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### Large-scale Networks for Attentional Biases

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The Oxford Handbook of Attention

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#### Abstract and Keywords

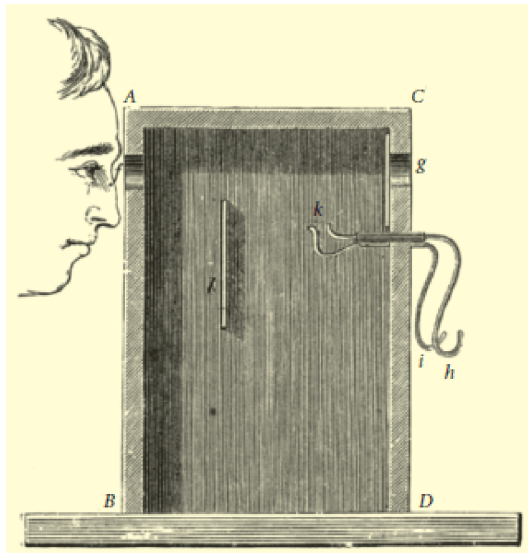
Selective attention is essential for all aspects of cognition. Using the paradigmatic case of visual spatial attention, we present a theoretical account proposing the flexible control of attention through coordinated activity across a large-scale network of brain areas. It reviews evidence supporting top-down control of visual spatial attention by a distributed network, and describes principles emerging from a network approach. Stepping beyond the paradigm of visual spatial attention, we consider attentional control mechanisms more broadly. The chapter suggests that top-down biasing mechanisms originate from multiple *sources* and can be of several *types*, carrying information about receptive-field properties such as spatial locations or features of items; but also carrying information about properties that are not easily mapped onto receptive fields, such as the meanings or timings of items. The chapter considers how selective biases can operate on multiple slates of information processing, not restricted to the immediate sensory-motor stream, but also operating within internalized, short-term and long-term memory representations. Selective attention appears to be a general property of information processing systems rather than an independent domain within our cognitive make-up.

Keywords: spatial attention, networks, top-down bias, information processing, memory

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THE core concept of ‘attention’ is a fundamental principle of cognition—the adaptive and proactive selectivity of our interface with the surrounding environment. Contrary to our intuition, we do not apprehend the complete and continuous stream of events unfolding around us. Instead, at any given moment we sample a handful of details that happen to be relevant or interesting within our current context and motivational state. Attention refers to the set of mechanisms that tune psychological and neural processing in order to identify and select the relevant events against all the competing distractions. This type of definition casts attention as function rather than as representation or as state. It is about orienting, focusing, and selecting.

#### Some History



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*Figure 5.1* Apparatus built by Helmholtz to investigate the scope of perception while avoiding ocular movements. A drawing was fastened (at position g) to the back of a hollow box painted black inside. The observer maintained fixation on a small hole pierced in the drawing that was visible at all times. The image was illuminated by making contact between two electrical wires (i and h), triggering a spark illuminating the drawing. A white piece of cardboard (l) protected the observer's eye while also reflecting the light from the spark onto the drawing. 'The sparks were produced by a large Ruhmkorff induction coil connected with the terminals of a Leyden jar. The contact in the primary coil was made or broken by hand' Reproduced from von Helmholtz, *Treatise on Physiological Optics, Volume III*, figure 32 © 2005, Dover Publications.

Some of the earliest known empirical studies of selective attention were by Herman von Helmholtz (1867). He built an apparatus akin to a tachistoscope, which could illuminate a display containing several letters for a fraction of a second (Fig. 5.1). Using it, he confronted the severe limitations in our perceptual abilities, noting that it was impossible to view all the letters simultaneously in a single glance. He then demonstrated our ability to orient attention to specific spatial locations at will, while still maintaining visual fixation on a single point. By orienting attention covertly to different locations of the array in turn, over multiple iterations, he could reconstitute the entire array. Summarizing early seminal experimental work and using introspective methods, William James (1890) provided insightful and lucid descriptions of varieties, effects, and mechanisms of attention, which remain rich and contemporary. According to James, attention is a pervasive faculty that shapes conscious experience: 'My experience is what I agree to attend to' (James 1890/1950: 403). At any given moment, the span of consciousness is limited to a single object or thought, attended to reflexively or voluntarily, due to immediate (intrinsic) or derived (associated) relevance. Focusing attention by anticipatory preparation (p. 106) using ideational centres concerned with the object to which the attention is paid results in adjustments in sense organs so that objects (or ideas of objects) are better perceived, conceived, distinguished, remembered, or more readily reacted to (James 1890/1950).

The early twentieth century witnessed a polarization of psychology between the psychoanalysts, who overemphasized the power of mental phenomena, and the behaviourists, who discredited it. The empirical study of attention regained a more balanced approach in the 1950s, when it became incorporated in the emerging 'information-processing' paradigm. Starting from the premise that our information-processing abilities are severely limited, the initial major experimental questions addressed the locus of the bottleneck. Experimental tasks were developed to test the consequences of focusing versus dividing attention in the presence of two or more competing streams (Cherry 1953). Opposing categorical views were put forward, which placed the information-processing limits at extremes of the information-processing stream: at very early, perceptual stages (Broadbent 1958) versus at late post-perceptual stages following semantic evaluation of stimuli (Deutsch (p. 107) and Deutsch 1963). The evidence was inconclusive in arbitrating between 'early selection' and 'late selection' theories, showing that it was possible to focus effectively on one stream of information based on physical characteristics of stimuli so that competing distractors generally did not reach awareness (compatible with early selection), but that high-level semantic or associative features of the unattended stream could nevertheless influence behaviour and occasionally break through into awareness (compatible with late selection; Treisman

1960) (for further discussion of this debate see Serences and Kastner (in chapter 4), this volume). A cogent theoretical model incorporating elements of both early and late selection was proposed by Anne Treisman (1960, 1969), in which modulatory mechanisms operating at perceptual levels attenuate processing of irrelevant material rather than blocking it completely, and in which stimulus representations have different thresholds of activation depending on their personal significance, conditional probability, or other contextual constraints (Treisman 1960). Nilli Lavie's 'perceptual-load theory' is another, contemporary hybrid model, which holds that a perceptual bottleneck only occurs when the perceptual demands of a task are high (Lavie 1995), see Lavie and Dalton (in chapter 3), this volume).

The present-day scene of attention research opens around the 1970s and 1980s as spectacular technological advances enabled increasingly sophisticated anatomical and functional brain studies in humans and non-human primates. The classical questions about the locus of capacity limitations quickly became obsolete, replaced by the clear realization that modulatory mechanisms operate at multiple levels of analysis in a distributed fashion in the brain (Nobre 2004; Nobre et al. 2011). Current research is directed toward characterizing the control and modulatory mechanisms of attention at the levels of individual neurons, neural systems, and large-scale networks. Orienting visual spatial attention according to task goals is the most widely investigated and, therefore, the most well understood paradigm.

### Scope of the Chapter

The main focus of this chapter is to consider the mechanisms of attentional control, with particular emphasis on the process of top-down signals biasing information processing. Starting from the paradigmatic case of visual spatial attention, we will present a theoretical account suggesting that attention is controlled by a large-scale 'frontoparietal' network of brain areas that combines representational mapping of physically salient and relevant events, motor programs for intended actions, and motivational factors. We will summarize some principles emerging from a network approach to the control of attention. We will review evidence refining the characterization of the functional anatomy of the network, and supporting its critical role in modulating information processing.

Stepping outside the well-trodden terrain of visual spatial attention, we reflect on the scope of attentional control mechanisms more broadly. We examine the various possible (p. 108) 'sources' of biases that can prepare perceptual mechanisms to improve interactions with the environment. In addition to the recognized effects of task goals, we entertain other possible potent modulators of ongoing information processing, such as long-term memories and motivational factors associated with anticipated events. We move on to consider the different 'types' of biases that can operate upon information processing. Whereas studies in the literature have probed how biases can facilitate neural processing according to receptive-field properties of neurons, it is clear that it is possible to anticipate stimulus properties that may not be easily mapped onto receptive fields, such as the timing of events or the meaning of words. Finally, we show that attention can act upon multiple 'slates' of information processing. We thus return to an old conception put forward by William James (1890) that attention is not restricted to operate upon objects from the sensory stream, but can also prioritize and select objects of thought. We describe a new body of work showing how attentional biases can act within representations maintained in visual short-term memory. To conclude, we discuss how this plurality of sources, types, and slates for attentional biases invites a reconsideration of the conceptualization of attention.

### Modulatory Biases

One of the more influential theoretical models for modulatory mechanisms of attention is the 'biased competition model' (Desimone and Duncan 1995). According to this model, the limits of perception arise because of the inherently competitive organization of perceptual systems. Through the visual hierarchy, convergence of inputs from afferent areas leads to increasingly complex receptive-field properties with increasingly lower spatial and temporal resolution. At downstream areas, such as in inferior temporal (IT) cortex, multiple objects or attributes can fall within the receptive field of the same neuron. Averaging the response across all the stimuli impinging on the receptive field would conflate the coding of the various stimuli and abolish discriminability. To be informative, the neuron should respond according to one of the multiple competing stimulus sources. To be adaptive, the neuron should respond according to the most relevant stimulus source.

