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Task-specific impairments and enhancements induced by magnetic stimulation of human visual area V5

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Transcranial magnetic stimulation (TMS) can be used to simulate the effects of highly circumscribed brain damage permanently present in some neuropsychological patients, by reversibly disrupting the normal functioning of the cortical area to which it is applied. By using TMS we attempted to recreate deficits similar to those reported in a motion-blind patient and to assess the specificity of deficits when TMS is applied over human area V5. We used six visual search tasks and showed that subjects were impaired in a motion but not a form 'pop-out' task when TMS was applied over V5. When motion was present, but irrelevant, or when attention to colour and form were required, TMS applied to V5 enhanced performance. When attention to motion was required in a motion–form conjunction search task, irrespective of whether the target was moving or stationary, TMS disrupted performance. These data suggest that attention to different visual attributes involves mutual inhibition between different extrastriate visual areas.

Keywords: magnetic stimulation; motion perception; visual search; V5; attention

1. INTRODUCTION

Several lines of evidence suggest that a region (V5) of human visual cortex, which lies in the occipital lobe posterior to the junction of the inferior temporal and lateral occipital sulci (Watson *et al.* 1993; Zeki *et al.* 1991), is specialized for the analysis of visual motion. Brain imaging studies report an increase in activation in and around area V5 when subjects are presented with moving checkerboards (Zeki *et al.* 1991; Watson *et al.* 1993), form-from-motion diplays (Gulyas *et al.* 1994), coherent or incoherent motion displays (McKeefry *et al.* 1997) and even illusory motion (Tootell *et al.* 1995). Neurological patients whose cortical damage includes area V5 have deficits in perceiving motion which range from an almost total inability to perceive the movement of objects to deficits in second-order motion only (see, for example, Zihl *et al.* (1983), Hess *et al.* (1989), Baker *et al.* (1991), Plant & Nakayama (1993) and Shipp *et al.* (1994)). There are areas of cortex other than V5 involved in the analysis of motion (see, for example, Dupont *et al.* (1994, 1997) and Orban *et al.* (1995)), and lesions which do not include human area V5 can also lead to prominent impairments in aspects of motion perception (Vaina & Cowey 1996; Vaina *et al.* 1998). Human areas V1, V2 and V3a, for example, are all activated by visual motion (McKeefry *et al.* 1997), V3 by motion in depth (de Jong *et al.* 1994), and V2 and V3a respond to illusory motion (Tootell *et al.* 1995), although to a lesser extent than V5 (Tootell *et al.* 1995).

Initial investigations of transcranial magnetic stimulation (TMS) applied over V5 appear to confirm the neuroimaging and neuropsychological data, severely and selectively impairing direction discrimination (Beckers & Homberg 1992; Hotson *et al.* 1994; Beckers & Zeki 1995). However, Beckers & Zeki (1995) emphasized the importance of applying TMS at −20 to +10 ms before or after the onset of the visual array, whereas Hotson *et al.*, (1994) reported the critical time to be 100–150 ms after stimulus onset. Evoked potential and magnetoencephalography studies also estimate different times for the critical involvement of V5 in response to motion stimuli (Probst *et al.* 1993; Holliday *et al.* 1997; Uusilato *et al.* 1997).

Of course, much of what is known about the cortical processing of motion comes from studies of receptive field properties of cells in the macaque visual cortex, which have shown that not only is V5 important for analysis of movement (Dubner & Zeki 1971; Zeki 1974) but that it is important for attention to movement (Treue & Maunsell 1996). This latter result is the first to demonstrate directly that V5 may be involved in more than purely sensory analysis, and this has been followed by a comparable functional magnetic resonance imaging study of human V5 (O'Craven *et al.* 1997), which showed that there is a greater increase of activation in areas MT-MST when subjects attend to the moving aspects of a display than when they attend to stationary elements of the same display. Given that cells in V1 and V2 are selective for direction and velocity (Hubel & Wiesel 1968) and kinetic boundaries (Lamme *et al.* 1993; Reppas *et al.* 1997), cells in V2 and V3a respond to 'real motion' (see Battaglini *et al.* 1996) and the effects of lesions confined to V5 on motion

