

R318 Dispatch

Visual attention: **Spotlight** on the primary visual cortex

Frank Sengpiel and Mark Hübener

Visual search tasks appear to involve spatially selective attention to the target, but evidence for attentional modulation in the visual area with the most precise retinotopic organization – V1 – has been elusive. Recent imaging studies show that spatial attention can indeed enhance visual responses in human V1.

Address: Max-Planck-Institut für Neurobiologie, Am Klopferspitz 18a, 82152 Martinsried, Germany.

Current Biology 1999, 9:R318–R321
<http://biomednet.com/elecref/09609822009R0318>

© Elsevier Science Ltd ISSN 0960-9822

The way we see the world is as much a reflection of our interpretation of the sensory input — the retinal image — as it is a truthful representation of the real world. Spatial attention, in particular, serves to accentuate objects or locations of interest, while a large amount of visual information is continually discarded. The role spatial attention plays in target detection is classically illustrated by a visual search task, such as that illustrated in Figure 1. Certain elementary features of visual objects — their orientation, colour, size and so on — appear to be processed in parallel across the visual field, and objects that differ in one of these features from surrounding objects ‘pop out’ (as the vertical blue bar does in Figure 1). The pre-attentive identification of such objects is effortless, and the reaction time generally does not depend on the number of non-target objects, or ‘distractors’. But when the target object is defined by the conjunction of two features of the surrounding distractors — such as ‘vertical’ and ‘red’, or ‘horizontal’ and ‘green’ in Figure 1 — objects have to be scrutinized serially, and in this case the time required for target identification increases almost linearly with the number of distractors [1,2].

In everyday life, attention tends to be overt — that is, eye movements are made towards the place or object that has captured an observer’s attention. In a search task, the observer’s gaze will shift from item to item. But the task can also be solved when fixation is held steady (see Figure 1). Spatial attention seems to act like a ‘spotlight’ that makes the target visible as soon as it is directed towards it. This so-called ‘covert attention’ paradigm has been employed extensively in psychophysical, neurophysiological and, most recently, neuroimaging studies of visual spatial attention.

As one might expect of such a striking perceptual phenomenon, attention can affect neuronal activity in most of the visual cortical areas where such modulation has been looked for. Stronger modulation effects have

been observed in areas higher in the visual hierarchy than those that carry out earlier stages of visual processing [3,4]. One would think, however, that the primary visual cortex (V1), where neurons have the smallest receptive fields and the retinotopic representation of space is most precise, would be best suited to being involved in a visual search task that requires a certain spatial resolution.

Paradoxically, many reports suggested that spatial attention had the least, if any, effect in V1. Electrophysiological studies in the past yielded conflicting results. Motter [5] recorded from macaques performing an orientation discrimination task. He reported that covert attention led to a significant increase in firing rate for 25% of V1 neurons, while 10% of the cells showed a relative decrease in responsiveness. Others found only minimal attentional modulation in V1 [6,7]. More recently, Roelfsema *et al.* [8] trained monkeys on an elegantly designed task in which animals had to trace one of two curves — the attended curve — while fixating a central spot. They found that firing rates of neurons in V1 were often significantly enhanced when their receptive fields were on the attended curve, compared with trials when they were on the second, distracting curve.

One of the main problems in demonstrating attentional modulation at the level of single neurons in V1 is that these neurons are sensitive to very small stimulus displacements and it is difficult to control for eye movements at that spatial scale. This makes it hard to ensure constancy of the physical stimulation, which is the essential prerequisite for attributing changes in neuronal response purely to changes in attentional state [4]. Furthermore, the small size of the receptive fields prevents placement of both target and distractor(s) within the receptive field of a single cell, a situation that is more likely to reveal attentional response modulation than when the distractor(s) are placed outside the receptive field [6,7]. Methods that measure the pooled activity of large numbers of neurons, such as event-related potential (ERP) or functional neuroimaging studies, overcome these difficulties. But earlier ERP and neuroimaging studies generally also failed to find any effect of spatial attention on activity in human V1 [9,10].

Recent functional magnetic resonance imaging (fMRI) studies have now shown that, in humans, spatial attention is indeed capable of modulating neuronal activity in V1. Tootell *et al.* [11] specifically addressed the issue of the extent to which spatial attention is retinotopically organized. They compared, for a number of visual areas,

the magnetic resonance activity pattern evoked by a visual stimulus when it was not being specifically attended to, on the one hand, and when it was, on the other. The visual stimulus in these experiments was composed of four randomly flickering vertical bars, each located in one quadrant of the visual field and some 11° peripheral to the central fixation spot.

