

A stimulating take on attention

Spearman Medal winner **Chris Chambers** looks at what human brain stimulation can tell us

Put a copper coil against the scalp, pass a current through it and the magnetic field produced temporarily interferes with the normal functioning of neurons in the cortex below. By measuring the behavioural consequences of this transcranial magnetic stimulation (TMS), we can infer which brain regions are required for specific behaviours, and when.

In recent years, studies using this technique have yielded some unique and unexpected insights into the cognitive neuroscience of attention. This article outlines this research, addressing questions such as whether disrupting normal functioning with TMS can actually facilitate attention, and whether there is a 'Fat Controller' at work in our brains.

questions

Which brain regions are necessary for attention in the healthy human brain, and when are they crucial in the timecourse of stimulus processing?

Do different neural mechanisms control attention to different stimulus properties (such as location or colour) and to different sensory modalities (such as vision, hearing or touch)?

resources

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Chambers, C.D. & Mattingley, J.B. (2005). Neurodisruption of selective attention: Insights and implications. *Trends in Cognitive Sciences*, 9, 542–0550.

The world is rich with information. Even as you read this sentence, your senses are being bombarded with a cacophony of stimuli – most of which you will never notice. If you could spend a moment in the 'life' of a stimulus, it may seem a gruelling existence. After passing through the peripheral receptors, you would encounter an immense traffic-jam of competing stimuli, each fighting desperately for neural representation. But the bottleneck is tight, and the likelihood that you are important for behaviour is slim. Even as your neighbours struggle to subdue you, higher-level brain systems would sweep through the ranks, culling the great majority of stimuli with ruthless efficiency. Within a fraction of a second, most of your rivals will have fallen, leaving little trace of their presence. As your competitors diminish, the odds on your own survival improve. It may be that you are a particularly bright or loud stimulus, or that you are the target of a deliberate search (such as a word on this page). For whatever reason, if you are one of the chosen few, then a gate will open to brain systems that control perception and action. You will become 'attended', gaining access to a level of neural representation that is forbidden to all but the most behaviourally important events.

Life for most stimuli might be unenviable, but life without attention would be virtually impossible. For more than a century, psychologists have puzzled over the question of how attention works. Many influential theories have been proposed, some describing the role of attention in binding together different

stimulus features (e.g. shape/colour/motion: Treisman and Gelade, 1980), and others likening spatial selection to a spotlight (Posner, 1980) or zoom lens (Eriksen & St James, 1986).

In the last 20 years, neurophysiology and cognitive neuroscience have provided a biological framework for these theories, emphasising the role of attention in determining the outcome of sensory competition (Duncan et al., 1997). Using neuroimaging methods such as functional magnetic resonance imaging (MRI) and electroencephalography (EEG), much has been discovered about the neural networks that are activated – and modulated – by attention (Corbetta & Shulman, 2002; Hillyard & Anllo-Vento, 1998; Kastner & Ungerleider, 2000). More recently, brain stimulation studies in humans have yielded some unique and unexpected insights into the neurobiology of selection. This article focuses, in particular, on recent advances in the cognitive neuroscience of attention using the technique of transcranial magnetic stimulation (TMS).

Understanding the where and when of attention in the brain

During TMS, an electric current is passed through an encased copper coil that is placed against the surface of the scalp. The current in the coil produces a transient magnetic field, which in turn induces an electric field in a discrete area of the underlying brain tissue. This electric field activates neurons in the cortex, thus interfering temporarily with their normal function. By measuring the behavioural consequences of TMS, we can infer which brain regions are required for specific behaviours. This logic contrasts with neuroimaging methods, which instead tell us which brain regions are *active* during behaviour, but which cannot reveal whether such activity is necessary.

One key contribution of TMS to cognitive neuroscience has been to establish not only *which* brain areas are crucial for behaviour, but also *when* a particular region is required. Psychological

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studies have provided an important guide to the timecourse of attention, showing that the selection process generally requires less than half a second. Evidence from EEG studies further suggests that selection may require at least two periods of cortical processing: an initial 'feedforward' wave of sensory activity, followed by a later 'feedback' sweep from attentional gatekeepers in the parietal and frontal cortex (Martinez, 1999; Noesselt et al., 2002). Some investigators have further proposed that such feedback is crucial for determining which stimuli enter conscious awareness (Lamme & Roelfsema, 2000).

Since a single TMS pulse generally has a very transient effect on brain activity, comparing the consequences of TMS at different onset times can reveal the timecourse of cortical involvement (Amassian et al., 1989). Using single-pulse TMS, previous studies have revealed an important role of the parietal cortex in attention over a range of times after the appearance of a visual stimulus, with some results suggesting a relatively early role (<150ms: Ashbridge et al., 1997) while other evidence points to later processing (>350ms: Müri et al., 2002).