One of the primary functions of attention is to set preparatory *biases* to influence the competitive interaction among multiple inputs in favour of the most behaviourally relevant stimulus. Biasing competitive interactions in this way facilitates selection of the attributes of relevant objects, and filtering out of irrelevant attributes, across populations of neurons. Interactions among neurons with spatially and temporally correlated activity further aid co-selection and integration of the features of the relevant objects (Desimone and Duncan 1995). Thus, as a corollary, such biasing signals are likely to play a major role in solving the difficult 'binding problem', by helping to reconstitute features of relevant events that may come to occupy awareness (Reynolds and Desimone 1999). (p. 109)

Our understanding of the cellular mechanisms for biasing neuronal activity, selecting target-related attributes, and integrating them into objects to guide awareness and action remains incomplete, but progress in this area is impressive, and several pieces of the puzzle are coming into view. Competitive interactions among neurons have been well described (Reynolds et al. 1999), as well as the influence of spatial (Moran and Desimone 1985), object-based (Chelazzi et al. 1993, 1998), and feature-based (Treue and Martinez Trujillo 1999) attention in resolving competitive interactions within multiple brain areas. For detailed accounts of the mechanisms being characterized, the reader is directed to the many excellent contemporary reviews of this literature (Reynolds and Chelazzi 2004). Although most experiments have concentrated on visual areas, there is clear evidence that analogous biasing mechanisms operate across sensory areas in other modalities (Mehta et al. 2000), as well as in motor (Cisek 2007; Pastor-Bernier and Cisek 2011) regions of the brain. The findings, therefore, argue against fixed points of limited capacity, and indicate instead that selective biasing mechanisms operate at multiple stages. Furthermore, the sites and temporal characteristics of modulatory mechanisms are likely to be highly task-dependent, and to be influenced by the specific types of features that need to be discriminated and the number of competing response tendencies that need to be handled for accurate task performance (Stokes et al. 2009) (for an early articulation of this flexible proposal see Kahneman and Treisman 1984).

### Control Mechanisms

What are the sources of these modulatory biases that play such a fundamental role in guiding perception and action? One generally accepted distinction is that between 'exogenous' and 'endogenous' shifts of attention. These are also referred to as 'reflexive' or 'automatic' and 'voluntary' or 'effortful' respectively. The distinction dates back at least to James, who separated passive/reflexive/non-voluntary/effortless from active/voluntary attention (James 1890/1950).

In exogenous shifts, physically salient stimuli attract attention. Biases are set 'bottom-up' by sensory-driven mechanisms that prioritize neural processing of events rendered conspicuous by virtue of their higher stimulus energy or local contrast (e.g. bigger, brighter, or faster) (Yantis and Jonides 1984; see Theeuwes (in chapter 8), this volume). These stimuli have acquired an edge through the evolution of our perceptual systems, and carry their own intrinsic biases to the competitive perceptual mechanisms. Their dominance can be considered a natural consequence of competitive interactions among unequal stimuli. Interestingly, however, these perceptually salient stimuli also leave a modulatory trail. They 'prime' their location, facilitating detection and discrimination of other events occurring at the same location over very brief intervals (Posner 1978, 1980). Unless the location turns out to be relevant or informative, the transient facilitation is subsequently replaced by suppression, thus freeing the system to explore other locations (Posner and Cohen 1984; Klein 2000; Chica et al. 2006; Lupiañez 2010). (p. 110)

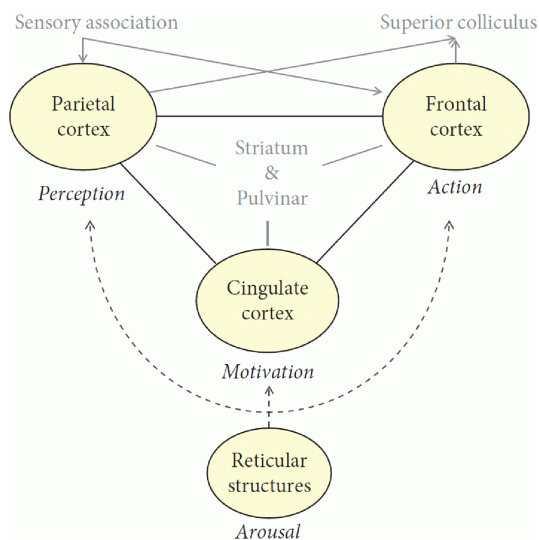
In endogenous shifts, focus is directed voluntarily to a location of choice. Biases operate 'top-down', driven by endogenous (mental) factors computed in high-level, associative areas, and influencing perceptual processing through feedback connections. Different scholars have emphasized different mechanisms of regulation for top-down biases. The biased-competition model proposes that top-down biasing signals are primarily mediated through working-memory representations of task-relevant items (Desimone and Duncan 1995). The alternative 'premotor theory' of attention emphasizes the role of motor intention, and proposes that computations in the oculomotor, as well as other sensorimotor systems, modulate perceptual analysis through feedback connections (Rizzolatti et al. 1987; Rizzolatti and Craighero 1998). Mesulam suggested a broader conceptualization, in which sensory, representational; motor, exploratory; and limbic, motivational biases combine to direct spatial attention through the action of a large-scale frontoparieto-cingulate attentional network (Mesulam 1981, 1990, 1999).

## Large-scale Network for Attention

### Original description

Everyone now agrees that the control of spatial attention depends on a large-scale network of brain areas. The first network model for attention was proposed by Mesulam in 1981, and subsequently refined and extended over the years (Mesulam 1990, 1999, 2005). The original proposed network architecture was based on clinical observations of patients with hemispatial neglect as well as on multiple sources of convergent data in non-human primates (Fig. 5.2). Four sets of brain areas, three cortical and one subcortical, constituted major nodes, each introducing a different functional specialization so that spatial attention emerged as a property of the network as a whole.

In the macaque, the three cortical nodes of this network were located in the dorsolateral portion of the inferior parietal lobule and lateral bank of the intraparietal sulcus (LIP) (area PG of von Bonin and Bailey, 7a of Brodmann), frontal eye fields (FEF) (area 8 of Brodmann), and the cingulate gyrus (areas 23–24 of Brodmann and the retrosplenial cortex). Anatomical tracer studies had shown these nodes to be monosynaptically interconnected (Mesulam et al. 1977). The parietal node was proposed to provide a multisensory perceptual map of the extrapersonal space weighted by physical salience and relevance of stimuli. The frontal node provided a hub for motor integration, which contained representations of motor programs for the distribution of exploratory actions. The cingulate node acted as a region for integration of limbic signals, assigning motivational relevance to events based on previous experience and current needs. Experimental lesions to any of these cortical nodes resulted in attention-related deficits akin to neglect (Bianchi 1895; Kennard 1939; Denny-Brown and Chambers 1958; Welch and Stuteville 1958; Heilman et al. 1970; Cowey and Latto 1971; Watson et al. (p. 111)



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Figure 5.2 Large-scale network for orienting visual spatial attention proposed by Mesulam (1981, 1990, 1999, 2005). Parietal, frontal, and cingulate cortices are the three primary cortical nodes. These act as local hubs for organizing and integrating signals related to perception, exploratory action, and motivation, respectively. The three cortical nodes are directly interconnected with one another, and are additionally interconnected through participating subcortical hubs in the striatum and the pulvinar nucleus of the thalamus. In addition to their intrinsic connections, the cortical and subcortical nodes also have connections to other areas with specialized sensory, limbic, and motor functions. The main nodes of the large-scale network each also receive modulatory reticular input from brainstem nuclei.

1973) and single-unit recordings showed modulation of neuronal activity by the relevance of the stimulus and nature of orienting responses it elicited (Hyvarinen and Poranen 1974; Mountcastle et al. 1975; Lynch et al. 1977; Bushnell et al. 1981). Each of these interconnected nodes had its own pattern of connections with functionally related areas, such as sensory association areas in the case of the parietal cortex, motor and premotor regions in the case of frontal eye fields, and other limbic nuclei in the case of the cingulate cortex. In addition, all three areas receive reticular input from a common set of thalamic, basal forebrain, and brainstem nuclei (see Mesulam 1990). These subcortical inputs comprised the fourth functional node of the network, and were proposed to play a central role in regulating the state of arousal, which underpins and interacts strongly with the selective control of spatial

attention (Hecaen et al. 1956). Brainstem reticular lesions have long been known to cause severe deficits in arousal and awareness, and lesions of the intralaminar thalamic nucleus in monkeys have been observed to result in neglect (Watson et al. 1974, 1978).

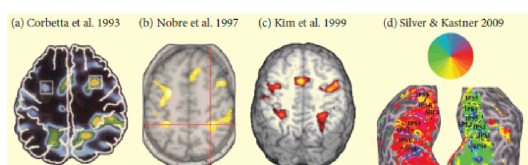
The network approach is intermediary to centrist approaches, in which complex functions are supported by exclusively dedicated brain areas (Spurzheim 1825), and (p. 112) holistic approaches, in which complex functions are equipotentially distributed across areas (Lashley 1950). It has several noteworthy properties. According to the large-scale network approach, individual cognitive domains are enabled through the interaction of interconnected areas, each with a relative specialization for a component function of that domain. Having a network of areas supporting a complex function means that impairments can arise from different lesion sites. The network also provides some protective compensatory mechanisms, so that severe and lasting impairments may not arise unless multiple nodes are damaged. The presence of multiple nodes with distinct functional specializations can also help explain the variety of deficits that arise from lesions to the different nodes, their interconnections, or their connections to other regions (see Geschwind 1965a, 1965b).

The interactions among the areas in an integrated system can blur the categorical distinctions between the functional specializations contributed by the different nodes. For example, the distinction between sensory and motor contributions across parietal and frontal nodes in the attention network was considered to be relative, with sensory and motor functions observable in each of these areas. Such a proposal, of course, is perfectly acceptable nowadays with our growing exposure to the sensory properties of neurons in the motor system, as in mirror neurons (di Pellegrino et al. 1992), and to increasing proposals of action-based active sensing mechanisms in perceptual systems (Fortuyn 1979; Schroeder et al. 2010).

Another feature of the large-scale network model is that brain areas with a given functional specialization need not be exclusively dedicated to one network. Conceivably, the same physiological specialization could underlie multiple complex functions. For example, similar neuronal profiles in posterior parietal cortex have been implicated in spatial attention, oculomotor control (Colby and Duhamel 1996; Snyder et al. 2000; Bisley and Goldberg 2010), decision-making (Leon and Shadlen 1998; Gold and Shadlen 2007; Gould et al. 2012), working memory (LaBar et al. 1999; Todd and Marois 2004; Buschman et al. 2011), and long-term memory (Wagner et al. 2005; Cabeza et al. 2008). The nodes of large-scale networks also add flexibility by acting as portals of interactions with other brain areas so as to integrate attention control with other complex functions, such as language, working memory, and long-term memory.