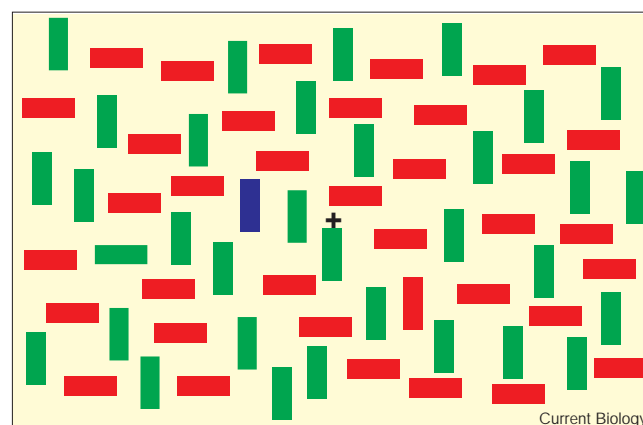
Without attention to a specific location — ‘passive viewing’ — the four bars evoked magnetic resonance activity in the expected retinotopic locations. With spatial attention cued to one of the four bars, the subjects’ task was to react with a button press to a transient change in the orientation of this bar. Tootell *et al.* [11] found that when their subjects attended to a specific stimulus location, there was a relative increase in the magnetic resonance signal at the representations of that stimulus in the various visual cortical areas. In areas that are not retinotopically organized — such as MT+, the presumed human homologue of the monkey motion-sensitive area MT — attentional modulation was nevertheless lateralized to the hemisphere contralateral to the attended stimulus. This indicated that, at the level of spatial resolution of fMRI, visual spatial attention is retinotopically organized. The attentional modulation in V1 was found to be much weaker than in the higher, extrastriate visual areas, but it was nevertheless significant.

A striking finding made by Tootell *et al.* [11] was the pronounced decrease of the magnetic resonance activity at retinotopic locations away from the representations of the four attended targets. The signal strength at these locations was even found to drop below the baseline level evoked by a uniform grey. This finding lends strong support to the notion that visual spatial attention involves a ‘push–pull’ mechanism, in which an increase in activity at an attended location is associated with a decrease in activity at non-attended locations.

An even more robust influence of spatial attention on neuronal activity in human V1 was observed in three other recent fMRI studies [12–14]. Somers *et al.* [12] compared the magnetic resonance signals in central and peripheral parts of V1 while their subjects were either attending to a rapidly presented series of letters in the centre of the visual field or performing a direction-of-rotation discrimination task on a peripheral stimulus. Like Tootell *et al.* [11], they found increases in the magnetic resonance signals in cortical regions corresponding to the attended stimulus and decreases in regions representing the non-attended stimulus.

Brefczynski and DeYoe [14] imaged the retinotopy of spatial attention using a dense array of targets that — unlike the four targets used by Tootell *et al.* [11] — filled the visual field. They found that, when the observer’s

Figure 1



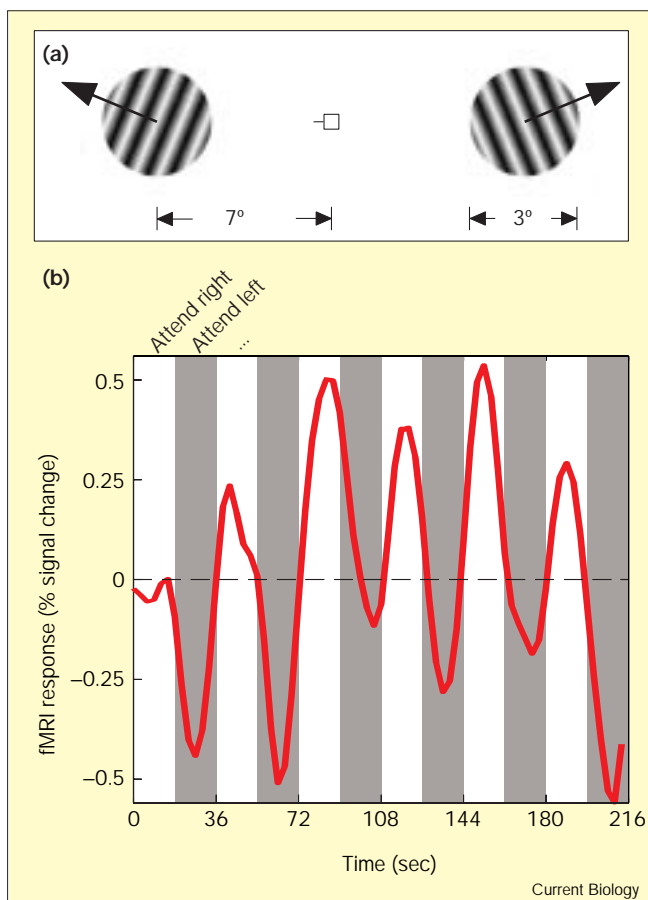
A demonstration of pre-attentive and attention-based mechanisms for image processing. While the blue bar ‘pops out’ immediately, an item-by-item search is necessary to identify the single horizontal green bar among the surrounding distractors. This task can also be carried out without eye movements (‘covert attention’): readers are encouraged to fixate the central cross and try to locate the vertical red bar. Attention must be shifted from object to object until the odd one is found.

