Fallah 2004), and that this microstimulation can also enhance stimulus-specific responses in V4 neurons (Moore and Armstrong 2003). One perspective on these computational and neurophysiological data (although not universally endorsed, see Awh et al. (2006) for discussion) is that they are consistent with the idea that spatial attention corresponds to the preparation to initiate an action, the "premotor theory of attention" (Rizzolatti et al. 1987). For the perception-action framework introduced at the beginning of this chapter, they provide explicit computational and neurophysiological demonstrations of the simultaneous and interactive recruitment of attention and of an eye movement plan as a consequence of the perception of a behaviorally relevant stimulus.

Attention and working memory.

Turning now to the STR of a location in space, one potent idea has been that of attention-based rehearsal, which holds that the STR of spatial information is accomplished via the covert allocation of spatial attention to one or more to-be-remembered locations (Awh et al. 1998; Awh and Jonides 2001). Behavioral evidence for this idea comes from the fact that the processing of stimuli presented at a location being held in memory shows the same benefits as those produced when attention is covertly allocated to that location, and that memory suffers when attention is pulled away during the delay period (Awh et al. 1998; Awh and Jonides 2001). Relevant physiological evidence includes the fact that the STR of spatial information biases event related potentials (ERP, computed from the electroencephalogram (EEG), Awh et al. 2000) and functional magnetic resonance imaging (fMRI) signals (Awh et al. 1999; Postle et al. 2004) in the same manner as does the covert allocation of spatial attention in tasks that make no overt demands on memory. This is illustrated in Figure 1, in which an attention-like bias is evident in delay-period activity across the entire cortical manifold of the posterior dorsal stream, the regions responsible for spatial perception and cognition. Inspection of this figure indicates that the magnitude of the putative attentional bias declines monotonically along the caudal to rostral axis, a phenomenon that may reflect the transition along this axis from cortical *sites* to cortical *sources* of attentional control. The superior parietal cortex and FEF have been identified as key sources of the endogenous control of attention in humans (e.g., Corbetta and Shulman 2002; Yantis and Serences 2003), and cortical sources of control might be expected to show less topographic variation of as a function of the location of attentional focus than the sites experiencing its effects (Ruff et al. 2006).

The concept of attention-based rehearsal can be tied directly to the perception-action framework by considering a recent study in which monkeys were trained to perform an attentional cuing task while activity was recorded from neurons in the FEF (Armstrong et al. 2009). Each trial began with a lever press, which triggered a visual cue to attend covertly to one of six locations at which oriented-grating stimuli would be presented. After a subsequent delay, an array of stimuli was flashed twice, and the animal signaled the detection of an orientation change in one of the stimuli by releasing the lever (or the absence of change by continuing to depress the lever). Critically, no eye movements were required, and breaks of central fixation were discarded from analyses. Recordings were made in FEF neurons whose movement fields encompassed the location of one of the stimuli. By reference to this group's earlier work (Moore and Fallah 2001; Moore and Fallah 2004), this is equivalent to saying that the "attention field" of the FEF neuron encompassed the location of one of the stimuli. The results indicated that cuing the location represented by an FEF neuron yielded sustained elevated activity across the cue-to-target delay, during the first flash, across the inter-flash-interval, and during the second flash. That this can be characterized as an *attentional* effect follows from the fact that behaviorally, change-detection performance benefitted from valid spatial cuing in the way that one would expect. That it can also be characterized as a *mnemonic* effect follows from the fact that the strength of the location-specific sustained activity, in the absence of visual stimulation, was predictive of performance on the task. By definition, then, the response fields of these neurons were shown to function as "memory fields" during portions of the trial when they represented regions of space in the absence of visual stimulation and in the absence of an overt motor plan. An overall conclusion from this experiment, then, which is consistent with a larger body of research not reviewed here (e.g., Sommer and Wurtz 2001), is that whether these cells support a motoric, an attentional, or a mnemonic function depends entirely on the behavioral and environmental circumstances of the moment. The same point has recently been demonstrated via a pattern classification-based decoding of fMRI data from the FEF of humans performing tasks of eye movements vs. visual attention vs. spatial working memory (Riggall et al. 2008). From this, one can conclude that the categorical distinctions implied by these labels are not be honored by the nervous system.