In one of our first TMS studies (Chambers, Payne et al., 2004), we wondered whether there may be multiple periods of attentional control in the parietal lobe, or whether this broad range instead reflects statistical variance between studies. Using single-pulse TMS, we stimulated the angular gyrus (a subdivision of the inferior parietal cortex) at one of many possible times while participants shifted their attention in space. The results revealed a surprising 'twin' timecourse, in which TMS of the angular gyrus disrupted shifts of attention either early (90-120ms) or late (210-240ms) after the target appeared.

Why should there be two periods of attentional processing in the parietal cortex? One possibility is that attention integrates visual sensory inputs that arrive in the angular gyrus at different times. Alternatively, the different periods may reflect separate processes involved in

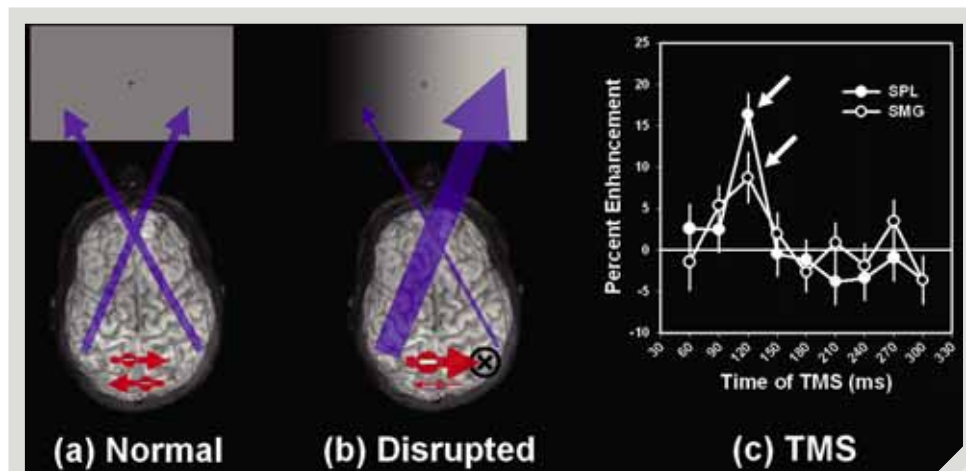


Figure 1. Attention and the cerebral hemispheres

Attention involves competition not only between stimuli, but also between cerebral hemispheres. In the normal healthy brain (a), the parietal cortices mutually inhibit one another. This relationship ensures a relatively balanced distribution of attention across the visual field, with each hemisphere controlling the selection of information on the opposite side. Following stroke (b), many patients suffer lesions to the right parietal lobe (indicated by the cross). This damage can lead to pathological inattention of the left visual field (thin blue arrow) and an attentional bias toward the right (thick blue arrow).

This deficit has been suggested to arise from disruption of the normal interhemispheric equilibrium. In particular, inhibitory signals from the damaged right hemisphere are weakened, leading to disinhibition (hyperactivity) of the left parietal cortex and a rightward attentional bias. Furthermore, the hyperactive left parietal cortex inhibits any remaining intact regions in the right hemisphere, exacerbating leftward neglect.

This pathological condition can be simulated mildly with TMS, especially when healthy participants are required to judge a target stimulus in the right visual field that occurs simultaneously with a distractor on the left (Hilgetag et al., 2001; Pascual-Leone et al., 1994). In this example (c), TMS was applied to the supramarginal gyrus (SMG) or superior parietal lobule (SPL) of the right hemisphere (Chambers et al., 2006), both of which are commonly damaged following stroke. The results revealed a remarkable enhancement of attention in the right visual field when stimulation was applied 120ms after target onset. This facilitation of performance provides evidence that rapid competition between hemispheres is crucial for normal spatial attention.

releasing attention from one location and then engaging it elsewhere. Finally, these different phases might indicate separate feedforward and feedback sweeps through the visual system. A key aim of our ongoing TMS studies is to determine which of these possibilities applies, thus understanding how selection unfolds in the brain over time.

Can stimulating the brain enhance attention?

It may seem reasonable to assume that the disruption of normal brain activity with TMS should generally impair, rather than improve, behaviour. Remarkably, however, TMS in normal participants can sometimes facilitate attention (Chambers

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et al., 2006; Hilgetag et al., 2001; Seyal et al., 1995). At first glance such results seem paradoxical, for how could interfering with a function possibly improve it? In this case, the answer appears to lie in the delicate balance of attentional control between left and right cerebral hemispheres.

