Priming of Motion Direction and Area V5/MT: a Test of Perceptual Memory

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Presentation of supraliminal or subliminal visual stimuli that can (or cannot) be detected or identified can improve the probability of the same stimulus being detected over a subsequent period of seconds, hours or longer. The locus and nature of this perceptual priming effect was examined, using suprathreshold stimuli, in subjects who received repetitive pulse transcranial magnetic stimulation over the posterior occipital cortex, the extrastriate motion area V5/MT or the right posterior parietal cortex during the intertrial interval of a visual motion direction discrimination task. Perceptual priming observed in a control condition was abolished when area V5/MT was stimulated but was not affected by magnetic stimulation over striate or parietal sites. The effect of transcranial magnetic stimulation (TMS) on priming was specific to site (V5/MT) and to task — colour priming was unaffected by TMS over V5/MT. The results parallel, in the motion domain, recent demonstrations of the importance of macaque areas V4 and TEO for priming in the colour and form domains.

Introduction

The specialization of different extrastriate visual areas for processing particular attributes in the visual scene is well accepted when considering mechanisms of simple stimulus detection and discrimination. For example, there is broad agreement that macaque area V4 and a ventral region in the human brain whose homology with V4 is disputed are important for some aspects of colour perception, and that area V5/MT is important for normal perception of visual motion (Heywood *et al.*, 1991; Cowey and Heywood, 1995; McKeefry and Zeki, 1997; Hadjikhani *et al.*, 1998; Walsh, 1999; Zeki *et al.*, 1999; Tootell and Hadjikhani, 2001). Many studies now employ the notion of regional functional specialization when examining the roles of sensory areas in 'higher' functions such as attention (De Weerd *et al.*, 1999), memory (Martin-Elkins *et al.*, 1989; Bisley and Pasternak, 2000; Magnussen, 2000) and perceptual constancies (Zeki, 1983; Walsh *et al.*, 1993; Schiller, 1995; Merigan and Pham, 1998). For example, perceptual priming of colour (defined as an enhancement in detection or discrimination of one colour if it was presented on a previous trial and a decrement in ability to detect it if a different colour was presented on the previous trial) is driven in a bottom-up manner that is independent of explicit knowledge of when a particular stimulus is going to appear (Maljkovic and Nakayama, 1994). In macaque monkeys, this colour priming depends on the integrity of areas V4 and TEO (Walsh *et al.*, 2000), suggesting a role for these areas in maintaining a representation based on a particular attribute. Recent psychophysical work has also demonstrated that subliminal priming for complex objects is restricted to the visual quadrant of the prime – consistent with the properties of neurons in extrastriate areas V4 and TEO (Bar and Biederman, 1999). Complementary evidence shows that macaque and human areas V5/MT are necessary for remembering the direction of visual motion (Magnussen and Greenlee, 1999; Bisley and Pasternak, 2000; Magnussen, 2000) [cf. also (Shulman *et al.*, 1999)].

One theoretical scheme (Tulving and Schacter, 1990) proposes that priming of physical attributes depends upon a perceptual representation system (PRS) that is preconceptual and widely distributed in the cerebral cortex. The proposed PRS is supported by a body of psychophysical work indicating that perceptual memory (of which priming is a component) of the basic attributes of a visual scene (colour, motion, orientation etc.) is subserved by low-level mechanisms of perception, located beyond V1 but prior to regions involved in visual object perception (Magnussen and Greenlee, 1999; Magnussen, 2000). Some neuropsychological patients with posterior cortex lesions have impaired perceptual priming but relatively intact conceptual priming (Carlesimo *et al.*, 1994; Gabrieli *et al.*, 1995). Other neuropsychological and imaging studies, however, indicate that priming of visual attributes depends on the parietal cortex (Farah *et al.*, 1993; Marangolo *et al.*, 1998), implying that the parietal cortex either holds a representation of the stimulus or in some way biases the feature codes of the attributes.

To examine the perceptual memory and PRS hypotheses we used repetitive transcranial magnetic stimulation (rTMS) to briefly disrupt visual processing in striate, V5/MT or parietal cortex during the intertrial interval of a motion discrimination task. The intention was to interfere with the intertrial storage of the previously presented direction of motion while leaving discrimination accuracy unaffected.