Oculomotor control and working memory

Of course, the neurons of the FEF that were the focus of the previous paragraph don't operate in isolation of the perception-action network in which they are located. Just one example of this is the fact that selective cooling of populations of neurons that show spatially tuned, sustained delay-period activity has comparably deleterious effects on delay-task performance whether the targeted tissue is in caudal PFC or in posterior parietal cortex (Chafee and Goldman-Rakic 2000). Indeed, similar response properties of neurons in these two regions (e.g., Chafee and Goldman-Rakic 1998), together with largely overlapping patterns of connectivity (Selemon and Goldman-Rakic 1988), makes it difficult to identify relative specialization of function of these two regions. Another region in the perception-action network whose function is less equivocal is the superior colliculus, the subcortical structure that constitutes the sole anatomical route to the muscles that control the position and movement of the eyes. The inferior layers of the superior colliculus are organized in a retinotopic saccade map that encodes current eye position and the location(s) of planned eye movements. As already summarized, the superior colliculus is anatomically and functionally connected with several cortical regions involved in visual perception, attention, working memory, and eye-movement control (Sommer and Wurtz 2001). A series of clever experiments by Theeuwes and colleagues has taken advantage of our understanding of this structure and its role in eye-movement control to demonstrate that "working memory is the same as programming an eye movement" (Theeuwes et al. 2009) (p. 110). For example, they have shown that remembering a location in space has the same deviating effect on eye movement trajectories as does the presence of a visual stimulus in that location (Theeuwes et al. 2005). Because this phenomenon has been linked to competitive interactions between represented locations in the superior colliculus (Sparks and Hartwich-Young 1989; Munoz and Istvan 1998), the implication is that the remembered location is represented in the superior colliculus as a suppressed saccade (i.e., as localized inhibition in the saccade map, Aizawa and Wurtz 1998). Theeuwes et al. (2009) hypothesize that a cortical control signal, perhaps from the FEF, inhibits a reflexive saccade to the remembered location, a hypothesis that is consistent with the difficulty that patients with FEF damage have in inhibiting reflexive eye movements (Pierrot-Deseilligny et al. 1991). The same mechanism of an "inhibitory tag", which is likely represented in parallel at several levels of the perception-action network, can account for the phenomenon of inhibition of return (IoR, Godjin and Theeuwes 2002) and in IoR-like phenomena observed during the STR of spatial information (Belopolsky and Theeuwes 2009). More generally, the dynamic interplay between the putatively visual, attentional, executive, and motoric elements of the perception-action network can also account for the benefits of responding to stimuli appearing at memorized locations (Awh et al. 1998), for the biasing of remembered locations in the direction of attention-capturing distractors (Van der Stigchel et al. 2007), and for interactions between working memory and visual search (Soto et al. 2005; Olivers et al. 2006; Soto et al. 2007).

This overview of the role of the perception-action network in many attentional, mnemonic, and motoric behaviors also accounts for the extensive literature on interactions between spatial working memory and several motor effector systems: Working memory for locations is selectively disrupted by concurrent finger tapping (Farmer et al. 1986; Smyth et al. 1988; Salway and Logie 1995), pointing (Hale et al. 1996), eye movements (Baddeley 1986; Hale et al. 1996; Lawrence et al. 2001; Pearson and Sahraie 2003; Postle et al. 2006), and arm movements (Baddeley and Lieberman 1980; Quinn and Ralston 1986; Logie and Marchetti 1991; Lawrence et al. 2001)). For example, Postle and Hamidi (2007) had subjects perform delayed recognition of either the identity or location of geometric shapes, and observed a selective pattern of disruption produced by nonvisual secondary tasks performed in the dark -- passive listening to nouns or endogenous generation of saccades, respectively. Event-related fMRI of this task indicated that the interference-specific effect corresponded to a relative increase of activity localized to regions associated with the secondary task in question: left hemisphere perisylvian cortex in the case of passive-listening distraction, and frontal oculomotor regions (the FEF and supplementary eye fields) in the case of saccadic distraction. Within these regions the neural interference effects were specific to voxels that showed delay-period activity on unfilled memory trials, and they predicted individual differences in the magnitude of the behavioral interference effect (Figure 2).

The dynamics of the perception-action network

To this point this chapter has considered the brain systems that support the STR of spatial information. We now turn to another level of analysis – task-related neural oscillations measured with EEG – to further explore the mechanistic bases of spatial working memory and related constructs. That is, what are the neural dynamics within the perception-action network that govern the balance between excitation and inhibition that was invoked earlier, and that implement the functions of attentional prioritization, motor preparation, and inhibition that can support the STR of spatial information?