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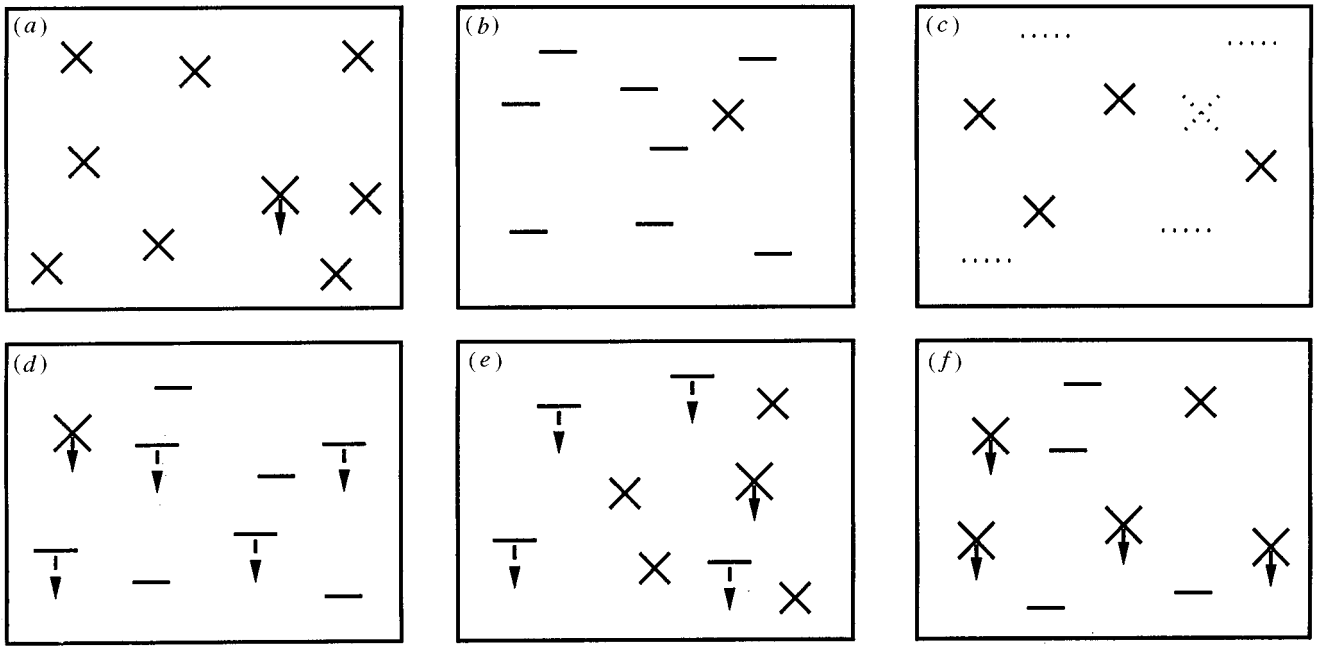

Figure 1. Schematic diagrams of six visual search tasks: (*a*) motion pop-out; (*b*) form pop-out; (*c*) colour × form conjunction (solid lines represent red and the dashed lines green); (*d*) motion irrelevant; (*e*) motion × form conjunction with moving target; and (*f*) motion × form conjunction with stationary target. The arrays are not drawn to scale and all show a target present. See § 2*c* for details. Arrows in the figure represent movement.

perception are often short-lived (Newsome *et al.* 1985; Newsome & Pare 1988), it is clear that V5 is not the only region of the macaque cortex which contributes to motion perception. Taken together, the findings of Treue & Maunsell (1996) and O'Craven *et al.* (1997) suggest that human V5 has a hitherto unsuspected role in visual attention and that focal lesions of V5 in human subjects could lead to impairments in movement perception which reflect this. To test this, we used TMS to explore the role of human V5 in a series of visual search tasks similar to those which have been used to test the visual search performance of the motion-blind patient L.M. (McLeod *et al.* 1989), whose large lesion includes area V5 (Shipp *et al.* 1994). Although TMS can be used to stimulate the cortex to produce crude visual percepts (Amassian *et al.* 1993), it more readily provides a means of disrupting the activity in regions of cortex with millisecond accuracy. It is in this disruptive mode that we used TMS. The technique has been used to study the timing and localization of visual processing and hemispheric asymmetry (Amassian *et al.* 1989, 1993), motion perception (Hotson *et al.* 1994; Beckers & Zeki 1995), attentional processes (Pascual Leone *et al.* 1994) and perceptual learning (Walsh *et al.* 1998).