Materials and Methods

Subjects

Seven subjects, five male and two female, aged between 23 and 29 years and all right handed, participated in the motion priming condition. Five subjects, three male, two female, aged between 25 and 39 years and all right handed, participated in the colour priming control. Five right-handed subjects, three male and two female, aged between 25 and 31 years, participated in the third experiment to control for non-specific response time (RT) decreases following TMS over a non-visually related area, in this case the vertex. All subjects were of a sufficient level of scientific education to understand the information given about magnetic stimulation and gave written, informed consent according to the Declaration of Helsinki. The experiment was approved by the local ethics committee, Oxford Research Ethics Committee.

Stimuli and Procedure

Stimuli were generated using a PC Pentium II, 400 MHz processor and presented on a Sony CPD-G200 Trinitron flat screen monitor (800 × 600 pixels, refresh rate 120 Hz) driven by a Rage IIC AGP display adapter. Stimuli were four virtual squares (1.9 × 1.9° of visual angle and black, like the background, 0.31 cd/m^2) regularly arranged around the centre of the screen and separated by 0.57° from the two adjacent squares (see Fig. 1). Each square contained 100 spatially random white pixels (57.2 cd/m^2), all moving either horizontally or vertically at 2.96°/s in the same direction within a square. In three of the squares the direction of motion was

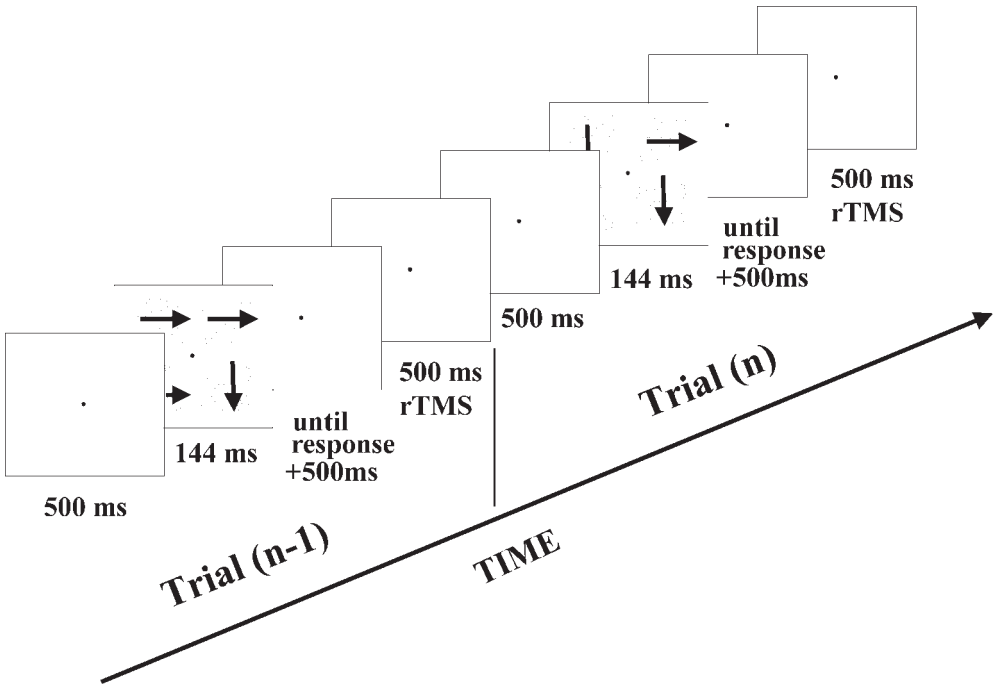

Figure 1. Schematic representation of the task. Subjects were presented with a fixation spot for 500 ms followed by the four panels containing random dots moving in the same direction in three panels and a different direction in the fourth. The stimuli were presented for 144 or 48 ms (motion experiment, colour experiment respectively) followed by a blank screen until the subject responded. Response was followed by a further 500 ms of blank screen after which rTMS was applied for 500 ms before the fixation point for the next trial.

identical, while in the fourth square it was orthogonal to the other three. This odd direction was the target to be detected by the subject. Each trial began with a white fixation point (0.2°, 57.2 cd/m^2) for 500 ms followed by the discriminanda presented simultaneously for 144 ms and followed by a blank screen. Stimulus conditions and procedures were identical for a colour priming task, designed to test for non-specific effects of TMS, with the exception that motion was in the same direction (top–bottom) in all four squares, the target was the odd colour [either green target (CIE.288.597) and red distracters (CIE.609.352) or vice versa] and stimuli were presented for 48 ms because good performance on the colour task required fewer frames than the motion experiment.