Alpha-band oscillations and visuospatial cognition

The first-ever published report of human EEG data described the phenomenon of oscillations recorded by posterior electrodes, centered on a frequency of 10 Hz, whose magnitude increased when the eyes were closed and decreased when the eyes were opened (Berger 1929). Replications and extensions of this finding have led to the widely accepted view that posterior alpha-band oscillations correspond to an "idling" state of brain, with higher-frequency oscillations predominating (i.e., in the beta and gamma bands) when the same networks are engaged in, for example, active visual processing. More recently, important roles for alpha-band oscillations have been established in visual attention and stimulus detection. In one highly cited study by Worden and colleagues (2000), for example, EEG data collected from subjects performing a Posner (1980)-style cued-attention task indicated that the onset of the attentional cue triggered an increase in the power of alpha-band oscillations in the hemisphere ipsilateral to that cue. That is, the shifting of spatial attention to one visual field prompted an increase in the magnitude of alpha-band oscillations in the other, unattended, visual field. Subsequent work has confirmed and extended this finding, demonstrating both decreases in alpha-band power at attended locations and increases at unattended locations. By one recent account, for example, alpha-band oscillations serve to prioritize internally directed processing (e.g., mental imagery) by gating the sensory processing of stimuli in the environment (Cooper et al., 2003). By another, shifts of attention are associated with transient decreases in alpha-band power over the selected region, whereas the sustained maintenance of attention to that area is associated with a later-developing and sustained increase in alpha-band power over unattended regions (Rihs et al. 2009).

The functional significance of these shifts in posterior alpha-band power is seen in their association with cortical excitability and visual performance. Spontaneous fluctuations in occipital alpha-band power predict cortical excitability, as indexed by the perception of TMS-induced visual phosphenes (Romei et al. 2008). They also predict successful detection of at-threshold visual stimuli, with lower power associated with superior detection performance (e.g.,Hanslmayr et al. 2007; van Dijk et al. 2008; Mathewson et al. 2009). Further, visual performance is also sensitive to the instantaneous phase angle (i.e., position in the cycle) of the spontaneous posterior alpha-band oscillation at the time of stimulus presentation (e.g., Busch et al. 2009; Mathewson et al. 2009). A related finding is that application of transcranial alternating current to visual cortex evokes phosphenes in a frequency-dependent manner, with maximal effects centered on 10 Hz when delivered in darkness, and shifting to higher frequencies, but still encompassing the alpha-band, when delivered in light (Kanai et al., 2008). From these, and additional, findings, Thut and Miniussi (2009) induce that "local α-amplitude carries information about the momentary (excitability) state of neurons within the dorsal processing stream" (p. 185).

Alpha-band oscillations and control

Alpha-band oscillations have also been ascribed an important role in the control of cortical processing. Although high-frequency oscillations are associated with information processing in local cortical modules (e.g., Uhlhaas et al. 2009), lower-frequency oscillations, including in the alpha band, have been proposed as a means of implementing top-down control, including the coordination of processing between anatomically distal modules (e.g., von Stein et al. 2000; Palva et al. 2005). One reason for this is that the physics of wave propagation make lower-frequency oscillators better suited to influence larger areas of tissue (Buzsaki 2006). A mechanism by which this control might be accomplished is by the synchronization of local higher frequency oscillations to a more "global" alpha-band oscillation (i.e., cross-frequency phase synchrony, Palva and Palva 2007). Numerous studies, in several species, have demonstrated the behavioral relevance of such large-scale synchrony, with between-region oscillatory synchronization associated with, for example, attention, working memory, and conscious sensory perception (for reviews, see Palva and Palva 2007; Uhlhaas et al. 2009). The fine-grained physiological basis for this type of top-down control has been demonstrated by simultaneous multicellular recordings made from multiple brain areas. These studies indicate that alpha-band oscillations in infragranular layers of higher-level cortical areas (i.e., deep layers that send feedback projections to upstream cortical areas) act as pacemakers that control the dynamics of alpha-band oscillations in the lower-level areas that receive these feedback projections. (For example, alpha-band oscillations in infragranular layers of parietal cortex govern expectancy-related alpha-band oscillations in primary visual cortex of the cat (von Stein et al. 2000), and laminar differences in alpha-band dynamics between interotemporal (IT) cortex vs. occipital areas V4 and V2 suggests a substrate whereby the former might control the attentional states of the latter two (Bollimunta et al. 2008).)

Brain stimulation as a tool to study the role of alpha-band oscillations in visuospatial cognition