### Imaging the attentional network

Over subsequent years, the large-scale model of attention was amply vindicated. Refinements to the model came from continued characterization of neglect symptoms and their dissociations, and from increasing knowledge about physiological properties and connectivity of brain areas (Mesulam 1990, 1999; Mesulam et al. 2005). The development of positron-emission tomography (PET), and then functional magnetic-resonance imaging (fMRI) methods, introduced a wealth of new information on the attentional network. Non-invasive brain imaging enabled the testing and extending of the network model, by mapping its constituent critical nodes and revealing areas that participate without being critical to spatial orienting. The core cortical parietal, frontal, and cingulate nodes were recognized to comprise functional mosaics of multiple areas with distinct but interrelated (p. 113) contributions to representational, intentional, and motivational functions. Other, highly related cortical areas for attention were also proposed to participate in some spatial attention functions, such as in the medial parietal cortex, supplementary eye fields (SEF), premotor areas in the case of orienting attention to near space, dorsolateral prefrontal cortex (BA 46), and possibly parts of temporal cortex. Also stressed was the role of subcortical areas, in particular the superior colliculus, striatum, and pulvinar nucleus of the thalamus (see also Saalmann and Kastner (in chapter 14), this volume).



*Click to view larger*

*Figure 5.3* Imaging the cortical areas involved in the control of visual spatial attention with increasing resolution. All images are from an axial perspective with the posterior part of the brain on the bottom and the right hemisphere on the right. (a) The seminal study by Corbetta et al. (1993) used positron emission tomography (PET) and relied on patterns of activation across a small group of participants. Data from Corbetta, M., Miezin, F. M., Shulman, G. L. and Petersen, S. E., A PET study of visuospatial attention. *Journal of Neuroscience*, 13, pp. 1202–26 © 2003, Society for Neuroscience. (b) Nobre et al. (1997) used PET to image the network in individual participants as well as in groups. It became possible to localize cortical activations to the intraparietal sulcus, frontal eye fields, and anterior cingulate cortices. Data from Nobre, A. C., Sebestyen, G. N., Gitelman, D. R., Mesulam, M. M., Frackowiak, R. S. and Frith, C. D., Functional localization of the system for visuospatial attention using positron emission tomography, *Brain*, 120 (Pt 3), pp. 515–33 © 1997, Oxford University Press. (c) Functional magnetic-resonance imaging greatly increased the functional anatomical resolution for investigating the spatial attention networks in groups and individuals in tasks with much greater experimental control. The example illustrated is from the study by Kim et al. (1999), showing the overlap in brain areas activated by voluntary/endogenous spatial orienting based on informative central cues and by automatic/exogenous spatial orienting based on non-informative peripheral cues. Data from Kim, Y. H., Gitelman, D. R., Nobre, A. C., Parrish, T. B., LaBar, K. S. and Mesulam, M. M., The large-scale neural network for spatial attention displays multifunctional overlap but differential asymmetry. *Neuroimage*, 9 (3), 269–77 © 1999, Elsevier. (d) By adapting procedures for retinotopic mapping to produce spatiotopic maps, it has become possible to subdivide the nodes of the spatial attention networks into multiple constituent functional regions. The example shows the subdivision of posterior parietal cortex into multiple functional regions with spatial specificity. Reproduced from Silver, M. A. and Kastner, S., Topographic maps in human frontal and parietal cortex, *Trends in Cognitive Sciences*, 13 (11), 488–95, © 2009, Elsevier.

The first visualization of the network for controlling spatial attention in the human brain came from studies using PET using an adaptation of Posner's visuospatial orienting task over a group of participants (Corbetta et al. 1993, 1995) (Fig. 5.3). We extended (p. 114) this work with the first functional anatomical characterization of the human 'frontoparietal network' using PET at the individual-subject level, which strongly supported Mesulam's model (Nobre et al. 1997). Three cortical areas were implicated in orienting spatial attention: posterior parietal cortex, straddling the intraparietal sulcus; dorsal premotor/posterior prefrontal cortex (in both lateral and medial Brodmann area 6); and anterior cingulate cortex (Brodmann area 24). We replicated these sites of activation with greater spatial resolution in an fMRI study using single-subject analyses and stringent behavioural controls (Gitelman et al. 1999). Studies investigating activity of spatial cues in isolation, separately from processing of subsequent targets, have verified that multiple brain areas participate in controlling spatial attention (Kastner et al. 1999; Corbetta et al. 2000; Hopfinger et al. 2000; Nobre et al. 2004; Woldorff et al. 2004).

By now, activation around the intraparietal sulcus and in dorsal premotor/prefrontal areas has been replicated by dozens of spatial attention imaging studies across labs worldwide (Vandenberghe et al. 1996; Fink et al. 1997; Kim et al. 1999; Hopfinger et al. 2000; Kastner and Ungerleider 2000; Corbetta and Shulman 2002; Giesbrecht et al. 2003; Pollmann et al. 2003; Woldorff et al. 2004; Molenberghs et al. 2007). Involvement of cingulate cortex in top-down regulation of behaviour according to motivational factors has also been convincingly demonstrated (Isomura and Takada 2004; Rushworth et al. 2007, 2011; Liu et al. 2011; Wallis and Kennerley 2011), and specifically noted in tasks involving spatial attention (Mesulam et al. 2001; Small et al. 2003, 2005; Dean et al. 2004; Mohanty et al. 2008; Kaping et al. 2011). Successive imaging studies have achieved increasing spatial and functional characterization of the mosaic of parietal and frontal cortical areas, as well as of the subcortical areas involved (e.g. Vandenberghe et al. 2001; O'Connor et al. 2002; Astafiev et al. 2004; Kastner et al. 2007; Kelley et al. 2008; Konen and Kastner 2008; Molenberghs et al. 2008; Silver and Kastner 2009; Szczepanski et al. 2010; Saalman and Kastner 2011; Serences 2011; Scolaro et al. 2012).

### Relationship between visuospatial attention and oculomotor control

In our original PET study (Nobre et al. 1997), the parietal and frontal areas were noted to resemble those highlighted by imaging studies of oculomotor control (Melamed and Larsen 1979; Fox et al. 1985; Petit et al. 1993; Anderson et al. 1994; Darby et al. 1996; Paus 1996), and were proposed to include the human homologues of macaque lateral intraparietal area (LIP), frontal eye fields (FEF), and supplementary eye fields (SEF). The strong functional interrelationship between visuospatial orienting and oculomotor control had been, and continues to be, suggested by a number of behavioural (Allport 1987; Sheliga et al. 1994) and neurophysiological (e.g. Colby and Duhamel 1996; Snyder et al. 1997, 1998; Gottlieb et al. 1998; Kusunoki et al. 2000) studies (see Deubel (in chapter 30), this volume). Human imaging studies comparing activations during spatial orienting of attention in the absence of eye (p. 115) movements (covert attention) and saccade generation confirmed a high degree of overlap in

activated brain areas (Corbetta et al. 1998; Rosen et al. 1999; Nobre et al. 2000a; Perry and Zeki 2000; Van der Stigchel et al. 2006). Contemporary research continues to explore the nature and degree of functional and neural overlap between eye movements and attention, as well as the mechanisms which enable the two functions to be dissociated during covert attention (e.g. Juan et al. 2004; Cohen et al. 2009; Khan et al. 2009; Lawrence and Snyder 2009; Bisley and Goldberg 2010; see also Deubel (in chapter 30), this volume, Theeuwes (in chapter 8), this volume; Gottlieb and Balan 2010; Wardak et al. 2011; Belopolsky and Theeuwes 2012; Gregoriou et al. 2012). Although oculomotor circuits may play a primary role in the network for spatial attention, studies have suggested that other sensorimotor circuits, specialized for different forms of spatially guided action (e.g. reaching or pointing movements), also display similar attentional modulations (e.g. Snyder et al. 1997, 1998; Astafiev et al. 2003; Van Der Werf et al. 2010; Deubel (in chapter 30), this volume).

### Endogenous versus exogenous spatial orienting

The different characteristics of endogenous versus exogenous spatial shifts of attention (see Posner 1978, 1980; Posner et al. 1982, 1984; Müller and Rabbitt 1989; Friedrich et al. 1998; Losier and Klein 2001; Berger et al. 2005; Sieroff et al. 2007; Lakatos et al. 2008; Wright and Ward 2008; Chica et al. 2013) have led to numerous brain-imaging studies comparing the neural systems involved in these two types of orienting.

Initial studies used blocked designs to contrast experimental conditions with high versus low requirement for voluntary orienting under well controlled stimulus conditions (Nobre et al. 1997), or to contrast conditions using symbolic cues that predict subsequent target location versus non-predictive transient peripheral cues (Kim et al. 1999; Koski et al. 1999; Rosen et al. 1999; Peelen et al. 2004). Surprisingly, the patterns of activations in endogenous and exogenous conditions reported were very similar, and consistent with engagement of the dorsal frontoparietal network in both cases (see Fig. 5.3c). These studies therefore suggested that endogenous and exogenous shifts of attention rely on the same general network of brain areas (Posner 1978; Jonides and Irwin 1981; Yantis 1998), though they could be supported by different dynamics and mechanisms within a common network.