2. MATERIALS AND METHODS

(a) *Applying TMS*

The stimulator was a single pulse MagStimTM Model 200 with a maximum output of 2 Tesla. Stimulation was applied at 70% of the maximum with a figure-of-eight 70 mm coil. The magnetic pulse is supplied to the coil from a storage capacitor charged to approximately 4 kV and has an estimated rise time of 0.2 ms and a duration of up to 1 ms (Jalinous 1991). The double coil windings in the figure-of-eight coil carry two currents in opposite directions and at the midpoint of the coil, where the two loops meet, there is a localized summation of current. A focal electric current is induced in the cortex by the magnetic pulse which undergoes minimal attenuation by the intervening soft tissue and bone. Using similar hardware, other investigators have reported spatially localized perceptual effects restricted to an area of approximately 1 cm (e.g. Hotson *et al.* 1994). It is important to note, however, that the total spread of induced electric current is of the order of several centimetres (Roth *et al.* 1991; see Ilmoniemi *et al.* 1997), although it is clear that some areas of current are below the threshold for affecting normal cortical function and the precise relationship between induced current and functionally effective current remains to be described. Thus, it remains possible that cortex surrounding area V5 was also stimulated during the experiments described.

(b) *Subjects*

Six subjects (aged 21–62) received TMS on the motion pop-out task (see below) and four of these (aged 21–35) went on to be tested on all six tasks. All subjects were right-handed, had normal or corrected-to-normal vision and reported an absence of epilepsy in their family medical history. Local ethical committee approval was granted for all procedures.

(c) *Stimuli*

Six search arrays were used (figure 1) based on those which had proved effective in a study of the motion-blind patient L.M. (McLeod *et al.* 1989). Stimuli were presented on a 270 mm × 200 mm (640 × 480 pixels) PC monitor at a distance of 100 cm from the observer, whose head was stabilized with a chin rest and head strap. The screen was divided into an eight-column × six-row array of 48 virtual boxes and on any trial each target or distractor could appear randomly in any one of these boxes: presentation was not restricted to a single hemifield, and because we did not intend to look at hemifield effects we did not bin data by the hemifield location of the target. To eliminate cues

from alignment of the stimuli, they were randomly displaced by ±0.3 degrees in horizontal and/or vertical directions. Subjects were required to report the presence/absence of a target by pressing one of two response buttons. Speed and accuracy were stressed in the instructions to the subjects. In the TMS conditions only one set size (eight distractors) was used. The target was present on 50% of trials. Each trial began with a 500 ms alerting tone and a fixation spot in the centre of the monitor. The fixation spot disappeared at the end of the tone. The search array was presented for 750 ms or until the subject made a response. Inter-trial interval was 4 s, as limited by the recharging requirements of the stimulator (Jalinous 1991).

In the motion pop-out task (figure 1*a*) the display was an array of stationary Xs in which the target was a downward moving X. In the form pop-out (figure 1*b*) the subjects were required to detect the presence of an X among an array of horizontal lines. In the colour/form conjunction task (figure 1*c*) the target was a green (CIEx/y .272/.609) X amongst an array of red (CIEx/y .649/.310) Xs and green horizontal dashes. Figure 1*d* shows the 'motion-irrelevant' condition in which the target was a moving X in an array of moving and stationary horizontal dashes. In this condition, although the target and some distractors were moving, the target was defined by its unique form; hence movement was neither a necessary nor a sufficient cue to detection. The two movement/form conjunction tasks are shown in figure 1*e*,*f*. The target in figure 1*e* is a moving X and the distractors are moving horizontals and stationary Xs, and in figure 1*f* the target is a stationary X in an array of moving Xs and stationary horizontals. The two oblique lines that formed the Xs subtended approximately 1.1 × 0.2 degrees of visual angle and those that formed the dashes subtended approximately 0.74 × 0.2 degrees. When there was movement in the display the moving stimuli drifted downwards at a rate of $1^{\circ}\,s^{-1}$ (the velocity used by McLeod *et al.* (1989)). In all conditions the background was black ($2.8\,cd\,m^{-2}$) and in all but the colour/form conjunction task the luminance of the targets and distractors was $21\,cd\,m^{-2}$.