The previous section suggests a strategy for developing a priori tests of the functional contribution of neuronal oscillations in different frequency bands. We have already reviewed how one study has used transcranial alternating current stimulation to map out the frequency tuning of visual cortex, and analogous approaches have also been applied to the motor system (Pogosyan et al., 2009). In a study targeting visuospatial cognition, Klimesch and colleagues (2003) have used repetitive transcranial magnetic stimulation (rTMS) to build on earlier EEG findings that subjects with high pre-trial alpha-band power tended to show greater task-related drops in alpha-band power (a phenomenon known as "event-related desynchronization" (ERD)), and tended to be better performers on a wide variety of tasks (Neubauer et al. 1995; Klimesch 1999). Importantly, this phenomenon was specific to the upper alpha band, the 2-Hz of the EEG immediately above each subject's individual resting alpha frequency (IAF; IAF varies considerably among healthy individuals (Doppelmayr et al. 1998)). For this experiment they reasoned that they might improve performance on a mental rotation task by exogenously increasing the pre-trial power of oscillations in the upper alpha band with a conditioning train of rTMS delivered immediately prior to the visual presentation of stimuli. Consistent with their predictions, they found that a train of 24 pulses of TMS, delivered to frontal or to parietal cortex at a rate of IAF + 1 Hz (to target the upper alpha band), produced improved accuracy. The control conditions of 24-pulse trains delivered at IAF – 3 Hz (i.e., the lower alpha band) and at 20 Hz, in contrast, had no significant effects on performance. A second experiment indicated that, for both frontal and parietal cortex, rTMS delivered at IAF + 1 Hz was associated with a greater task-related ERD than was sham stimulation of the same areas (Klimesch et al. 2003). Although they didn't record the EEG during the delivery of rTMS, the authors speculated that the IAF + 1 result was produced by an rTMS-induced increase in pretrial power in the upper alpha band. (Another study, although not involving spatial processing, has demonstrated highly specific effects (midline parietal but not left dorsolateral prefrontal; delay period but not probe period; 5 Hz but not 1 Hz or 20 Hz) of rTMS on the STR of letters (Luber et al., 2007).)

The role of neuronal oscillations in the STR of location information

Early in this chapter is was suggested that the dynamic state of processing at different levels of the perception-action network will determine whether the behavior to which it gives rise will be attentional, motoric, or mnemonic. Subsequent sections established the importance of alpha-band oscillations in determining these dynamic states, and the immediately preceding section introduced a methodological approach for carrying out a priori tests of the functional relevance of oscillations. Here these threads come together in a set of studies establishing that alpha-band oscillations also play an important role in the STR of spatial information. In the initial study we applied 10 Hz rTMS to the intraparietal sulcus (IPS), the superior parietal lobule (SPL), the FEF, and the dorsolateral (dl)PFC during the delay period of a spatial delayed-recognition task (Hamidi et al. 2008). This frequency of rTMS, which corresponds to the alpha band of the EEG, had previously been effective at disrupting other targeted cognitive processes (e.g., Postle et al. 2006; Feredoes et al. 2007), and the results of this study, too, revealed a selective effect of delay-period rTMS of IPS, SPL, and FEF relative to dlPFC and a control area in the primary somatosensory cortex of the postcentral gyrus (PoCG). The direction of this effect, however, was the opposite of what we had predicted: rTMS of IPS, SPL, and FEF produced a selective *decrease* in RT, and no reliable effects on accuracy; that is, it produced improved performance (Hamidi et al. 2008). Although such behavioral facilitation effects are not without precedent (e.g., Walsh and Pascual-Leone 2003; Luber et al. 2007), we felt it important to follow up with a replication study in which we concurrently recorded the EEG, so as to get a better understanding of how rTMS had produced these effects.

The rTMS/EEG study, like an earlier fMRI study (Postle and Hamidi 2007), required the STR of either the locations or the identities of four serially presented shapes. On half the trials, unpredictably, a train of 10 Hz rTMS was delivered during the 3 sec of the delay period, either to the SPL or the PoCG control area. On $\text{rTMS}_{\text{absent}}$ trials, the delay period of both location and identity trials was characterized by sustained elevated power in the upper alpha band of the EEG (~10-13 Hz). rTMS produced nonspecific effects that were commonly observed when it was delivered to PoCG and/or during identity trials. In contrast, specific to location memory trials when rTMS was delivered to SPL, the magnitude and direction of the effect of rTMS on delay-period alpha-band power predicted the magnitude and direction of the effect of rTMS on behavior.

Specifically, the two were negatively correlated, such that rTMS-related increases in alpha-band power were accompanied by decreases in accuracy, and decreases in alpha-band power were accompanied by increases in accuracy (Fig. 3, Hamidi et al. 2009).

An additional result from this study, which also fits with the computational considerations spelled out earlier in this chapter, is that rTMS of SPL also influenced alpha:gamma phase synchrony in a task-specific manner, such that rTMS-related increases of 1:4 phase synchrony (i.e., 10 Hz:40 Hz) predicted improved performance on location trials and impaired performance on identity trials. (This effect was independent of the relationship between delay-period alpha-band power and performance.)