In contrast to these findings and interpretations, Corbetta and colleagues proposed that different circuits supported endogenous versus exogenous orienting of spatial attention (Corbetta et al. 2000; Corbetta and Shulman 2002). They proposed that the dorsal frontoparietal network mediated voluntary, endogenous shifts of spatial attention; whereas a ventral network, comprising the temporal parietal junction (including supramarginal gyrus and superior temporal gyrus) and inferior frontal gyrus, mediated reflexive, exogenous shifts. Their proposal was based on the different patterns of activations triggered by spatial cues versus subsequent targets in event-related fMRI tasks. In agreement with the previous literature (Kastner et al. 1999), spatial cues activated dorsal parietal and premotor/prefrontal cortices. Targets, on the other hand, engaged a (p. 116) more widespread network of areas, including the temporal parietal junction and inferior frontal gyrus, in addition to dorsal frontoparietal areas. Furthermore, the ventral parietal and frontal regions responded more strongly to targets that had been invalidly cued, appearing at unexpected locations. Corbetta and colleagues reasoned that unexpected (e.g. invalidly cued) targets trigger predominantly exogenous shifts of attention to their location, and do more so when voluntary attention had been directed somewhere else by the preceding cue. Their findings, but even more so their interpretations, led to their influential subdivision of attention into two functionally distinct 'dorsal' and 'ventral' attention networks (shortened to DAN and VAN respectively) (Corbetta and Shulman 2002).

The strict correspondence of the ventral network to exogenous orienting, however, could be challenged. The account does not explain the consistent similarity of cortical activation patterns between blocked endogenous versus exogenous attentional shifts (Kim et al. 1999; Koski et al. 1999; Rosen et al. 1999; Peelen et al. 2004). Furthermore, comparing the processing of unexpected targets to informative cues is not the same as comparing exogenous to endogenous orienting. The appearance of an invalidly cued target may trigger disengagement of attention from its previous site and a reflexive shift toward its location, but it may also engage a number of other processes: e.g. signalling a mismatch between current expectations about stimulus contingencies to direct action, updating learning of stimulus contingencies, switching stimulus-response associations between expected and novel patterns, as well as the motivational and emotional factors of violated expectations (see Nobre et al. 1999). The conceptualization of the 'ventral attention network' therefore conflates various putative factors that are not restricted to the control of attention (for further discussion on the 'VAN', see also Beck and Kastner (in chapter 9),



this volume).

The conditions in which ventral parietal and frontal areas become activated have become better characterized through careful subsequent experiments. Findings argue clearly against the hypothesis that ventral frontoparietal regions play a special role in directing exogenous shifts of attention (Kincade et al. 2005). Using an ingenious and well controlled design, Corbetta's group compared activations triggered by predictive central cues versus non-predictive peripheral cues, as well as by validly versus invalidly cued targets in the endogenous and exogenous cueing contexts (Kincade et al. 2005). As expected, endogenous spatial cues activated the dorsal frontoparietal network. Contrary to their predictions, however, exogenous cues did not activate either dorsal or ventral frontoparietal areas. Valid and invalid targets in both endogenous and exogenous cueing conditions activated both dorsal and ventral frontoparietal regions. Furthermore, higher activation for invalid targets compared to valid targets only occurred in endogenous cueing conditions, when spatial expectations were breached. These occurred in some of the dorsal (e.g. FEF) as well as ventral (e.g. supramarginal gyrus) regions. Targets at an invalid location after a non-informative cue did not recruit frontoparietal areas (for related results see Peelen et al. 2004; Natale et al. 2009). Additional experiments have also shown that irrelevant salient events fail to engage frontoparietal areas; only task-relevant target events, or distractors sharing target features, occurring at (p. 117) unattended or unpredicted locations engage ventral parietal and frontal regions (Serences et al. 2005; Indovina and Macaluso 2007; Serences and Yantis 2007).

Taken as a whole, the evidence shows that the 'ventral attention network' is a misnomer. Ventral parietal and frontal areas do not participate directly in shifting attention exogenously or in resetting attentional weights. These areas are not engaged by stimuli that trigger exogenous shifts of spatial attention, such as transient non-informative cues. Instead, they are activated by the appearance of imperative target stimuli (or distractor stimuli sharing target features), which require decisions or responses; and their activation is enhanced when target appearance is unexpected. Elucidating the precise functional roles these areas play will require continued experimentation. Though the functions are likely to interact closely with the control of attention in spatial orienting tasks, they should not be construed as spatial attention functions in their own right. Many possibilities remain, such as functions related to motivational or emotional responses to breaches in expectation, sensory prediction-error signals, and/or updating representations of stimulus contingencies relevant to behaviour. Dropping the misleading nomenclature is an important first step in achieving clarity and making progress in understanding the nature of and interrelationship among the various types of control functions.

### Temporal dynamics within the attention network

The high degree of interaction among nodes of the frontoparietal network has been fully supported by studies of functional connectivity in humans and macaques. The similarity in functional profiles of areas like FEF and LIP has long been noted (e.g. Chafee and Goldman-Rakic 1998), and indeed it is difficult to distinguish them other than in a relative way (e.g. Lawrence and Snyder 2009; Muggleton et al. 2011; Wardak et al. 2011). During tasks requiring spatial attention, correlations have been noted to increase among network areas (e.g. Buchel and Friston 1997; Gitelman et al. 2002; Buschman and Miller 2007; Vincent et al. 2008; Ozaki 2011; Vossel et al. 2012).

A key question in this field concerns the identity of the prime mover in shifting the focus of spatial attention. Given the high degree of proposed interaction and coordination across the nodes of the large-scale network for attention, it is unlikely that a clear and consistent temporal hierarchy of contributions can be identified. Hemodynamic imaging methods lack the resolution to measure timing differences at the scale necessary to resolve a sequence of events across the network of attention. Studies using event-related potentials show that lateralization of cortical activity triggered by predictive spatial cues starts posteriorly, suggestive of a parietal origin, and then progresses anteriorly, suggestive of frontal engagement (Harter et al. 1989; Hopf and Mangun 2000; Nobre et al. 2000b; but see van Velzen and Eimer 2003; Praamstra et al. 2005; Murray et al. 2011). A similar posterior-to-anterior progression is observed in non-lateralized brain activity triggered by cues that instruct a shift of spatial attention versus maintenance of attention at the same locations (Talsma et al. 2005, 2011; (p. 118) Brignani et al. 2009), though spatial shifts compared to a cued rest period elicit a different pattern (Grent-'t-Jong and Woldorff 2007). Stepping back, it is important to realize that the sequence of effects within the attention network may largely depend on what triggers a spatial shift—an instructional cue, a working-memory representation of an anticipated target, or a salient perceptual event. Buschman and Miller (2007) neatly demonstrated this context dependency of

the temporal hierarchy among spatial attention control areas. Recording simultaneously from different brain areas in the macaque, they showed that LIP was the first to signal a target within a search array when it popped out based on sensory features; but that FEF and lateral prefrontal areas took the lead when target detection required effortful matching of the target to a template held in working memory.

### Interactions between the attention network and visual areas

The large-scale network for spatial attention—bringing together perceptual representations, intentions, and motivations—is proposed to act as the main source of spatial biases to prioritize the selection and integration of relevant events during the competitive processing in visual, and other sensory areas (Hopfinger et al. 2000; Kastner and Ungerleider 2000; Mendenorp et al. 2011). Single-unit and local field-potential recordings taken from multiple brain regions simultaneously in macaques show task-related correlations between visual areas and FEF and LIP (Buschman and Miller 2007; Saalman et al. 2007; Gregoriou et al. 2009). In humans, analyses of functional interactions among brain areas using fMRI (Buckel and Friston 1997; Gillebert et al. 2012) or MEG (Siegel et al. 2008) also show enhanced coupling between frontoparietal nodes and visual areas with attention. Strong confirmation that frontal and parietal areas play a causal role in modulating excitability of visual neurons has come from studies using interference methods to change activity in FEF or posterior parietal areas while simultaneously measuring visual activity. Pioneering studies by Moore and colleagues showed that microstimulation of FEF neurons led to changes in the firing rate of V4 neurons with compatible receptive fields, and improved visual discriminability of targets therein (Moore and Armstrong 2003; Moore and Fallah 2004; Armstrong et al. 2006; Armstrong and Moore 2007). In humans, studies using transcranial magnetic stimulation (TMS) to FEF or posterior parietal areas while simultaneously measuring visual activity using fMRI or EEG have confirmed that frontal and parietal areas play a causal role in modulating visual excitability (e.g. Paus et al. 1997; Ruff et al. 2006, 2008; Taylor et al. 2007; Capotosto et al. 2009; Blankenburg et al. 2010; Driver et al. 2010).

These studies provide convincing evidence that the frontoparietal network acts as a source of top-down signals to influence perceptual analysis at sensory sites. Future work combining interference and correlational methods should help describe differences in the types and timings of top-down influences originating from different areas within the (p. 119) large-scale attention network. It will be equally important to test for alterations in visual excitability in patients who have sustained focal cortical lesions to different functional regions within posterior parietal, frontal, and cingulate areas (see Knight et al. 1980; Woods and Knight 1986; Woods et al. 1993; Vandenberghe et al. 2012).

### The network for visuospatial attention and hemispatial neglect

Neglect, a neurological syndrome of disrupted spatial attention, is often associated with parietal lesions (Brain 1941; Vallar and Bolognini (in chapter 33), this volume), but can also occur after frontal, temporal, thalamic, or striatal damage (Karnath et al. 2002; Husain and Rorden 2003). This multiplicity of neglect-causing lesion sites is incorporated into the large-scale network model of spatial attention (Mesulam 1981, 1999). However, the fit between the location of neglect-causing lesions in neurological patients and of areas activated by attentional tasks in healthy subjects is far from perfect. Human brain-imaging studies of visuospatial attention have implicated parietal areas around the middle segment of the intraparietal sulcus (Nobre et al. 1997, 2003, 2004; Kastner and Ungerleider 2000; Nobre 2000; Corbetta and Shulman 2002; Giesbrecht et al. 2003; Woldorff et al. 2004), in the posterior segment of the intraparietal sulcus (Vandenberghe et al. 1997, 2005; Silver and Kastner 2009), and in the superior parietal lobule (Vandenberghe et al. 2001; Yantis et al. 2002; Molenberghs et al. 2007; Serences and Yantis 2007). In contrast, ‘parietal’ lesions, which are the most common cause for neglect, occur at more inferior locations such as the angular gyrus (Vallar and Perani 1986; Hillis et al. 2005; Verdon et al. 2010; Vossel et al. 2011), supramarginal gyrus (Committeri et al. 2007; Golay et al. 2008), the temporal–parietal junction (Driver and Vuilleumier 2001), or the posterior superior temporal gyrus (Karnath et al. 2001; Hillis et al. 2005; Verdon et al. 2010).