Subjects had to select one of four response buttons, using the thumb and first fingers of each hand, to indicate which square contained the target. The rTMS pulses were applied 500 ms after the response (i.e. in the second 500 ms of the intertrial interval) and were followed by the fixation spot for the next trial. A target was present on every trial. To avoid possible effects of spatial priming the target never appeared in the same square on any two consecutive trials, a fact of which the subjects were not informed and which they did not realize during the experiment. This manipulation also ensures that the priming data are not confounded either by spatial priming effects or repetition of finger responses. The direction of the moving dots and the location of the target was pseudorandomized between trials. In the motion experiment, subjects were given 320 trials in blocks of 40, and received 80 TMS trials per stimulation site (V1, V5/MT and PPC) and 80 control trials. In the colour experiment subjects were given 240 trials in blocks of 40, and received 80 TMS trials per stimulation site (V5/MT and PPC) and 80 control trials. In any given block TMS was given either on every trial or none of the trials. In TMS experiments there is a choice between delivering TMS predictably or randomly. In our experience the best method depends on the experimental design and the task being performed. In this experiment we chose a block design to avoid an interaction between trials that were preceded by TMS or no TMS; this would have been theoretically uninformative in the context of our hypothesis, and would have required twice the number of TMS and non-TMS trials. Practice blocks were allowed to ensure that the subjects could perform the task accurately and that the priming effect was present.

In the motion experiment, the independent variable was the direction of the dots in the target square. The direction could either be the same as or different from the previous trial, and the aim of the statistical analyses carried out was to assess the effects of TMS on the relative reaction times of trials in which the preceding target was moving in the same direction versus those trials in which the target was preceded by a different direction. In the colour experiment, the colour of the dots in the target square was the independent variable. Throughout we refer to these as Same and Different trials respectively.

A third experiment was carried out to ensure that any decreases in reaction time could be attributed to intersensory facilitation and not to the effects of pre-activating visual cortex by applying TMS over visually related areas, V1, V5/MT and PPC during the intertrial interval. In this control experiment the visual stimuli and magnetic stimulation parameters were identical to those used in the motion experiment with the exception that TMS was applied over the vertex. The subjects were stimulated by TMS and also by the sound of the discharge and the tactile sensation on the scalp. Conceivably, subjects might respond more quickly because the TMS had a non-specific alerting effect which could decrease reaction times to an irreducible level at which it is not possible to interpret differential effects of primed and non-primed trials.

Magnetic Stimulation

The stimulator was a MagStim 200 Super-Rapid stimulator delivering current to a 70 mm figure-of-eight coil. Details of the stimulator, coil selection and the focality of stimulation have been given in detail elsewhere (Ashbridge *et al.*, 1997). Repetitive pulse TMS was applied to three sites. For V5/MT stimulation the coil was held tangential to the skull with the handle pointing backwards at ~90° to the axis of the spinal cord and for parietal stimulation the handle pointed backwards at ~45° to the spine. For V1 stimulation, the coil handle was oriented vertically. Pulses were delivered at an intensity of 60% of maximum output of the stimulator at 10 Hz for 500 ms.

The posterior occipital site was located between 2 and 4 cm above the inion at the midline. We shall refer to this site as striate cortex or V1. We are aware that it is unlikely that only V1 was stimulated, but the shorthand is justifiable on several grounds. First, the interpretation of the phosphene data is consistent with the topography of striate cortex (Kastner *et al.*, 1998; Kammer, 1999). On behavioural grounds V1 is also the most frugal interpretation since single and repetitive pulse TMS produce effects consistent with interference to V1 whether one considers the time course