(d) *Procedure*

Before the stimulation sessions, the subjects performed 100 trials with each of the six different search displays with mixed set sizes of four, eight and 16 distractors. Subjects then received 120 consecutive trials with TMS being delivered once on each trial, with a stimulus–TMS onset asynchrony of either 0, 50, 100, 150, 200 or 250 ms. Only one search array was presented in any block of 100 control or 120 TMS trials, thus subjects knew from trial to trial which task was to be performed. The stimulation times were selected on the basis of pilot experiments and the success of previous studies within this time window. Non-TMS trials were not intermingled with TMS trials because of possible subjective expectation effects. During TMS, the coil was placed tangential to the surface of the skull and the centre of the coil was positioned approximately 3–4 cm above the mastoid-inion line and 5–6 cm lateral to the midline in the sagittal plane. The coordinates were selected on the basis of previously successful studies with TMS (Hotson *et al.* 1994; Beckers & Zeki 1995). We also compared magnetic resonance imaging scans of three of the subjects' brains and these were used to verify stimulation sites. In addition, in pilot experiments we used a variant of a 'win-stay/lose-shift' paradigm to locate regions on the scalp which seemed to result in motion deficits over a small number of trials (Ashbridge *et al.* 1997). Stimulation was always applied to the left hemisphere. A typical testing session of TMS and non-TMS trials lasted between 60 and 90 min. Eye movements were not monitored. Feedback was not given on performance.

Table 1. *Slopes, intercepts and mean reaction times for the baseline trials on which TMS was not applied*

(The task column gives the location of each task in figure 1.)

task	slope (ms per item)		intercept		eight distractors	
	target present	target absent	target present	target absent	target present	target absent
figure 1*a*	−1.3	−2.8	442	512	425	500
figure 1*b*	−3.1	−3.1	350	354	323	312
figure 1*c*	−2.9	0.3	454	472	430	495
figure 1*d*	−8.6	13.4	358	312	430	408
figure 1*e*	38.1	41.9	315	380	578	690
figure 1*f*	29.0	48.9	400	331	630	680

3. RESULTS

The baseline performances of the subjects are shown in table 1. Because the effects of TMS were assessed using only one set size (eight), reaction times on TMS trials were compared with the reaction times on the same set size in the baseline trials. TMS had no effects on error rates in any of the tasks (subjects made a mean of 1.9% errors on non-TMS trials and 2.3% on TMS trials). The reaction times were analysed by analysis of variance for main effects and by Dunnett's test for multiple comparisons with a control condition (Dunnett 1964).

(a) *Trials on which the target was present*

TMS produced clear lengthening of reaction times on three tasks in which motion was a relevant stimulus parameter (the tasks shown in figure 1*a*,*e*,*f*). There was significant quickening on two tasks and no effect on the form pop-out. As is clear from figure 2*a*, TMS delivered in synchrony with the onset of the moving pop-out array made subjects significantly slower than on control trials ($p<0.05$). No effects were seen at other stimulation times. Elevations in reaction time were also seen in the two movement/form conjunction tasks. In the task that required detection of a moving X from stationary Xs and moving horizontals (figure 1*e*), performance was slower when TMS was applied with onset asynchronies of 0 ($p<0.05$), 100 ($p<0.01$), 150 ($p<0.01$) and 200 ($p<0.05$) ms (figure 2*e*). When the conjunction tasks required detection of a stationary X embedded in moving Xs and stationary horizontals (figure 1*f*), performance was impaired at onset asynchronies of 0 ($p<0.05$), 100 ($p<0.05$), 200 ($p<0.05$) and 250 ($p<0.05$) ms (figure 2*f*). In the stationary form pop-out task (figure 1*b*) there were no effects at any stimulation time. TMS had a facilitatory effect on the colour/form conjunction task (figure 1*c*) at all but zero asynchrony: 0 ms TMS onset asynchrony ($p>0.05$), 50 ($p<0.01$), 100 ($p<0.05$), 150 ($p<0.01$), 200 ($p<0.01$) and 250 ($p<0.05$) (figure 2*c*). Similar effects occurred when motion was present but irrelevant (figure 1*d*) with the facilitation present at all onset-asynchrony times (figure 2*d*; $p<0.01$ in all six cases).