Neurologists and neuropsychologists have long known that stroke patients who have suffered parietal brain damage are likely to show attentional deficits (Driver & Mattingley, 1998). Many such patients present with lesions to the right hemisphere, and exhibit a pathological

gradient of attention towards the right visual field (or hemifield). This syndrome, termed unilateral neglect, occurs in the absence of primary sensory loss, and is believed to arise from disruption of normal inhibitory interactions that operate between the left and right parietal lobes (Kinsbourne, 1977; Figure 1a, b). Following damage to the right parietal cortex, the left hemisphere becomes 'disinhibited', causing a rightward attentional bias and a leftward inattention.

For several decades, unilateral neglect has been regarded as supportive evidence for the role of interhemispheric inhibition

in spatial attention. Nevertheless, studies in brain-damaged patients seem to tell us only part of the story. In particular, if interhemispheric inhibition is indeed crucial for attention, then right parietal damage should not only cause left neglect, but should also boost attentional selection above normal levels in the right visual field. Such evidence, however, has proven lacking (Snow & Mattingley, 2006), possibly due to the effects of additional non-specific deficits that accompany brain damage.

The use of TMS in healthy subjects has helped to complete this missing link by

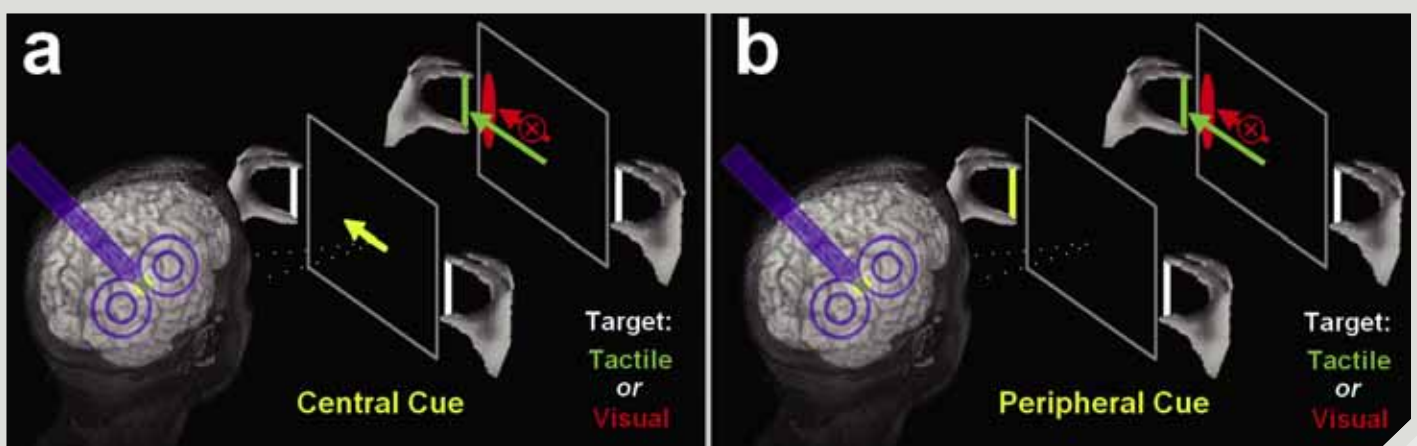


Figure 2. Putting the 'Fat Controller' hypothesis to the test

If a common neural mechanism controls spatial attention in different senses, then the attentional interference caused by TMS in one sensory modality (e.g. vision) should always occur simultaneously with effects in other modalities (e.g. touch, hearing).

In this experiment (Chambers, Stokes et al., 2004), a central arrow cue (yellow) told participants on which side of the computer screen a target stimulus was likely to occur. Whilst maintaining their gaze centrally, participants made a perceptual decision about the target, which was presented in vision (red) or in touch (green). To test whether the parietal cortex is required for spatial attention in multiple modalities, TMS was applied during the cue stimulus to the right supramarginal gyrus. Crucially, TMS impaired the ability to orient attention strategically to visual targets (red cross), but not to tactile targets that occurred in the same location (green). Parietal stimulation thus 'decoupled' visual and tactile spatial attention, which should not be possible if a single mechanism controls both senses.

More recently (Chambers et al., 2007), we applied the same TMS protocol, but this time participants ignored an initial tactile cue (yellow). Here, parietal stimulation reduced the involuntary shift of attention between the tactile cue and visual target (red cross), while once again having no effect on perception of the tactile target (green).

Taken together, these studies provide clear evidence against the existence of a single Fat Controller. Instead, attention in different senses appears to be controlled by multiple gatekeepers that are anatomically separate but functionally linked.