of the effects (Corthout *et al*., 1999), the phenomenology of stimulation on perceptual recognition (Kosslyn *et al*., 1999; Cowey and Walsh, 2000) or the disruptive effects of stimulation (Amassian *et al*., 1993). A left hemisphere lateral occipital site was located 3 cm dorsal and 5 cm lateral to the inion (individual subjects' coordinates varied between 3 and 4 cm dorsally and 5 and 6 cm laterally). We refer to this site as V5/MT on the basis of previous anatomical data showing that this site overlies extrastriate area V5/MT and on the numerous previous studies that have selectively impaired visual motion perception with TMS over this site (Hotson *et al*., 1994; Pascual-Leone *et al*., 1999; Stewart *et al*., 1999). As in previous studies we designated the V1 and V5/MT sites on the basis of phosphene production; the V1 site was selected as the point of stimulation which gave the most consistent phosphene in the central few degrees of the visual field and the chosen V5/MT site was where TMS produced a clear moving phosphene [for descriptions of how moving phosphenes are established and how they vary see (Stewart *et al*., 1999)]. To establish the appropriate parietal cortical site we used a visual search task as a behavioural assay, and the region at which stimulation produced a deficit on this task was taken as the critical parietal location for visuospatial processing. The details of TMS and visual search have been given in several sources (Ashbridge *et al*., 1997; Walsh *et al*., 1998a,b). Figure 2 shows anatomical MRI scans illustrating the correspondence between the position of the TMS coil and the location of V5/MT and parietal cortex.

Results

Motion Priming (Fig. 3)

Baseline trials in the absence of TMS showed a clear priming effect – reaction times on Same trials were ~40 ms faster than on Different trials (paired sample *t*-test, $t = 3.3$, df = 6, $P = 0.016$). A two-way analysis of variance (ANOVA) was carried out with factors stimulation site (three levels: V1, V5/MT and parietal) and priming (two levels: Same prime, Different prime). There was a significant effect of priming ($F = 8.609$, $P = 0.026$) and a significant interaction between priming and TMS stimulation site ($F = 11.465$, df = 2, $P = 0.002$). TMS over V5/MT in the intertrial interval abolished the priming effect (Different trials were marginally, though not significantly, faster than Same trials), and *post hoc* contrasts showed that the interaction of TMS site and priming were due to the effects of TMS at V5/MT relative to V1 ($F = 10.776$, df = 1, $P = 0.017$) and relative to the parietal site ($F = 16.847$, df = 1, $P = 0.006$). Repetitive pulse TMS in the intertrial interval decreased reaction times across all conditions with no differences between V5/MT, V1, or parietal TMS induced RT decreases ($F = 1.05$, df = 2, $P = 0.38$). Thus TMS over V5/MT had a specific effect on reaction time – it changed the relative differences between Same and Different trials. The overall decrease in reaction times has been seen in many TMS experiments and is an example of non-specific inter-sensory facilitation. An elegant solution to the problem of evaluating this kind of speeding was presented by Marzi *et al*. (Marzi *et al*., 1998), who interpreted differences between facilitations as the real deficit caused by TMS. In our study this rationale is particularly relevant since the effect of interest was not merely a predicted difference between TMS stimulation sites but a predicted difference within (Same versus Different) and