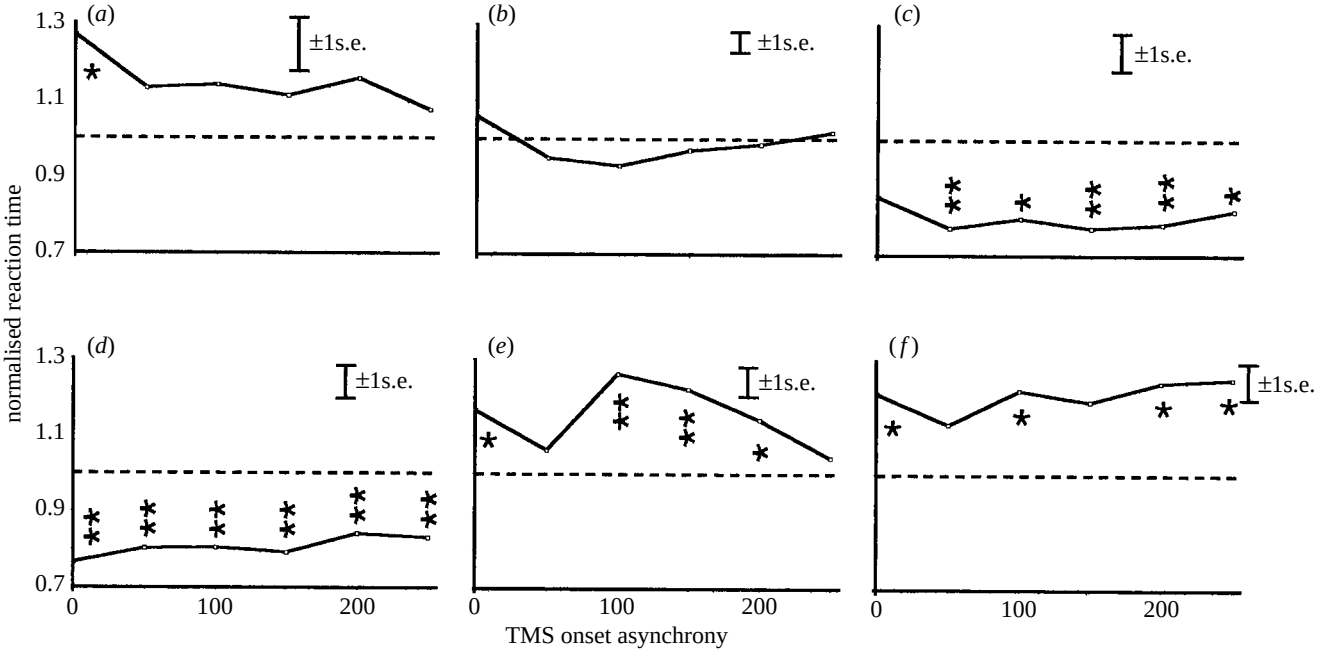

Figure 2. Reaction times when a target was present on TMS trials normalized to the performance on non-TMS trials with 8 distractors. (*a–e*) correspond to the tasks shown in figure 1*a–e*. * indicates $p<0.05$, and ** $p<0.01$.