An important point to make about all of the results from the Hamidi et al. (2009) study is that they can not be discounted as somehow "atypical" or not representative of how the brain normally functions because they may have resulted from imposing on the brain an exogenous oscillatory regime that is not typical of its normal functioning. Rather, they clearly reflect a biasing of the endogenous pattern of task-related oscillations. Indeed, a head-to-head comparison of these rTMS data with EEG data in which 10 Hz visual flicker was delivered during the delay period clearly illustrates that the latter produces much stronger entrainment of posterior neural systems than does the former (Johnson et al., 2010). Thus the results from this study indicate that, as is the case for visuospatial perception and attention, oscillations in the alpha band have a functional role for the STR of spatial information.[1]

Toward a unified account of visuospatial cognition.

In the first half of this chapter we have seen how the dynamic interplay of elements in the perception-action network gives rise to such nominally varied behaviors as visual attention, oculomotor control, and the STR of spatial information. The second half of the chapter suggests *how* this dynamic interplay may be controlled: It may be that alpha-band oscillatory dynamics, and their interactions with other frequency bands, control the tuning and output of the perception-action network. Although there is a solid theoretical basis for this model (Palva and Palva 2007), its critical evaluation will require that several outstanding question be addressed. Many of these question either require, or lend themselves to, the combined rTMS-EEG method:

- *Will the pattern of individual differences of the effects of 10 Hz rTMS on delayed-recognition (Hamidi et al., 2009) generalize to non-memory tasks, such as tests of the endogenous and exogenous control of attention, of oculomotor control, and of visual target detection?* (E.g., will someone whose spatial working memory performance improves with 10 Hz rTMS to the SPL also show improvements on these other tasks?)
- *What factors account for the individual differences in the effect of 10 Hz rTMS on alpha-band power and on behavior (Hamidi et al. 2009)?*
- *Once these factors are understood, will varying them systematically as parameters in an rTMS study lead to predictable improvement and impairment of performance within individual subjects?*

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[1] Note that oscillatory dynamics in other frequency bands have also been implicated in working memory function, as well as in other domains of cognition (e.g., Siegel et al., 2009; Jensen et al., 2007). Because these do not relate directly to spatial working memory, however, they will not be considered in this chapter.

- *How do the effects of rTMS differ as a function of whether it is delivered prior to or during a task?* (Note that this is of interest, because whereas Klimesch et al. (2003) assumed that pretrial rTMS entrained cortical oscillations to the stimulation frequency, our data suggest that delay-period rTMS does not entrain the EEG to its driving frequency, but, rather, modulates the gain of components of the endogenous, behaviorally related EEG (Johnson et al. 2010).)

Addressing these questions will constitute modest steps toward answering the ambitious question that has been the focus of this chapter: How does spatial working memory work?