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revealing the effects of parietal stimulation on competitive interactions between stimuli in opposite visual fields (Chambers et al., 2006; Hilgetag et al., 2001; see Figure 1c). These experiments have shown that TMS of the right parietal cortex can indeed facilitate the selection of stimuli in the right hemifield. Furthermore, such benefits can be fast, occurring within 130ms of stimulus onset (Chambers et al., 2006). Considered alongside unilateral neglect, these observations suggest that parietal interference tips the delicate balance of attention between the hemispheres, causing an involuntary 'over-attention' to the right side of space.

Multiple gatekeepers or a single 'Fat Controller'?

An emerging question in the cognitive neuroscience of attention concerns the functional specificity of control. To what extent does a common neural mechanism determine the selection of different stimulus characteristics, such as location, colour or shape? Is there a global system that operates across the sensory modalities of vision, hearing and touch? In other words, is there a 'Fat Controller' in the parietal or frontal lobe that oversees all aspects of attentional control?

If a Fat Controller did exist, it could provide a parsimonious account of how attention binds together an attended object and all of its features (Duncan et al., 1997). Interestingly, observations from human neuroimaging studies have provided some evidence of such a mechanism. When allocating attention to different stimulus dimensions, such as location or colour, we see a remarkably similar pattern of activity in frontal and parietal areas (Giesbrecht et al., 2003; Slagter et al., 2007). Furthermore, functional MRI and EEG studies have found that orienting spatial attention in vision, hearing or touch produces largely indistinguishable patterns of activity in the parietal and temporal lobe, leading some investigators to conclude that attention is controlled by a 'supramodal' system (Eimer

& van Velzen, 2002; Macaluso et al., 2002).

Behavioural evidence, however, has raised doubts about the commonality of attentional control. On the one hand, psychological studies could be said to support a global mechanism by showing that spatial attention cannot be fully divided between different sensory modalities: When a cue predicts the location of a target in just one modality (e.g. vision), attention is nevertheless oriented in multiple modalities (e.g. vision and touch; Spence & Driver, 1996; Spence et al., 2000). But, importantly, attention shifts tend to be much stronger in the 'primary' modality, implying a degree of separation between the senses.

These seemingly conflicting results highlight an important caveat of neuroimaging methods. Do common patterns of brain activity (as observed through EEG or fMRI) necessarily indicate common cognitive processes? In the case of multisensory attention, might overlapping activity in vision and touch instead reflect the coordinated activation of modality-specific systems? Consider, for instance, the scenario in which areas 1, 2, 3 and 4 are brought 'online' during visual or tactile attention. According to the Fat Controller hypothesis, all of this activity would be required for orienting in both modalities. Alternatively, however, some of the activity may reflect the mutual activation of modality-specific systems, even if only one modality is required in a particular situation. Thus, areas 1 and 2 may be uniquely visual, while areas 3 and 4 may be uniquely tactile. These explanations are indistinguishable because brain imaging cannot tell us which activations are necessary for visual or tactile attention.

Using TMS, it is possible to apply a more direct test of this hypothesis (Figure 2). If a common neural mechanism orients attention in different senses, then the same

control regions in the parietal lobe should be necessary for spatial selection in vision and touch. However, as shown in Figure 2, this is not the case: at least some parietal regions appear to be uniquely specialised for orienting attention to visual stimuli (Chambers et al., 2007; Chambers, Stokes et al., 2004). It thus seems clear that spatial attention is coordinated by a series of modality-specific 'gatekeepers', rather than a single Fat Controller.

Future directions

The use of TMS in cognitive neuroscience has revealed novel insights into the neural basis of attentional control. This article has considered just a few of these:

- | that there are at least two critical periods underlying attentional control in the parietal cortex;
- | that mutual inhibition between the hemispheres is important for maintaining an even distribution of attention across space; and
- | that while the psychological concept of attention may appear singular, it nevertheless arises from a series of distinct neural processes.

What does tomorrow hold for attention research in cognitive neuroscience? One key development is the combination of TMS with neuroimaging methods such as fMRI (Ruff et al., 2006) and EEG (Fugetta et al., 2006). In our lab, we have begun to combine TMS with fMRI to determine simultaneously the effects of parietal stimulation on attention and the neural representation of stimuli in the visual cortex. The hope is that this combination of techniques will enable us to gain new insights into the role of 'top down' signals from parietal to visual cortex, and between higher-level regions in opposite hemispheres.

More generally, the future will depend on a happy marriage between an increasingly advanced set of neuroscience methods and a well-established body of behavioural paradigms from experimental psychology. It is this unique bridging of disciplines that places cognitive neuroscience at the forefront in linking the biology and psychology of human attention.

"Is there a global system that operates across sensory modalities?"

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