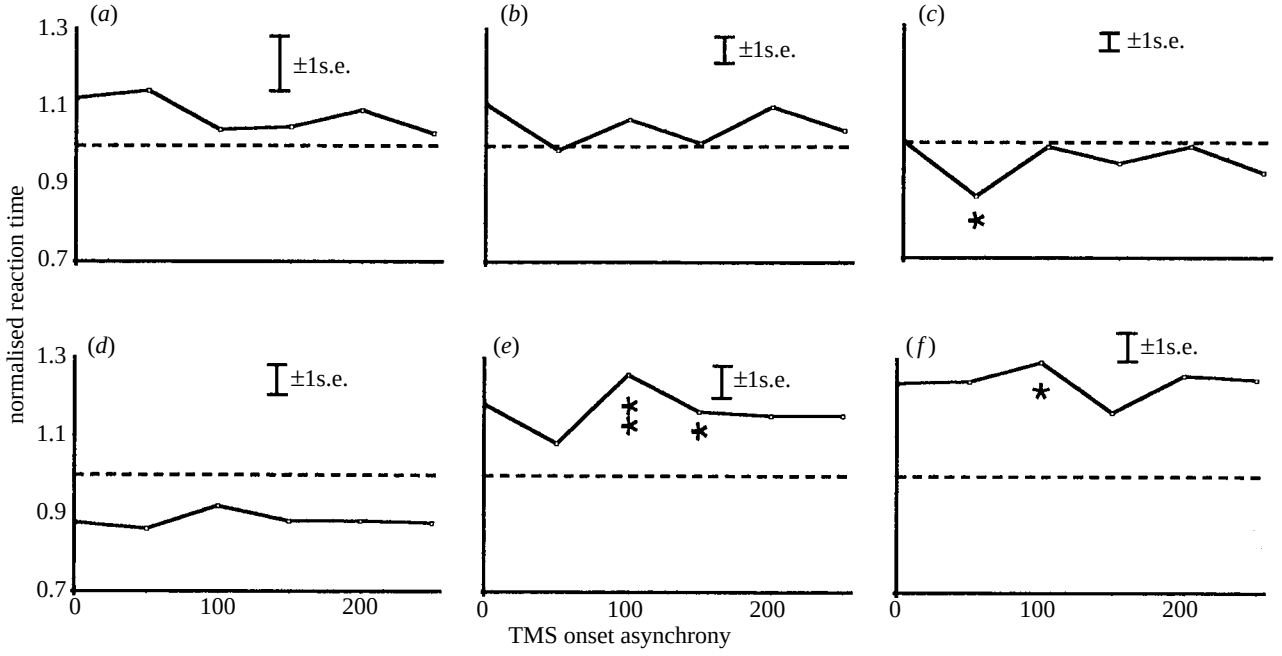

Figure 3. As for figure 2 but for trials when the target was absent.

(b) ***Trials on which the target was absent***

In previous studies of the effects of TMS on motion perception, motion was always present and relevant during stimulation. In contrast, in the present experiment, on 50% of trials no target was present and thus in some tasks, where the target and/or distractors moved, motion processing was required only on target present trials. This is true for motion pop-out (figure 1*a*) and our motion-irrelevant pop-out (figure 1*d*). We therefore only expected effects of TMS on target-absent trials in the two movement/form conjunction tasks (figure 1*e*,*f*) because movement was a relevant parameter on these tasks even on target-absent trials. There were no significant elevations of reaction time at any TMS onset asynchrony in the motion pop-out (figure 3*a*), form pop-out (figure 3*b*) or the motion-irrelevant (figure 3*d*) tasks. Only one enhancement was observed in the colour/form conjunction (figures 1*c* and 3*c*) at 50 ms stimulus–TMS asynchrony ($p<0.05$). In the two tasks that did require motion processing on target-absent trials, the effects of TMS were nearly identical with the effects on present trials, but only two times reached significance in the

conjunction with a moving target (TMS asynchrony $=100$ ($p<0.01$), 150 ($p<0.05$). In the conjunction with the stationary target (figure 3*f*) only TMS at 100 ms after stimulus onset yielded a significant effect ($p<0.05$).