attention was directed at one target within the dense array, cortical response modulation occurred at precisely the site where activity was generated when the target was presented alone. This relationship was so accurate, and the modulation so strong, that the location of a subject’s focus of attention could potentially be determined directly from the pattern of visual cortical activation.

In the experiments carried out by Gandhi *et al.* [13], subjects in the fMRI scanner had to perform a speed discrimination task on one of two moving gratings that were presented simultaneously in the periphery of the left and right visual hemifields (Figure 2a). The shape of a fixation mark centred between the two grating stimuli cued subjects to attend to either the left or right grating. A clear modulation of the magnetic resonance signal in V1 with the attentional cueing was found: in each hemisphere, activity increased when subjects attended to the stimulus in the corresponding (contralateral) hemifield, and decreased when they attended to the stimulus in the opposite (ipsilateral) hemifield (Figure 2b). Control experiments showed that performance in the speed discrimination task was better when attention was cued compared to a situation where no cue was given, proving that subjects had in fact made use of the cue to shift their attention. The attentional modulation in V1 had a magnitude about 25–30% of the activity difference due to the presence or absence of the (attended) stimulus.

In the same study [13], strong attentional modulation of magnetic resonance activity was also evident in area MT+. This is not too surprising, as subjects had to discriminate

Figure 2



Attentional modulation of activity in human V1 [13]. (a) A sketch of the visual stimulus. Two moving gratings were presented simultaneously in the left and right visual hemifields, while subjects had to fixate the central mark. A tiny bar next to the fixation mark cued subjects to attend either to the right or, as in this case, to the left grating; the bar switched orientation every 18 seconds. The task consisted of detecting whether the speed of the attended grating increased or decreased during the trial; seven such discriminations had to be performed during an 18 second epoch. (b) Magnetic resonance signal amplitude in V1 during attentional cueing. The curve shows the difference between the relative magnetic resonance responses in the left and the right hemisphere. The signal evidently changes with the attentional cueing and is always larger in the contralateral hemisphere, where the attended grating is represented.

speeds, a bread-and-butter task for area MT, and as neurons in area MT have previously been shown to be very susceptible to attentional load ([15] for example). It is surprising, however, that, in one of the two subjects tested, the magnitude of the attentional modulation in area MT+ was not any larger than in V1.

The studies discussed above have shown that, depending on the visual task, attentional modulation of responses does indeed occur in the primary visual cortex. For the region of V1 representing that part of the visual field to

which spatial attention is directed, neuronal responsiveness increases; conversely, when attention is directed away from a particular location there appears to be a consequent decrease in responsiveness in the retinotopically corresponding V1 region. Furthermore, it has at least partly been confirmed that the magnitude of attentional modulation increases with hierarchical position of the cortical areas examined.

What do these findings mean for our understanding of attentional mechanisms? It has been shown before that neurons in the macaque V1 respond differentially to texture stimuli in a context-dependent manner [16]. V1 is therefore likely to play a role in figure-ground segregation and similar pre-attentive image segmentation processes. The immediacy of 'pop-out' effects and their independence of cognition would seem to support a 'bottom-up' neural model of visual attention. In line with this view, the context-specific enhancement of responses in monkey V1 to texture stimuli is delayed by just 30–40 milliseconds relative to the onset of the visual response itself [16], which does not leave much time for modulatory influences from beyond extrastriate visual cortical areas.