This potential mismatch can be partially resolved by considering that neglect is caused by lesions disconnecting the communication between network nodes or between the network and input and output areas (see Geschwind 1965a, 1965b; Gaffan and Hornak 1997; Thiebaut de Schotten et al. 2005; Bartolomeo et al. 2007). Studies using diffusion-tensor imaging methods to measure damage of white matter tracts in patients with and without neglect

symptoms have confirmed that structural damage to the superior longitudinal fasciculus (SLF), linking parietal and frontal nodes of the attention network, contributes significantly in determining the occurrence of persistent neglect symptoms (Doricchi and Tomaiuolo 2003; Doricchi et al. 2008; Urbanski et al. 2008, 2011; Ciaraffa et al. 2013). In a similar vein, it has also been proposed that effective lesions exert their influence remotely (Corbetta et al. 2005; He et al. 2007; Corbetta and Shulman 2011).

Whereas it is easy to imagine how differences in the prevalence of certain brain lesions, consequences of disconnection, and remote effects could have led to the current picture of clinic-pathological associations, it remains important to verify whether lesions to the areas implicated in spatial attention functions by imaging and neurophysiology studies (p. 120) impair spatial attention. An early study testing patients with parietal lesions in a simple spatial orienting task suggested a role for dorsal parietal cortex in orienting attention to a spatially unpredicted stimulus (Posner et al. 1984, 1987), but methods were not available at the time to perform accurate lesion localization. A subsequent study using the same experimental task but improved lesion localization separated a group of fifteen patients according to whether they had lesions to the temporal-parietal junction including the superior temporal gyrus, or lesions involving the parietal but not the superior temporal region (Friedrich et al. 1998). Extinction-like spatial orienting deficits were specific to patients in the temporal-parietal junction group. These data have been very influential in framing the thinking about the critical parietal areas for mediating shifts of attention. However, as recently pointed out by Vandenberghe and colleagues (2012), the patient groupings in the study by Friedrich and colleagues (1998) were potentially misleading in titrating the contributions of superior parietal versus inferior parietotemporal areas.

In a series of elegant and methodologically rigorous studies, Vandenberghe's group has investigated the effects of focal parietal lesions that spare white matter on visuospatial orienting functions. They used an adaptation of the Posner spatial orienting task in which unilateral targets appear at correctly spatially cued positions most of the time. On remaining trials, unilateral targets appear at the non-cued side, requiring reorienting of spatial attention; or bilateral targets appear, requiring filtering of the irrelevant item. In initial group studies, they showed that lesion overlap included inferior parietal, temporal-parietal, and intraparietal regions (Molenberghs et al. 2008; Gillebert et al. 2011). When locations of effective lesions were compared to brain activations in a group of control participants performing the same task, there was clear overlap between lesion and activation sites in the intraparietal sulcus (Molenberghs et al. 2008). In order to test whether intraparietal lesions alone can disrupt spatial orienting, studies were carried out on individual patients with rare, small, circumscribed lesions (Gillebert et al. 2011). A lesion to the left posterior intraparietal cortex resulted in large deficits to detect contralesional targets when these were invalidly cued or accompanied by an ipsilesional distractor. A lesion confined to the right middle intraparietal area showed a similar pattern of effects, though with a more distributed reorienting deficit to both contralesional and ipsilesional targets. Functional MRI measures of these patients showed no abnormalities in the activity of more inferior parietal regions, ruling out explanations based on remote effects of the dorsal lesions. A patient with a small bilateral lesion of the medial wall of the SPL was described separately (Vandenberghe et al. 2012). In this case large bilateral deficits in reorienting attention, but no deficits in filtering were observed. Corroborating results came from a study correlating different types of spatial attention deficits with location of lesion using a region-of-interest approach in twenty neglect patients (Ptak and Schnider 2011). Though the maximum lesion overlap was in the temporal-parietal junction, spatial orienting effects were more strongly associated with damage to the intraparietal sulcus. Studies such as these raise caution about overrating centres of lesion overlap, which may primarily reflect vascular variables rather than any measure of the brain-behaviour relationships of interest.

This rigorous experimental approach involving combined behavioural and imaging measurements in patients with focal and informative lesions, and comparison of (p. 121) results to those obtained on healthy volunteers, is redressing the apparent inconsistency between the neuropsychological and imaging literatures. Future work of this kind should continue to add clarity and important insights to the study of spatial attention.

### Lateralization in lesion and imaging studies

Clinico-pathological observations of patients with neglect suggest that the network for spatial attention displays a strong right-hemisphere dominance (Heilman and Van Den Abell 1980; Mesulam 1981; Weintraub and Mesulam 1987). Neglect is much more frequent and severe following right-hemisphere lesions in humans (Mesulam 1981; Weintraub and Mesulam 1987), an asymmetry which is not observed in non-human primates. Mesulam (1981)

proposed a model by which each hemisphere controlled attention toward the contralateral hemispace, but in which the right hemisphere dedicated more synaptic space to attentional functions and additionally controlled attention to the ipsilateral hemispace.

Some spatial attention imaging studies have reported larger or stronger activations in the right hemisphere (e.g. Corbetta et al. 1993; Nobre et al. 1997; Gitelman et al. 1999; Hopfinger et al. 2010), but this pattern has not been consistently observed (e.g. Sommer et al. 2008; Shulman et al. 2010). Instead, studies mapping the spatiotopic organization of parietal and frontal areas suggest symmetrical involvement of the hemispheres in directing attention to the contralateral space (Kastner et al. 2007; Konen and Kastner 2008; Silver and Kastner 2009; Szczepanski et al. 2010; Szczepanski and Kastner 2013), in line with the simpler inter-hemispheric competition account of spatial attention and neglect (Kinsbourne 1977). In particular, studies by Szczepanski and colleagues combined sustained spatial attention manipulations with spatiotopic mapping to investigate the degree of inter-hemispheric bias in the different functional regions in the posterior parietal cortex (Szczepanski et al. 2010; Szczepanski and Kastner 2013). Different regions showed different patterns of bias, though across the network of areas the biases were well balanced across participants (Szczepanski et al. 2010). The degree of overall inter-hemispheric spatial biases varied among individual participants and correlated with performance measures on an independent test of spatial bias. Furthermore, applying to topographically identified areas consistently shifted the spatial bias toward the ipsilesional visual field (Szczepanski and Kastner 2013) (for further discussion of hemispheric dominance in spatial attention, see also Beck and Kastner (in chapter 9), this volume).

There may be multiple ways to reconcile these apparently discrepant findings. It is possible that specific functional regions with systematic hemispheric biases contribute disproportionately to spatial deficits in neglect. Alternatively, the balance of spatial biases within the frontoparietal network may be disrupted by remote lesions. Corbetta and his colleagues have proposed that neglect occurs as a result of damage to the right temporal parietal junction creating a hemispheric imbalance in activity within the dorsal frontoparietal network (Corbetta et al. 2005; He et al. 2007; Corbetta (p. 122) and Shulman 2011). Finally, it may be prudent to conceptualize neglect as a syndrome to which multiple deficits may contribute, in addition to those involved in orienting spatial attention. Patients with verified visuospatial orienting deficits do not always fulfil the criteria for neglect (e.g. Posner et al. 1984; Gillebert et al. 2011). Other deficits may interact with spatial deficits and play an important role in determining the range, severity, and duration of neglect, such as problems with alerting, sustaining attention, or maintaining information in working memory (Robertson 2001; Husain and Rorden 2003).

It is also important to bear in mind the limits of imaging methods to reveal the mechanisms of hemispheric dominance. Hemodynamic imaging methods may lack the temporal resolution to reveal short-lived neural mechanisms that may contribute to hemispheric dominance. Even if activity occurs bilaterally, activity in one hemisphere may lead in time or last longer. For example, asymmetries have been noted in event-related potentials linked to attention control and modulation (e.g. Nobre et al. 2000a; Miniussi et al. 2002). Structural imaging methods may also provide clues. Structural diffusion-imaging tractography has recently revealed hemispheric differences in the branches of the superior longitudinal fasciculus, with variability in the lateralization of one of the branches correlating with performance in line bisection performance and speed of target detection across the visual fields (Thiebaut de Schotten et al. 2011). The substrate of hemispheric asymmetry in spatial attention may therefore involve fibre pathways as well as cortical activation patterns.

Correlational methods alone, however, will ultimately be insufficient to reveal asymmetries in the causal influence of spatial attention areas on sensory processing. By combining TMS with fMRI, Ruff and colleagues (2009) were able to demonstrate different patterns of visual modulation when stimulating left versus right frontal or intraparietal sulcus. For example, in parietal areas, only right stimulation led to changes in hemodynamic activity in visual areas. The powerful combination of interference (TMS or lesions) and correlational (fMRI or MEG/EEG) methods may be the most effective way to make headway on this intriguing question of hemispheric asymmetry in spatial attention in humans (see also Blankenburg et al. 2010; Driver et al. 2010; Heinen et al. 2011).