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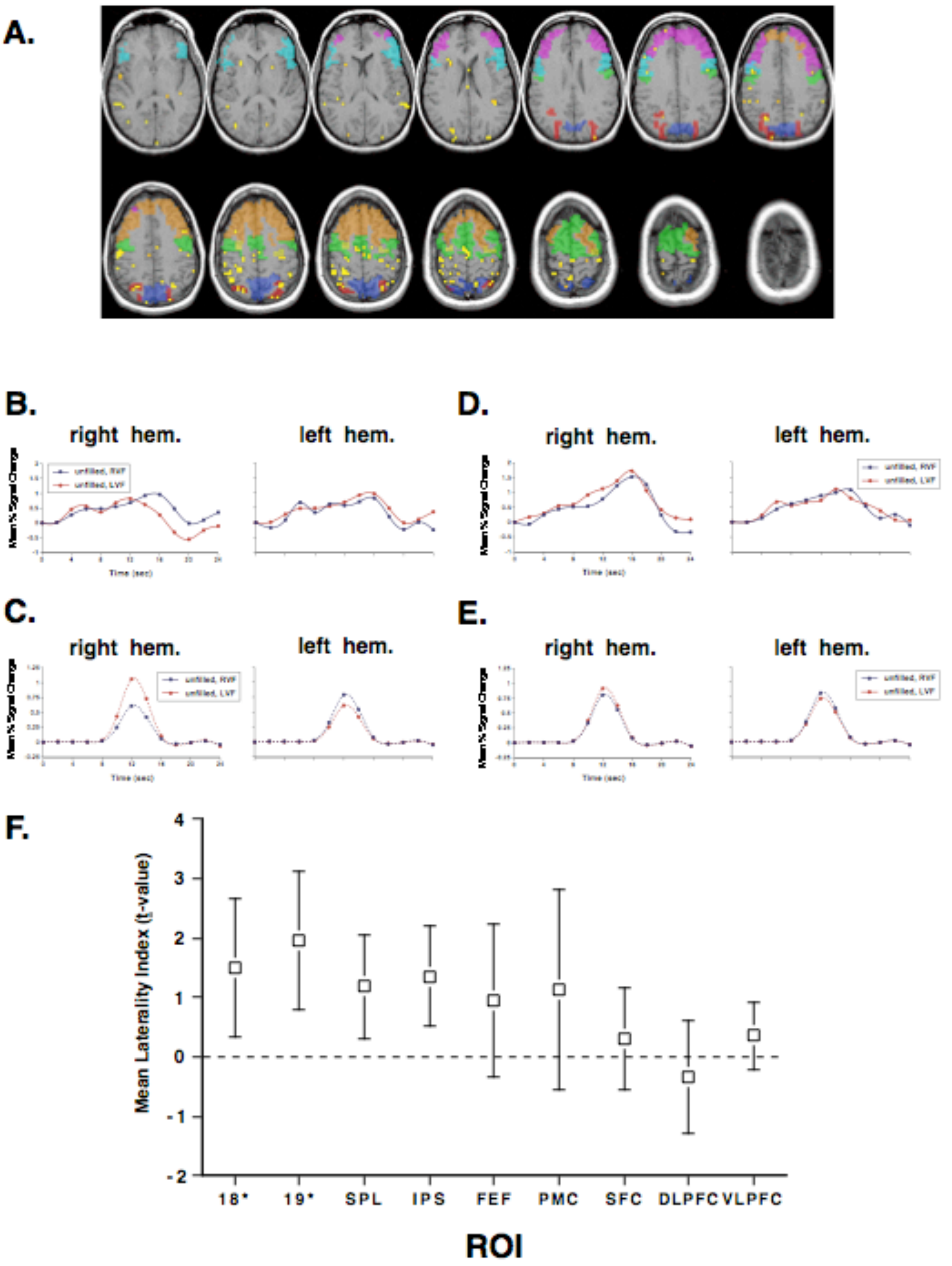
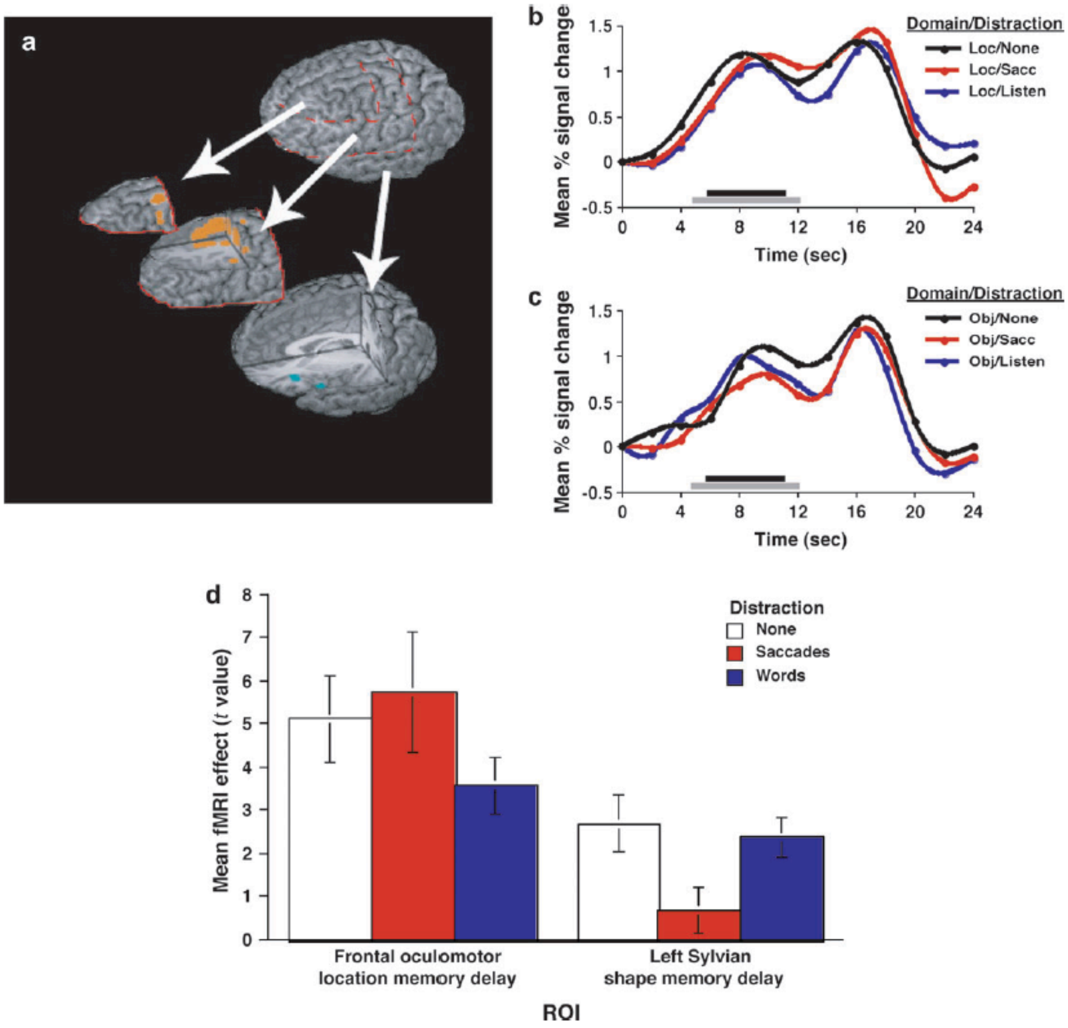
Figure Legends