In contrast, the hierarchically graded strength of attentional effects across cortical areas, and the apparent absence of such effects in V1, seemed to support 'top-down' neural models of visual attention. Inputs from the posterior parietal cortex and/or pulvinar are likely sources of a spatial attentional bias that gates information processing in visual cortical areas [3]. Central control of where attention is focused is obviously essential for this phenomenon to be behaviourally useful. But it also seems sensible to assume that, at various stages of visual processing, attention modulates the extraction and perception of those features that the respective visual areas are 'specialized' for. In V1, these would include location and orientation of contours. Attention may bias the competition between different objects for the processing capacity for any of their properties [3], and so affect each processing level.

There are several possible reasons why it has been difficult in the past to detect attentional modulation in V1. It has been suggested that attentional modulation may more often take the form of suppression — for non-attended objects and locations — in areas early in the visual processing stream, while enhancement — of attended objects and locations — may predominate in higher areas. The assumption underlying this view is that neurons in early visual areas already respond at close to maximal rates to their preferred stimuli during passive viewing (or even under anaesthesia), while in the highest cortical areas, cells become active only when specific tasks are performed [3]. But while attentional suppression was indeed seen in V1 by Tootell *et al.* [11] and Somers *et al.*

[12], its magnitude was actually no greater than the attentional suppression seen in higher areas [11].

Alternatively, it is possible that, in the earlier studies, the tasks were not sufficiently demanding. In the new studies, maximum attention was ensured by choosing stimulus parameters so that tasks were difficult and only 70–90% correct responses were achieved. It would be interesting to know whether trials with poorer performance were correlated with weaker attentional modulation, and better performance with stronger modulation. Neuroscientists are still a long way from seeing on an fMRI scan what you have just been thinking about, but they may be close to telling you what you have been looking at.

Acknowledgements

We thank David Heeger and Geoffrey Boynton for making the data included in Figure 2 available to us.

References

1. Treisman A: Preattentive processing in vision. *Comp Vis Graph Image Proc* 1985, 31:156-177.
2. Posner MI, Dehaene S: Attentional networks. *Trends Neurosci* 1994, 17:75-79.
3. Desimone R, Duncan J: Neural mechanisms of selective visual attention. *Annu Rev Neurosci* 1995, 18:193-222.
4. Maunsell JHR: The brain's visual world: Representation of visual targets in cerebral cortex. *Science* 1995, 270:764-769.
5. Motter BC: Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli. *J Neurophysiol* 1993, 70:909-919.
6. Moran J, Desimone R: Selective attention gates visual processing in the extrastriate cortex. *Science* 1985, 229:782-784.
7. Luck SJ, Chelazzi L, Hillyard SA, Desimone R: Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *J Neurophysiol* 1997, 77:24-42.
8. Roelfsema PR, Lamme VAF, Spekreijse H: Object-based attention in the primary visual cortex of the macaque monkey. *Nature* 1998, 395:376-381.
9. Heinze HJ, Mangun GR, Burchert W, Hinrichs H, Scholz M, Münte TF, Gös A, Scherg M, Johannes S, Hundeshagen H, et al.: Combined spatial and temporal imaging of brain activity during visual selective attention in humans. *Nature* 1994, 372:543-546.
10. Clark VP, Hillyard SA: Spatial selective attention affects early extrastriate but not striate components of the visual evoked potential. *J Cognit Neurosci* 1996, 8:387-402.
11. Tootell RBH, Hadjikhani N, Hall EK, Marrett S, Vanduffel W, Vaughan JT, Dale AM: The retinotopy of visual spatial attention. *Neuron* 1998, 21:1409-1422.
12. Somers DC, Dale AM, Seiffert AE, Tootell RBH: Functional MRI reveals spatially specific attentional modulation in human primary visual cortex. *Proc Natl Acad Sci USA* 1999, 96:1663-1668.
13. Gandhi SP, Heeger DJ, Boynton GM: Spatial attention affects brain activity in human primary visual cortex. *Proc Natl Acad Sci USA* 1999, 96:3314-3319.
14. Brefczynski JA, Deyoe EA: A physiological correlate of the "spotlight" of visual attention. *Nature Neurosci* 1999, 2:370-374.
15. Treue S, Maunsell JHR: Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature* 1996, 382:539-541.
16. Lamme VAF: The neurophysiology of figure-ground segregation in primary visual cortex. *J Neurosci* 1995, 15:1605-1615.