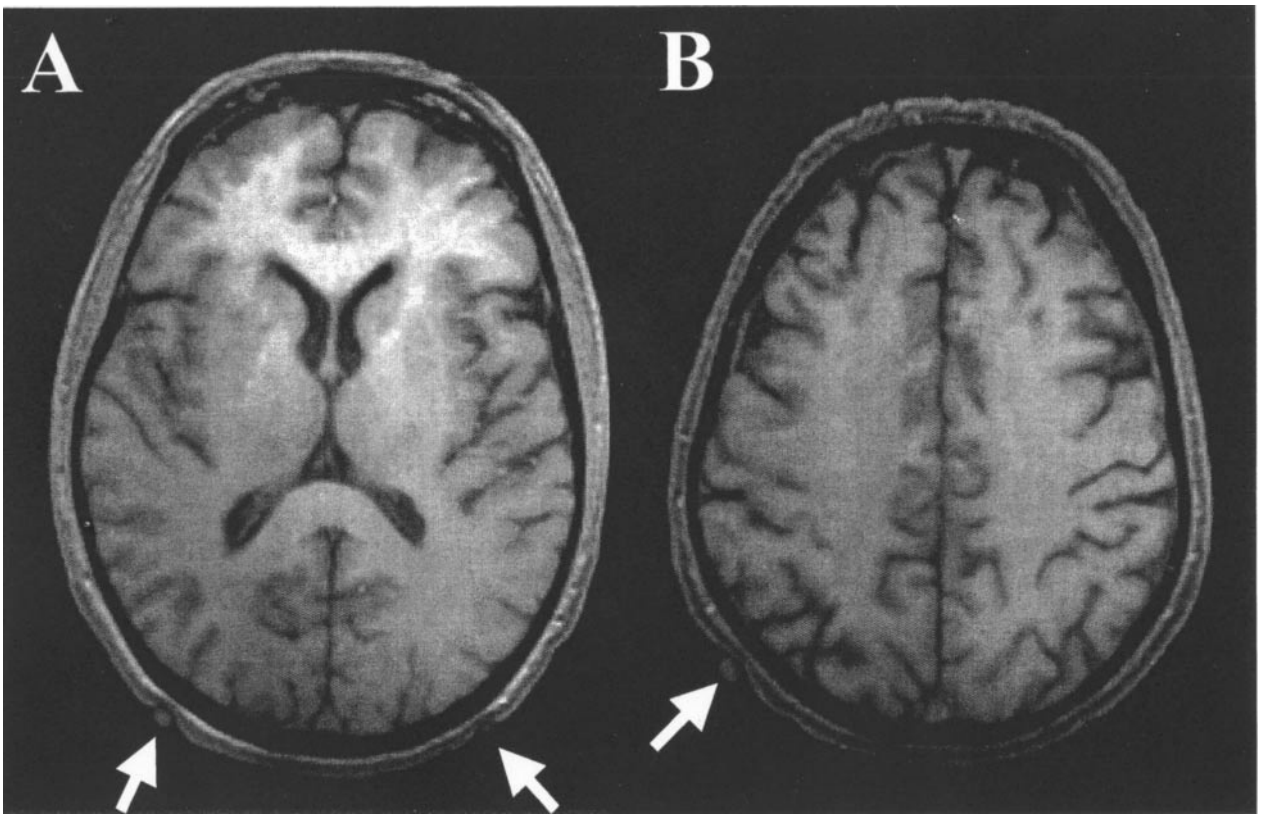

Figure 2. Structural images from one subject showing the location of the stimulation sites used for MT/V5 and posterior parietal (PPC) cortex. Images were T1-weighted (TR = 15 ms, TE = 6.9 ms, TI = 600 ms, flip angle = 12°, field of view = 256 (256 mm, matrix = 256 (256, 64 (3 mm slices with no gap between slices). An oil capsule was placed over the regions stimulated. For MT/V5 the arrow on each side indicates the position of the ascending limb of the inferior temporal sulcus, which was traced over successive slices from its more ventral origin. It was much clearer on the right than left. The arrow on the right section indicates the right angular gyrus. TMS applied to the MT/V5 site shown here has consistently produced moving phosphenes, disrupted the motion after effect and disrupted motion discriminationin previous experiments. The PPC site shown here has also frequently been used in experiments in which TMS disrupts visuospatial processing.