4. DISCUSSION

TMS applied over human cortical area V5 disproportionately impairs performance on visual search tasks which require attention to motion and enhances performance when attention is directed to attributes other than motion. The bi-directional specificity of the results precludes an explanation based on eye-movements, eye blinks or other non-specific effects of TMS: it is difficult to conceive for example of how interference with eye movements or blinks may have a beneficial effect when the array is stationary or movement is irrelevant but an adverse effect when movement is relevant. Our first result, deficits on tasks requiring attention to motion, is further evidence of a role for V5 in selective attention to movement (Treue & Maunsell 1996; O'Craven *et al.* 1997). The improvement observed when attention is directed to attributes other than motion is an unexpected, new finding and suggests that the role of V5 in selective attention may be more complex than suggested by physiological or brain imaging studies. A related finding has been reported by Seyal *et al.* (1995) who were able to demonstrate that sensitivity to tactile stimuli was increased in the hand ipsilateral to the hemisphere which received magnetic stimulation.

The results extend the previous demonstrations of TMS effects on motion perception (Beckers & Homberg 1992; Hotson *et al.* 1994; Beckers & Zeki 1995) and suggest that the different critical TMS onset asynchrony times observed in these earlier studies may have been influenced by the short stimulus presentation times (50 ms by Hotson *et al.* (1994) and 28 ms by Beckers & Zeki (1995)) or the speed of the dots in their displays ($30^\circ\,s^{-1}$ by Hotson *et al.* (1994) and $11^\circ s^{-1}$ by Beckers & Zeki (1995)). Our much longer presentation times and slower velocity reveal that V5 is involved in a continuous assessment of visual motion. It is important to note, however, that whereas the other studies assessed the effects of TMS on errors, we assessed the effects of TMS on reaction times since it is our experience that single pulse TMS can delay but not otherwise impair performance of cognitive tasks (see Walsh & Cowey 1998). The earlier studies also reported differences in hemifield effects with unilateral TMS. Beckers & Zeki (1995) argue that left hemisphere TMS has no effect on left hemifield perception whereas Hotson *et al.* (1994) found that TMS over the left hemisphere impaired direction discrimination in both visual hemifields. We did not intend to address these differences because our arrays were presented bilaterally and one would therefore expect visual search to involve both hemifields (see also Ilmoniemi *et al.* 1997).

The data do not precisely replicate the performance of patient L.M. (McLeod *et al.* 1989), who did not show any superiority with stationary displays requiring attention to colour and form. This difference between the effects of real lesions and disruption by TMS can be explained in two ways. The lesion suffered by L.M. covered a far larger area than that disrupted by TMS. Thus the difference between the real and virtual patients could be a simple matter of lesion size. A more interesting and equally plausible explanation, however, is that the differences reflect the mechanisms involved in normal attention, in facilitatory effects in general (see Kapur 1996) and in recovery processes. It is established that areas of extrastriate cortex are important for selective attention (Moran & Desimone 1985; Corbetta *et al.* 1991; Chelazzi *et al.* 1993) and that stimuli can compete for the processing capacities of different visual areas (Chelazzi 1995; Treue & Maunsell 1996; O'Craven *et al.* 1997). The asymmetry of the effects, target-present trials being affected more than target-absent trials, suggests that V5 is particularly important in target detection or in suppressing attention to moving non-target elements when the target becomes the object of focal attention. An alternative to this competing stimuli view is to think of the visual areas themselves as competing for limited resources such as blood flow and access to other regions, such as the parietal and frontal cortices, which are involved in voluntary selective processes (Jueptner *et al.* 1997). Binocular rivalry may be thought of in the same context; it is not stimuli that compete in rivalry, but the processing channels from each eye that do so. Thus the facilitatory effects of TMS over V5 could arise from a disinhibition of areas involved in colour and form processing, caused by disrupting the customary contribution from V5. Similar disinhibitory effects are well known (Sprague 1966) and evidence from neuropsychology (Morland *et al.* 1996) also suggests an inhibitory relationship between the colour and motion systems. Such competition between areas will of necessity be dynamic in order to be able to respond to changes in task demands, probabilities of specific events occurring, states of arousal and experience. It seems likely therefore that under most conditions facilitation as a function of brain damage would be short lived: hence the lack of enhancements in L.M.'s performance.

We conclude, in agreement with physiological studies in the macaque (Treue & Maunsell 1996) and brain activation studies in humans (O'Craven *et al.* 1997), that visual area V5 is important for attention to motion. Additionally, we suggest that visual areas compete for processing resources and that disruption of V5 allows greater resources to be directed to areas attending to stimulus elements other than motion.

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