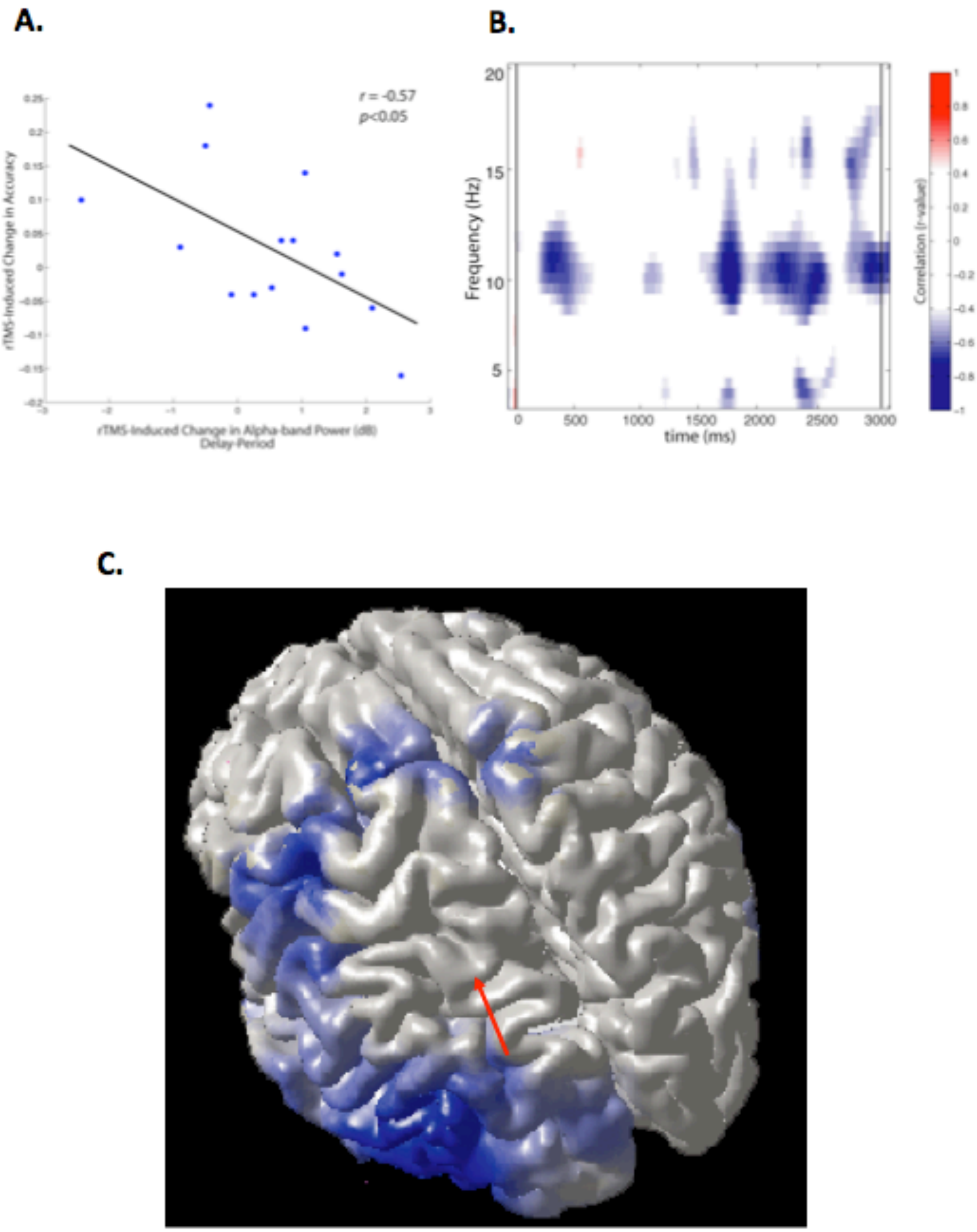
Figure 1. Results from Postle et al. (2004). (A) illustrates the delay-evoked ROIs in a representative participant. Structural ROIs are identified by translucent colors—SPL (dark blue), IPS (red), PMC (green), FEF (red), SFC (orange), DLPFC (fuchsia), VLPFC (light blue)—are overlaid by delay responsive voxels, which appear yellow and orange. (B) illustrates that, at the group level (mean and 95% confidence interval), the laterality of delay-period activity was significantly biased in favor of the hemisphere contralateral to the remembered location (quantified by a laterality index that was significantly different from 0 in extrastriate BAs 18 and 19, and in IPS and SPL, but not in any of the frontal cortical ROIs). These results suggest that attention-based rehearsal is supported by the type of "baseline shift" that is often observed in studies of sustained attention. (C) illustrates trial-averaged fMRI data from unfilled trials for the two hemispheres of the SPL delay-evoked ROI of the participant illustrated in (A). (D) illustrates quantitatively the delay effects (delay-epoch covariates scaled by their parameter estimates) estimated by the GLM from the data illustrated in (C). (E) illustrates trial-averaged fMRI data from unfilled trials for the two hemispheres of the IPS delay-evoked ROI of this same participant. (F) illustrates quantitatively the delay effects (delay-epoch covariates scaled by their parameter estimates) estimated by the GLM from the data illustrated in (E).