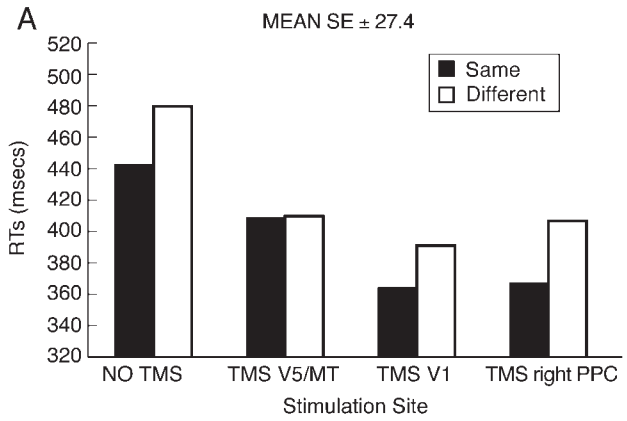

Figure 3. Motion priming. (*A*) Reaction times from stimulus onset as a function of Same/Different trials and TMS site. The first pair of histograms shows a priming effect [Same faster than Different: mean RTs (SE) in ms from stimulus offset, 284 (32) and 319 (40) respectively], so too the third and fourth pairs, which show reaction times for trials when TMS was applied over striate or parietal cortex. The priming effect in these was maintained [mean RTs (SE) in ms: TMS over V1, Same trials, 220 (18); Different trials, 247 (27); TMS over PPC, Same trials, 222 (19); Different trials, 262 (29)]. As the second pair of histograms shows, there is no priming effect when V5/MT was the targeted region of TMS [Same trials 264 (28), Different trials 265 (28)]. (*B*) Accuracy data as a function of Same/Different trials.

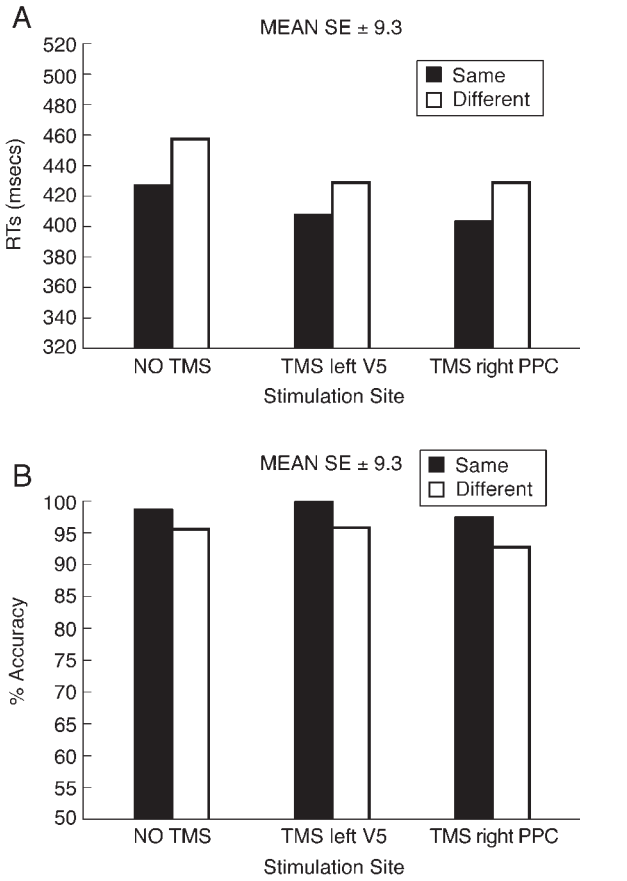

Figure 4. Color priming. (*A*) Reaction times from stimulus onset as a function of Same/Different trials and TMS site. The priming effect (Same faster than Different) is seen in the baseline condition [mean RTs (SE) in ms from stimulus offset: Same trials 379 (9), Different 409 (14)]. This behavioural pattern is unaffected either by V5/MT or right parietal cortex stimulation. V5/MT TMS mean RTs (SE): Same trials, 360 (9), Different trials 381 (8); PPC TMS mean RTs (SE): Same trials 356 (6), Different trials 383 (10). (*B*) Accuracy data as a function of Same/Different trials.

between (V1, V5/MT, parietal) sites. The effects of TMS were not due to an overall decrement in performance as measured by accuracy (Fig. 3*B*). A 3 × 2 ANOVA with factors stimulation site and prime showed that performance on Same trials was more accurate than on Different trials (F = 11, df = 1, P = 0.016) but there was no significant effect of stimulation site (F = 0.201, df = 2, P > 0.05) nor an interaction between TMS and accuracy on primed and unprimed trials (F = 0.56, df = 2, P > 0.05).