### Expanding the Scope of Attention

Whereas the bulk of attention research has considered spatial or object-based attention operating within vision or other perceptual domains, the scope of attention is much wider. The essence of selective attention is the biasing of

neural activity to favour selection and integration of items that are relevant and adaptive within the current context. This definition leaves open several aspects, regarding what constitutes the sources of bias, what type of information they may carry, the representational slates upon which they can operate, and what behavioural purpose they ultimately support. (p. 123)

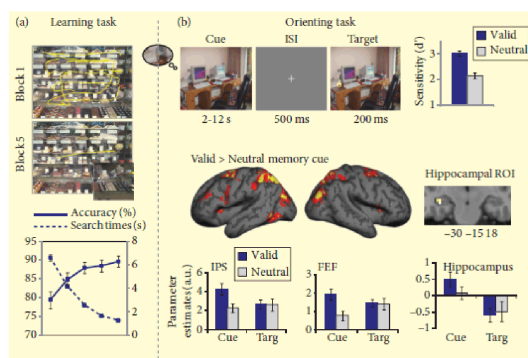
## Sources of Bias

In most attention studies, it is the current *task goal* that guides attention. Perceptual cues are typically used to define the target events or to predict their location (e.g. Hillyard et al. 1973; Posner 1980).<sup>1</sup> Depending on the theoretical account, these perceptual cues in turn establish task-relevant working-memory representations (Desimone and Duncan 1985), action intentions (Rizzolatti et al. 1987; Rizzolatti and Craighero 1998), or predictive priors (Rao and Ballard 1999; Feldman and Friston 2010), which serve as sources of top-down signals to influence neural activity within sensory areas or further along the processing stream.

## Guidance by long-term memory

Experimental paradigms using perceptual cues have served as powerful platforms for dissecting the mechanisms of attention control and modulation, but they also leave out arguably the most common source of attentional biases: those coming from prior experience and stored as long-term memory (LTM). The critical role memory plays in guiding perception has been long recognized (al-Haytham 1021/1989; Helmholtz 1867). According to Helmholtz, perception is a process of unconscious inference, arising from testing predictions acquired through experience against incoming stimulation. A contemporary and computational articulation of these notions is found in Friston's Free Energy Principle (Friston 2009; Feldman and Friston 2010).

Contemporary attention research is repossessing the notion of memory-guided attention and beginning to reveal the neural mechanisms involved (see also Kuhl and Chun (in chapter 28), this volume). The most established paradigm is that of 'contextual cueing' within visual search (Chun and Jiang 1998, 2003). Response times to identify targets within search arrays decrease as the same spatial configurations of distractors repeat through the experiment, even when participants are unaware of these contingencies (Chun and Jiang 1998, 2003). Associative links between objects in a search array can also affect performance during visual search (Moore et al. 2003). Contextual cueing effects are particularly strong when rich and naturalistic scenes provide the contextual background to guide target identification (Brockmole et al. 2006; see also Becker and Rasmussen 2008), and when the contextual information is presented ahead of the search array, providing time for memory-based guidance to develop (Kunar et al. 2008). Critically, LTM has extremely high storage capacity, greatly outperforming working memory in the number of specific contextual, object, and spatial associations that can be used to guide perception (Brady et al. 2008; Stokes et al. 2012).



[Click to view larger](#)

**Figure 5.4** Behavioural and brain-imaging results from the study by Stokes et al. (2011) showing orienting of spatial attention based on long-term contextual spatial memories. (a) Leftmost panel illustrates the pattern of eye movements (yellow lines on the scene pictures) as participants search for the location of a small pre-designated target stimulus (a key) within 192 complex scenes. Half of the scenes contained a target and the other half did not (counterbalanced). Over five blocks of searching, participants become proficient at finding keys. Whereas they search extensively in the first block, eye movements and the duration of search are greatly reduced by the final block. The bottom graph plots the systematic increase in the number of targets found (solid line) and the decreasing response times to find the target over the

successive experimental blocks. Data from Stokes, M. G., Atherton, K., Patai, E. Z. and Nobre, A. C., Long-term memory prepares neural activity for perception, *Proceedings of the National Academy of Sciences of the USA*, 109, E360–7 © 2012, the National Academy of Sciences. (b) The orienting task was performed on the following day during fMRI scanning. Studied scenes (without any target) were presented as cues. Cue duration was lengthy and jittered in order to enable analysis of cue-related fMRI responses. After a brief interval, the scene was repeated briefly with or without an embedded target. Participants were required to make a speeded, forced-choice discrimination response. Scenes in which participants had successfully located the target during the learning session acted as 'valid memory cues', providing 100% predictive information about the spatial location of the upcoming target when present. Scenes in which no targets had been present in the previous learning task acted as 'neutral memory cues', providing no specific information about the likely upcoming target location. The perceptual sensitivity ( $d'$ ) graph shows that participants were reliably better at discriminating the presence of a target after valid memory cues. Equivalent results are obtained when the pacing of the task is quicker and cue durations are reduced to 200 ms (not shown). Brain-imaging results are taken from the simple contrast of cue-related activations when these were 'valid memory cues' compared to when they were 'neutral memory cues'. Memory cues carrying valid predictive information were reliably associated with higher levels of activation in a network of frontoparietal regions linked to visual spatial attention (see Fig. 5.3). Plots show that the enhanced activations in frontoparietal regions and in the hippocampus are specific to the cue period. Data from Summerfield, J. J., Lepsien, J., Gitelman, D. R., Mesulam, M. M. & Nobre, A. C., Orienting attention based on long-term memory experience, *Neuron*, 49 (6), pp. 905–16 © 2006, Elsevier.

Nobre's laboratory has recently adapted contextual cueing tasks to investigate the neural mechanisms of memory-guided orienting of attention (Fig. 5.4). The experimental paradigm is designed to separate mechanisms related to learning context-target (p. 124) (p. 125) associations, orienting attention based on learned contexts, and identifying and selecting target items within contexts (Summerfield et al. 2006). In an initial session, participants learn to locate target items across a large set of complex scenes until they reach a stable and high level of performance. On a subsequent day, they perform a memory-guided spatial orienting task, in which the familiar scenes are used as attention cues. Scenes are presented briefly before the appearance of the target item, requiring a detection or discrimination response. Performance is compared for targets appearing at the remembered location from the learning task (valid), a location different to that learned (invalid), or in a scene in which no target location had been learned (neutral). Behavioural measures show reliable benefits of memory-guided orienting on response speed (Summerfield et al. 2006, 2011) and perceptual discrimination (Patai et al. 2012; Stokes et al. 2012; Doallo et al. 2013). The effects develop surprisingly rapidly, being reliably observable at 100 ms cue–target intervals (Summerfield et al. 2006). Electrophysiological recordings during the orienting task show that memory cues induce lateralized alpha-band modulations in anticipation of the target, in a similar pattern to that observed during perceptual visual spatial orienting tasks (Summerfield et al. 2011; Stokes et al. 2012). Recordings during target processing reveal modulation of early visual potentials, but also raise the possibility that some of the modulatory mechanisms may differ from those arising from perceptual cues (Summerfield et al. 2011; Patai et al. 2012; Doallo et al. 2012). For instance, contrary to what is observed during visual spatial cueing (Leblanc et al. 2008; Seiss et al. 2009; Brignani et al. 2010; Schankin and Schubo 2010), the N2PC potential related to detecting a target within a visual search array is reliably attenuated by memory cues (Doallo et al. 2012; Patai et al. 2012). fMRI studies show that memory cues trigger activity in the hippocampus as well as in dorsal frontoparietal areas involved in visual spatial attention (Summerfield et al. 2006; Stokes et al. 2012). Ongoing studies continue to characterize the network and dynamics involved in top-down biasing of perception by LTM. One intuitive possibility is that neural mechanisms associated with externally cued attentional orienting are also co-opted for biasing perception according to past experience stored in LTM, with the hippocampus and possibly other areas participating in spatial contextual memories serving as a critical link. Alternatively, activity in brain areas related to spatial contextual memories could influence early visual or other sensory areas directly through feedback, re-entrant connections, independently of the frontoparietal network. Both types of mechanisms could also coexist. The use of interference methods, such as TMS or lesions, will be of crucial importance to determine the extent of overlap and interaction between memory and dorsal frontoparietal attention systems in the dynamic modulation of perception. (p. 126)

### Guidance by motivation

Another widely recognized source of adaptive behavioural control relates to the attainment of rewards and fulfilment of motivational drives (Thorndike 1901). A network of cortical and subcortical areas is thought to guide decision-making and behavioural responses through reinforcement learning, including the ventral tegmental area of the midbrain, the nucleus accumbens in the ventral striatum, and prefrontal and cingulate cortices (O'Doherty

2004). During reinforcement learning, several factors may contribute to behaviour, such as the value and quantity of predicted and obtained reward, action representations, and utility functions.

Research is being increasingly aimed at revealing whether and how motivation and reward-related functions are capable of biasing perceptual functions (see Pessoa (in chapter 25), this volume). So far, results have demonstrated improved perceptual discrimination of stimuli that are motivationally significant, through physiological or monetary reward associations or incentives (e.g. Della Libera and Chelazzi 2006, 2009; Engelmann and Pessoa 2007; Engelmann et al. 2009; Raymond and O'Brien 2009; Kristjansson et al. 2010; Piech et al. 2010; Rutherford et al. 2010; Della Libera et al. 2011). Reward incentives or prior history have also been shown to enhance excitability in visual areas (Serences 2008; Engelmann et al. 2009; Hickey et al. 2010a; Baines et al. 2011; Tosoni et al. 2012).

Understanding whether reward-related influences necessarily occur through the spatial attention network is of major interest. Direct connections between the reward network and sensory areas, such as those between the amygdala and extrastriate cortex, could mediate reward-based perceptual biases originating from areas such as the orbitofrontal cortex (OFC) (Kringelbach and Rolls 2004). Alternatively, reward and motivation could act through the attention-control system (e.g. Padmala and Pessoa 2011), through linking points such as the posterior cingulate (Mesulam et al. 2005) or intraparietal sulcus (Gottlieb and Balan 2010; see Gottlieb (in chapter 12), this volume). A combination of both routes may also occur, and their interaction may depend on the interplay between voluntary and instinctive factors. Separating the functional contributions of reward associations and task goals within a given task can be challenging. These are conflated in many common task designs (see Maunsell 2004), and it may be difficult to prevent voluntary shifts of attention to stimuli with motivational relevance even in designs that formally orthogonalize these factors (see Hickey et al. 2010a, 2010b).