Figure 2. Results from Postle and Hamidi (2007).
a. Loci of memory-delay responses in the *no distraction* conditions for location (orange) and object (green) memoranda, in a single subject (#9). The top-left cutout features activity in the FEF and the SEF; the bottom-right cutout in the left Sylvian fissure.
b. Trial averaged time series from the location memory-delay voxels in panel a. Gray line along horizontal axis indicates duration of delay period; black line indicates duration of secondary-task period.
c. Trial averaged time series from the object memory-delay voxels in panel a.
d. Group data from frontal oculomotor location memory-delay and left Sylvian shape memory-delay ROIs, illustrating a region by secondary-task interaction. This neural double dissociation mirrors the behavioral effects, and illustrates that interference-specific neural effects are anatomically specific.

Figure 3. Results from Hamidi et al. (2009).
A. Plot showing individual differences in the effect of rTMS of SPL on delay-period alpha-band power and performance.
B. Time-frequency plot of *r* values during the 3 sec of the delay period, thresholded to show the time points during which delay period activity correlated significantly with behavior. In this plot the beginning of the delay period is labeled “0” msec and the end of the delay period “3000” mesc.
C. Source localization of the regions carrying the correlation illustrated in A. and B. These included a large region of cortex extending from the left inferior parietal lobule, along the intraparietal sulcus (BA 39) to the left extrastriate cortex (BA 18), a region covering the left precentral sulcus (BA 6) and superior frontal gyrus, which included the putative FEF, as well as a region in the right medial temporal lobe corresponding to the hippocampus (not shown). The red arrow indicate the region of SPL targeted with rTMS.


A.
B.
right hem.
left hem.
Mean % Signal Change
Time (sec)
unfilled, RVF
unfilled, LVF
C.
right hem.
left hem.
Mean % Signal Change
Time (sec)
unfilled, RVF
unfilled, LVF
D.
right hem.
left hem.
Mean % Signal Change
Time (sec)
unfilled, RVF
unfilled, LVF
E.
right hem.
left hem.
Mean % Signal Change
Time (sec)
unfilled, RVF
unfilled, LVF
F.
Mean Laterality Index (t-value)
4
3
2
1
0
-1
-2
18*
19*
SPL
IPS
FEF
PMC
SFC
DLPFC
VLPFC
ROI


a
b
Mean % signal change
1.5
1
0.5
0
-0.5
0
4
8
12
16
20
24
Time (sec)
Domain/Distraction
Loc/None
Loc/Sacc
Loc/Listen
c
Mean % signal change
1.5
1
0.5
0
-0.5
0
4
8
12
16
20
24
Time (sec)
Domain/Distraction
Obj/None
Obj/Sacc
Obj/Listen
d
Mean fMRI effect (t value)
8
7
6
5
4
3
2
1
0
Distraction
None
Saccades
Words
Frontal oculomotor location memory delay
Left Sylvian shape memory delay
ROI


A.
r = -0.57
p<0.05
rTMS-Induced Change in Accuracy
0.25
0.2
0.15
0.1
0.05
0
-0.05
-0.1
-0.15
-0.2
-3
-2
-1
0
1
2
3
rTMS-Induced Change in Alpha-band Power (dB)
Delay-Period
B.
Frequency (Hz)
20
15
10
5
0
500
1000
1500
2000
2500
3000
time (ms)
Correlation (r-value)
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
C.