Colour Priming (Fig. 4)

The difference between the effects of TMS over V5/MT, PPC and V1 provided controls for specificity of TMS stimulation site. A colour condition was included to control for specific task demands to ensure that the effects of V5/MT stimulation were specific to motion and not any priming task. Baseline trials in the colour priming condition also showed a clear priming effect in the predicted direction with a mean RT advantage of 30 ms for Same over Different trials (t = 5.55, df = 4, P < 0.005). TMS over V5/MT or parietal cortex had no effect on colour priming. An ANOVA with prime (Same versus Different) and rTMS site (V5/MT versus parietal) as factors showed the effect of the prime to be significant (F = 38.83, df = 1, P < 0.005) but no effect of TMS site (F = 0.012, df = 1, P > 0.05) and no interaction between TMS site and prime (F = 0.383, df = 1, P > 0.05). A 3 × 2 ANOVA with factors stmulation site and prime showed that performance on Same trials was slightly more accurate than on Different trials (F = 7.42, df = 1, P = 0.053: Fig. 2B), and there was no significant effect of stimulation site (F = 1.3, df = 1, P > 0.05) and no interaction between TMS and accuracy on primed and unprimed trials (F = 0.185, df = 1, P 0.05). In other words, the effect of TMS over V5/MT was specific to motion.

Vertex Stimulation and Motion Priming (Fig. 5)

A two-way ANOVA (condition: TMS/non-TMS; priming: Same/Different) showed that the priming effect of Same direction was maintained (F = 26.34, df = 1, P = 0.007) when TMS was applied over the vertex to control for visually related reaction time enhancements. The reaction time enhancements caused by non-specific intersensory effects of TMS were significant (F = 7.8, df = 1, P = 0.049), and there was no interaction between the effects of prime and TMS (F = 3.06, df = 1, P = 0.155), indicating that TMS over vertex did not interfere with motion priming.

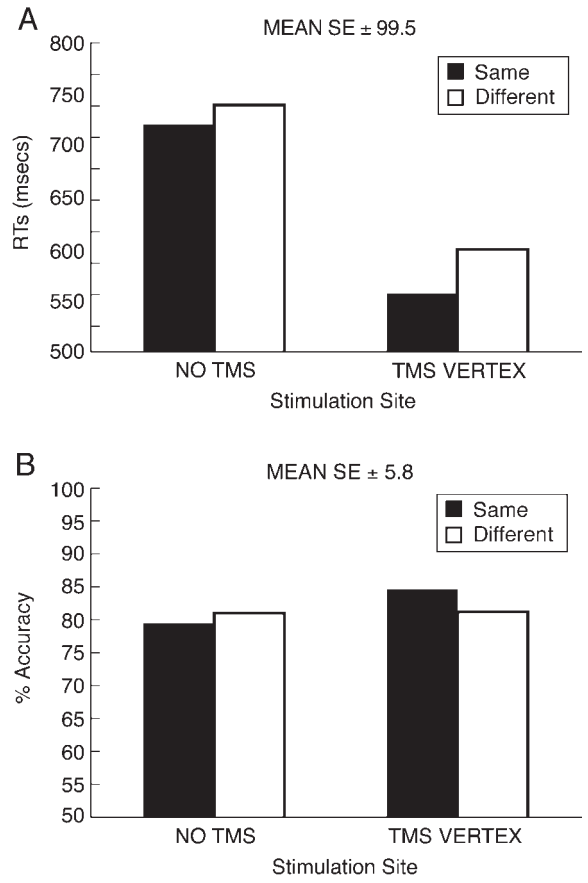

Figure 5. Vertex stimulation. (*A*) Reaction times as a function of Same/Different trials. The priming effect (Same faster than Different) is present in the non-TMS and TMS trials [mean RTs (SE) in ms from stimulus offset: Same (non-TMS/TMS trials) 574/612, Different (non-TMS/TMS trials) 461/598]. (*B*) Accuracy data as a function of Same/Different trials.

Discussion

TMS over V5/MT in the intertrial interval of a motion discrimination task disrupted visual priming of motion. This effect was specific to stimulation site (V5/MT but not PPC or V1) and to stimulus requirements (visual motion priming but not colour priming).

The results provide strong support for the notion of a PRS (Tulving and Schacter, 1990; Schacter, 1994; Schacter and Buckner, 1998) and the perceptual memory hypotheses (Magnussen and Greenlee, 1999; Magnussen, 2000), whereby priming and memory for simple visual attributes engage areas between primary visual cortex and higher visual areas concerned with the formation of structural descriptions of more complex objects. They also support the rationale of using the cortical visual specializations to investigate cognitive capacities in terms of sensory modules (Bisley and Pasternak, 2000). The results also complement the recent studies of perceptual priming that have demonstrated the importance of extrastriate cortex (Bar and Biederman, 1999; Walsh *et al.*, 2000).