Behavioural and neural measures in humans (Kiss et al. 2009; Hickey et al. 2010a, 2010b, 2011; Anderson et al. 2011a, 2011b; Krebs et al. 2011; Anderson and Yantis 2012; Hickey and van Zoest 2012) and non-human primates (Peck et al. 2009; Gottlieb and Balan 2010) show that stimuli with reward value capture attention automatically, even when task-irrelevant or distracting. Brain-imaging studies combining manipulations of spatial attention and reward incentives have shown that reward incentives can enhance activity in areas involved in control of spatial attention as well as recruit activation in additional limbic regions (Small et al. 2005; Mohanty (p. 127) et al. 2008, 2009; Engelmann et al. 2009; Tosoni et al. 2012). Studies also implicate posterior cingulate cortex and its connection to parietal cortex as candidates for mediating the interaction between attention and motivation, though there are different interpretations regarding the extent to which this region carries primarily reward-related signals (Tosoni et al. 2012) or also contributes to the integration of reward and spatial orienting functions (Mesulam et al. 2005; Small et al. 2005; Mohanty et al. 2008).

Both additive and interactive effects have been noted between attention and motivation (see Pessoa and Engelmann 2010; Pessoa (in chapter 25), this volume). By comparing effects during manipulations of reward incentives versus the requirement to shift attention in control areas, Tosoni and colleagues (2012) have concluded that the two sources of control may operate largely independently. Single-unit studies in area LIP of macaques have also revealed largely independent effects of reward and spatial orienting (Bendiksby and Platt 2006). Direct comparisons of visual responses according to manipulations of attention versus reward incentives also show that modulatory mechanisms are not coextensive, and that reward-related changes in visual excitability may occur independently of spatial or object-based attention (Serences and Saproo 2010; Baines et al. 2011).

### Multiple sources of bias

In real life motivational signals are often bound to memories. The reward outcomes of experiences play an important role in shaping what we will approach or avoid in the future (Shohamy and Adcock 2010). In order to start unravelling how memories of past reward outcomes influence ongoing perceptual processing, Doallo and colleagues (2013) manipulated reward outcomes during the learning phase of the memory-based orienting task (Summerfield et al. 2006; Patai et al. 2012). They found that even one single exposure to a monetary reward outcome after learning a spatial contextual association for a target was sufficient to enhance subsequent behavioural and neural markers of memory-based orienting. The experimental paradigm provides a way to start investigating the interplay between motivation, memory, and task goals in shaping perception.

Future work should continue to explore the multiplicity of sources of top-down biasing mechanisms. Are top-down biases from various types of sources such as task goals, memories, and motivation consistently funnelled through a common large-scale frontoparietal attentional network? Or, are there various lines of bias that can interact with one another or act independently to influence perception? The latter possibility may call into question the existence of ‘attention’ as an autonomous psychological domain, and instead reveal the selective biasing of information processing as a general property of cognitive systems. (p. 128)

### Types of Bias

In most, if not all, contemporary theories, attentional biases operate upon receptive-field properties. Anticipatory signals increase spontaneous firing levels of neurons coding the relevant or predicted location or features. Prioritized selection of these attributes in turn leads to suppression of activity in neurons coding other, competing locations or features (Desimone and Duncan 1995; Driver and Frith 2000; Reynolds and Heeger 2009). Understanding how assemblies of neurons with spatially congruent receptive fields can come to be selected to integrate representations of spatially attended objects is intuitive (e.g. Treisman and Gelade 1980; Koch and Ullman 1985) even if figuring out the implementation details is far from trivial. Understanding how feature-based attention can organize cell assemblies (see Chelazzi, et al. 1998; Stokes, et al. 2009) is more difficult, given the lack of clear anatomical segregation according to features within visual areas and the lack of feature-based organization of connections between areas. Nevertheless, it is possible to imagine how flexible, adaptive coding mechanisms (Duncan 2001; Freedman et al. 2001) can set up coalitions of neurons with relevant receptive-field properties and tune excitability through some kind of reverberating (Hebb 1949) or oscillatory activity (Grossberg 1982; Fries 2005).

Ultimately, however, attention models based on prioritization of receptive field properties are insufficient to explain the varieties of attention. Clearly we are able to anticipate and prioritize events based on information that does not map directly onto receptive field properties. Let us illustrate what we \_\_\_\_\_. Presumably the reader was able to anticipate an end to the previous statement.

### Semantic expectations

Seminal early work by Anne Treisman demonstrated that semantic context effects can override selection based on simple features to drive disambiguation and interpretation of stimuli within dichotic listening paradigms (Treisman 1960). Using an orienting paradigm, Neely, and Posner and Snyder, showed that it was possible to direct attention voluntarily to semantic categories of words (Posner and Snyder 1975a 1975b; Neely 1976). Building on this work, Nobre and colleagues compared neural mechanisms of orienting attention to semantic categories versus location of words (see also Moores et al. 2003). An ERP study showed that similar patterns of behavioural facilitation arise from very different modulatory mechanisms (Cristescu and Nobre 2008). fMRI showed selective activation of brain areas involved in semantic analysis (see Gough et al. 2005) when orienting attention to semantic categories, in addition to recruitment of the dorsal frontoparietal network associated with control of spatial attention (Cristescu et al. 2006). Following a similar approach, Miniussi and colleagues (2005) showed behavioural benefits of anticipating different—spatial or verbal—task sets brought about through (p. 129) different modulatory mechanisms. These studies indicate that theoretical and computational models of attention modulation will need to move beyond simple receptive-field biases to take into account the ability to focus selectively on high-level, associative types of representations that are likely to be coded in large populations of neurons across multiple brain regions.

### Temporal expectations

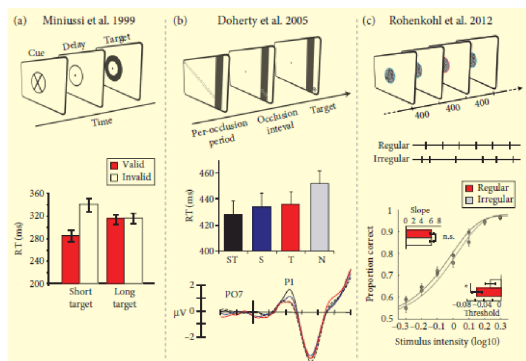
Another critical dimension framing our behaviour missing from current models is the ‘timing’ of events. Building on early work showing facilitation of behaviour by alertness (Posner and Boies 1971) and by predictable intervals between events (foreperiods) (Woodrow 1914; Alegria and Delhaye-Rembaux 1975; Niemi and Näätänen 1981), Nobre and colleagues have demonstrated our ability to orient attention voluntarily and flexibly to predicted or relevant times of target events (Coull and Nobre 1998; Nobre et al. 2011; see Nobre and Rohenkohl (in chapter 24), this volume) (Fig. 5.5). Temporal orienting of attention has proven to be a robust phenomenon, observed in different sensory modalities and across many types of experimental paradigms (see Nobre et al. 2007; Nobre and Rohenkohl (in chapter 24), this volume). Regular rhythmic patterns of stimulation also lead to strong benefits in



behavioural performance and perceptual discrimination of target events (Jones 1976; Rohenkohl et al. 2012). The investigation of temporal orienting mechanisms has intensified, and is beginning to tackle the puzzling question of how temporal predictions can be coded and influence perceptual analysis in the absence of temporal receptive fields. Studies comparing temporal versus spatial orienting of attention under controlled experimental conditions show that similar magnitudes of behavioural facilitation come about through distinct modulatory mechanisms (Griffin et al. 2002; Doherty et al. 2005). In addition, when both temporal and spatial expectations are present, these two types of biases can interact synergistically to enhance modulatory mechanisms based on spatial receptive fields (Doherty et al. 2005; Rohenkohl and Nobre 2011). Current research indicates that oscillatory brain activity may play an important role as a conduit for temporal expectations to regulate neural excitability (Lakatos et al. 2008; Schroeder and Lakatos 2009).

## Slates for Biases

There is no single locus at which attention operates. Most attention researchers investigate its effects within vision. Even within the narrow confines of visual perception, modulations can occur at multiple levels of processing (see Serences and Kastner (in chapter 4), this volume) depending on the features that discriminate targets from distractors, the types of attentional biases available, and the requirements of the task. Beyond visual perception, we know attention operates across the different sensory modalities (Spence (p. 130)



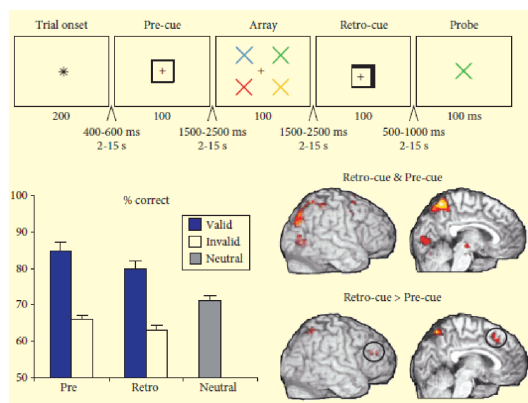
[Click to view larger](#)

**Figure 5.5** Examples of temporal orienting tasks. (a) Task and reaction-time results in the study by Miniussi et al. (1999). Foveally presented symbolic cues predicted (80% validity) whether the target would appear after a short (600 ms) or long (1400 ms) interval after cue onset. Targets were easy to discriminate and required a simple speeded detection response (there were 10% of catch trials containing no target). Data from Miniussi, C., Wilding, E. L., Coull, J. T., and Nobre A. C. D., *Orienting attention in time. Modulation of brain potentials*, *Brain*, 122 (Pt 8), pp. 1507–18 © 1999, Oxford University Press <http://brain.oxfordjournals.org/>. (b) Task and results from Doherty et al. (2005). Spatial and temporal expectations were manipulated orthogonally, according to the spatial and temporal regularity with which a disc traversed the monitor in discrete jumps before it disappeared under an occluding band. Participants had to discriminate whether a small dot appeared with the disc on its reappearance after occlusion, and make a go/no-go response accordingly. Plot of reaction times shows that participants were significantly faster to detect targets appearing at predictable spatial locations (S) or temporal intervals (T) compared to the non-predictive condition (N). Effects of spatial and temporal expectations on reaction times were additive, leading to even faster response times when participants had combined spatio-temporal expectations (ST). Visual event-related potentials over contralateral visual electrodes (plotted for PO7) revealed a marked interaction between spatial and temporal expectations during early visual processing. The early visual P1 potential elicited by targets in the temporal-expectation condition (plotted in red) was no different than the P1 elicited for targets in the non-predictive condition (plotted in dashed line). Targets occurring at predicted spatial locations elicited an enhanced P1 potential (plotted in blue). When combined with spatial expectations, temporal expectations (ST, plotted in black) significantly boosted the gain modulation of the visual P1. Data from Doherty, J. R., Rao, A., Mesulam, M. M. & Nobre, A. C., *Synergistic effect of combined temporal and spatial expectations on visual attention*, *Journal of Neuroscience*, 25, pp. 8259–66 © 2005, Society for Neuroscience. (c) Task and results by Rohenkohl et al. (2012) showing modulation of perceptual processing by temporal expectations under the right experimental conditions. Gaussian noise-patch stimuli occurred in a temporally predictive, rhythmic stream (50 ms duration, 400 ms onset asynchrony) (shown) or in a non-predictive, arrhythmic stream (50 ms duration, 200–600 ms onset asynchrony). Target Gabor patches were superimposed on a minority (10%) of the noise patches. These were indicated by a pink surrounding placeholder, which prompted participants to make a forced-choice discrimination about the clockwise or counter-clockwise orientation of the target. Targets appeared at one of seven luminance contrast levels, anchored to individuals' 75% accuracy performance in a previous

session. The intervals surrounding the targets were kept exactly the same for the regular and irregular condition. Performance was significantly improved for the predictive, regular condition (plotted in red) than in the non-predictive, irregular condition (grey). The psychometric function shows enhanced contrast sensitivity levels, with improved threshold levels, for the regular condition. The slope of the psychometric function remained unchanged. Response times were also significantly and consistently improved for the regular condition (not shown). Modelling (not shown) suggested that rhythmic temporal expectation in this task enhanced the signal-to-noise gain of the sensory evidence upon which decisions were made. Data from Rohenkohl, G., Cravo, A. M., Wyart, V., and Nobre, A. C., Temporal expectation improves the quality of sensory information, *Journal of Neuroscience*, 32, pp. 8424–8 © 2012, Society for Neuroscience.

(p. 131) and Driver 2004) and upon motor representations (Rushworth et al. 1997, 2001) to facilitate our interface with the boundless incoming sensory stream. But, attention does not only face the incoming sensory stream. In fractionating the ‘varieties of attention’, James suggested a subdivision between ‘sensorial attention’, directed toward objects of sense, and ‘intellectual attention’, directed at ideal or represented objects.

Certainly, intuition suggests an ability to orient attention to selective aspects of internalized memory representations that can be independent of continual sensory stimulation. For some time, however, it appeared this intuition was wrong. Early empirical work suggested that the ability to orient spatial attention to memory was confined to fractions of a second, when representations were said to be in an ‘iconic’ state (Sperling 1960; Averbach and Coriell 1961). Spatial cues prompting selective retrieval (post-cues) after this brief iconic period were found to be ineffective at improving performance (Phillips and Baddeley 1971; Phillips 1974). The more enduring form of visual short-term memory (VSTM) is highly limited in capacity, and is usually considered the result of attention operating on the sensory stream to direct selective encoding and to support maintenance (Cowan 1995; Awh and Jonides 2001; Postle 2006). Its contents were considered not to be susceptible to further selective modulation (Sperling 1960; Sternberg 1966).



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**Figure 5.6** Initial demonstrations of the ability to orient spatial attention within arrays maintained in visual short-term memory. The top panel illustrates the behavioural task used in Griffin and Nobre (2003, Experiment 1) and adapted for fMRI in the study by Nobre et al. (2004). Intervals for blank displays in between the trial events were shorter in the task used for the behavioural study (top row) than for the fMRI study (bottom row). In the behavioural study, participants viewed an array of four different colours. At the end of the trial they viewed a probe array and made a forced-choice response to indicate whether the probe had been present or absent in the previous array (50% likelihood). Spatially predictive cues (80% valid) were presented either before (pre-cue) or after (retro-cue) the array. In the example shown, a valid retro-cue points to the location in which the target was present. The accuracy plot shows that participants are more accurate when predictive spatial cues are provided compared to trials in which only neutral cues are presented. Their accuracy is significantly worse when spatial cues are misleading (invalid). Interestingly, the magnitude of the cueing effects was similar for retro-cues and pre-cues. In the imaging study, pre-cues and retro-cues cues were imperative, and participants judged whether the probe matched the cued item. The imaging results show activations specific for spatial pre-cues and retro-cues (compared to non-spatial cues at the same trial frame). Both types of spatial cues activated a similar frontoparietal network of regions, including the intraparietal sulcus and the frontal eye fields, as shown in the conjunction analysis (retro-cue and pre-cue). Retro-cues showed enhanced activations in some of the parietal areas and engaged additional lateral and medial prefrontal regions (circled). Data from Nobre, A. C., Coull, J. T., Maquet, P., Frith, C. D., Vandenberghe, R., and Mesulam, M. M., Orienting attention to locations in perceptual versus mental representations, *Journal of Cognitive Neuroscience*, 16, pp. 363–73 © 2004, Massachusetts Institute of Technology.

Two groups of researchers independently re-examined the question of attentional control over the contents of VSTM (Griffin and Nobre 2003; Landman et al. 2003). They presented cues in the period during which a memory array was being maintained in VSTM indicating the location of the item from the memory array that was likely to be required for a subsequent memory-based judgement (Fig. 5.6). These retrodictive cues (retro-cues), enabling orienting of spatial attention to selective locations of VSTM representations, conferred clear behavioural advantages. Retro-cueing effects are robust and by now are firmly established through numerous replications (see Nobre and Stokes 2011; Gazzaley and Nobre 2012; Stokes and Nobre 2012; Kuhl and Chun (in chapter 28), this volume). (p. 132) (p. 133)

Retro-cues are different from post-cues. They do not prompt immediate retrieval, but instead trigger top-down biasing mechanisms that operate on representations being maintained in VSTM to guide subsequent performance. The mechanisms by which attentional orienting can facilitate maintenance and/or retrieval of representations in VSTM are still being detailed. Brain-imaging studies so far suggest involvement of similar control mechanisms as during orienting to perceptual representations with possible recruitment of additional, selective regulatory mechanisms mediated by prefrontal areas (Nobre et al. 2004; Lepsien and Nobre 2007; Bledowski et al. 2009; Nee and Jonides 2009; Lepsien et al. 2011; Tamber-Rosenau et al. 2011). Modulation of visual processing similar to that which occurs during perceptual orienting has also been observed (Lepsien and Nobre 2007; Sligte et al. 2009; Higo et al. 2011), although it is sometimes challenging to separate modulation of maintenance-related activity in posterior visual areas participating in VSTM from modulation related to anticipating the subsequent probe stimulus (Lepsien and Nobre 2007; Lepsien et al. 2011). Similar behavioural and neural patterns of effects have also been observed after cues prompting participants to refresh their current focus in VSTM by thinking back to a specific previously viewed item (Johnson et al. 2007; Yi et al. 2008; Johnson and Johnson 2009).

The existence of a form of James' 'intellectual' attention has thus been confirmed. Prioritization and selection of information is not confined to operate upon the incoming sensory stream and immediate perception–action cycle. Instead, selective attention can also operate on internalized, 'off-line' representations that are no longer supported by sensory stimulation to facilitate behaviour.

A natural extension of 'off-line' attention is to consider its putative role in the voluntary retrieval of selective long-term memories (see Nobre and Stokes 2012; Kuhl and Chun (in chapter 28), this volume; Kuhl et al. 2012). A recent model, for example, proposes that mechanisms of endogenous versus exogenous orienting of attention mediate voluntary and spontaneous long-term memory retrieval respectively (Cabeza et al. 2008). Others suggest that separate functional anatomical mechanisms mediate perceptual attention control and memory retrieval (Hutchinson et al. 2009; Sestieri et al. 2010), which may be in competition with one another (Guerin et al. 2012). This is clearly a fascinating area of fundamental interest, which deserves further investigation (see Kuhl and Chun (in chapter 28), this volume).

### Summary

Bringing together goals, expectations, intentions, memories, and motivations to guide our perception, choices, actions, and memories through biases about the locations, features, timings, and associations of anticipated events, the functions of attention pervade every aspect of our cognitive life. This plurality of sources, slates, and types of attentional biases invites a reconsideration of the very conceptualization of attention. It may be time to do away with narrow views of 'attention' that delimit it as an independent domain (p. 134) within cognition operating through a set of consistent modulatory mechanisms, and instead embrace the notion that selective biasing is a hallmark embedded property of information processing throughout cognitive functions. Through mechanisms of voluntary control 'each of us literally chooses, by his ways of attending to things, what sort of a universe he shall appear to himself to inhabit' (James 1890/1950: 425–426).

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### Notes:

(1) . Task relevance and likelihood of events are, of course, conceptually separable and can be manipulated independently (Summerfield and Egnor 2009). However, in practice, these two types of manipulations are often combined or used interchangeably to prompt shifts in spatial or object-based attention. It could be argued that these constructs go hand-in-hand, and show a large degree of interaction. In the limit, it may seem absurd to set goals about highly unlikely or impossible events, and wasteful to generate expectations about any and all possible irrelevant events. Nevertheless, the mechanisms that underpin these different types of biasing signals may rely on fundamentally different neural mechanisms. It will be interesting and important to characterize each of these in turn, as well as how they interact, in order to understand the repertoire of attention mechanisms and their implications in psychological, neuropsychiatric, and neurological disorders. Initial investigations along these lines are beginning to yield alluring findings (Wyart et al. 2012). *Proceedings of the National Academy of Sciences USA*.

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