The delivery of TMS in the intertrial interval of a task may have alerted subjects non-specifically and thus decreased reaction times. There is also the possibility that a decrease in reaction time might mask differences between conditions. These two possibilities need to be explored in the interpretation of TMS data in paradigms which reduce reaction times. The RT decrease across all TMS conditions relative to control trials clearly shows that intersensory facilitation was present. This cannot be attributed to disruptions of the visual system alone because TMS over vertex had the same effect. The possibility that floor effects may have masked priming effects in the V5/MT TMS condition is also not tenable in this experiment for two reasons. First, the reaction time decrease was not significantly different from that caused by TMS applied to V1 and PPC, in which priming was preserved, suggesting that a floor had not been reached. Secondly, the reaction time decrease caused by TMS applied over the vertex was even greater than that caused by the TMS over visual areas, indicating both that a floor had not been reached by V1, V5/MT or PPC TMS and that the reaction time decreases were due to non-visual effects.

While the results of this study are in agreement with psychophysical studies of perceptual memory, they question the claim that parietal cortex mechanisms underpin attribute priming (Marangolo *et al.*, 1998). First, not all effects of brain lesions indicate of the role of the damaged area – rather, they may often be an expression of the way the brain has reorganized in response to long-term damage (Lomber 1999). Secondly, the patients with parietal cortex damage who showed a failure of colour priming when the probes (i.e. the primed rather than the priming stimuli) were presented in the contralesional field also failed to show normal spatial priming (Marangolo *et al.*, 1998). In the absence of normal spatial priming in these patients it is more parsimonious to attribute their apparent colour priming deficit to a failure in the spatial domain rather than to some form of top-down control of V4 by parietal cortex. We also follow parsimony in trying to explain sensory priming in terms of sensory cortex rather than parietal cortex influence. Feature and location priming operate independently (Maljkovic and Nakayama, 1994, 1996). It is simpler to imagine two separate mechanisms operating independently than two distinct aspects of a single mechanism; in the cases of colour, motion and space, if the mechanisms are separate then the best candidate areas for these specializations are separate visual areas (V4, V5/MT and parietal cortex respectively). The simplicity of this approach is encapsulated in Malkjovic and Nakayama's proposal that 'the salience of many different properties of a stimulus (different features and different positions) are all stored separately, and the valence for each, either positive or negative, is incremented and decremented independently' (Malkjovic and Nakayama, 1996). Further, if one considers the circuitry required for parietal control of priming, it is also more elaborate than the circuitry required if one tries to account for priming in terms of extrastriate cortex. It is simpler to suggest that the independent mechanisms proposed could operate by changing the firing weights of neurons via intra-areal connections. This would satisfy a long standing principle of cortical organization – that of keeping the neural interconnections as short as possible (Cowey, 1979). Finally, considering other evidence, it is noteworthy that the spatial extent of priming seen in a recent study of object priming reflects the spatial organization of human extrastriate areas V4 and TEO (Bar and Biederman, 1999), not that of parietal cortex and, as Connor *et al.* discovered (Connor *et al.*, 1997), extrastriate attention operates on spatial scales that mirror the spatial resolution of extrastriate neurons. Again, it would require an extra step to explain why the parietal lobe might be required to inform the extrastriate cortex of its own spatial properties, which themselves have been shown to be modulated without recourse to dorsal mechanisms (Motter, 1994; Treue and Maunsell, 1996).

The perceptual memory approach is a particularly promising means of combining psychophysics with TMS – a feat only a few

studies have managed (Miller *et al.*, 1996; Corthout *et al.*, 1999; Kammer, 1999) as a result of the spatial and temporal overlap of processing in striate cortex. Work on visual cognition has, as a result, concentrated on parietal cortex (Walsh and Cowey, 1998; Oliveri *et al.*, 1999; Fierro *et al.*, 2000). However, for further studies of sensory processes, the perceptual memory hypothesis widens the time window of processing and increases the number of cortical regions of interest to which TMS can be applied.

Notes

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