



The effect of expectation on facilitation of colour/form conjunction tasks by TMS over area V5

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Abstract

In an earlier paper, we reported task-specific impairments and improvements caused by applying TMS over cortical visual area V5 [Proceedings of the Royal Society of London B 265 (1998) 537]. The phenomenon is further investigated in the present study using two of the previous tasks: a motion/form conjunction in which TMS impaired performance and a colour/form conjunction in which performance was enhanced with TMS. In the earlier experiment, subjects were presented with blocks of trials of one task type perhaps allowing some of the observed effects to arise from knowing the type of stimulus to be discriminated. When blocks of trials consisted of randomly mixed moving/form and colour/form conjunction tasks, TMS over V5 still impaired target-present responses for the moving/form conjunction, but the facilitation seen for colour/form conjunction target-present responses disappeared. We suggest that the competitive inhibition postulated between visual movement areas and colour areas in the brain, in our previous paper, are subject to expectation or knowledge of forthcoming stimulus type.

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1. Introduction

Transcranial magnetic stimulation (TMS) of cortical visual area MT/V5 disrupts performance on tasks that require visual motion processing (Walsh, Ellison, Battelli, & Cowey, 1998). This finding is consistent with neuroimaging and single unit studies (Dubner & Zeki, 1971; O'Craven, Rosen, Kwong, Treisman, & Savoy, 1997; Treue & Maunsell, 1996; Zeki, 1974), which provide evidence that activity in area V5 is related to the extent to which visual motion is a task-relevant attribute. TMS over V5 also leads to an improvement in performance on tasks that require processing attributes other than motion, e.g. colour and form (Walsh et al., 1998). These results collectively suggest that independent processing of the various visual elements in a scene may be limited or moderated by the

extent to which other attributes are relevant to a task. Indeed, half a century of experimental psychology testifies to this fact (e.g. Broadbent & Broadbent, 1987; Cherry, 1970; Pashler, 1987; Treisman, 1991). In this paper, we show that these competitive interactions between different sensory elements is determined by two factors: one factor is priming—what one has just seen/done has an effect on how efficiently one can see/do in the following seconds (Bichot & Schall, 1999; Desimone, 1996; Maljkovic & Nakayama, 1994; Maljkovic & Nakayama, 1996); the second factor is the strength of competition from other attributes. To demonstrate this, we compared the effects of TMS over V5/MT on tasks that demanded detection of motion or of colour and form targets in conditions when the same kind of attributes appeared on every trial or when the attributes to be detected were randomised from trial to trial. The results suggest that competition between cortical areas is an important factor in visual processing, and that competition is affected by knowledge or expectation of forthcoming visual events.

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2. Method

2.1. TMS equipment

A Magstim™ model 200 was used and stimulation was applied at 70% of the stimulator’s maximum power, with a 70 mm figure of eight coil. With this configuration, the magnetic pulse has an estimated rise time of 0.2 ms and a duration of up to 1 ms (see Ashbridge, Walsh, & Cowey, 1997) for details).

2.2. Subjects

Twelve subjects (aged 21–62 years) volunteered to take part in this experiment. 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.

2.3. Stimuli

Stimuli were presented on a 270 mm × 200 mm PC monitor at a distance of 100 cm from the observer, whose head was stabilised with a chin rest and head strap. The screen was divided into an 8 column × 6 row array of 48 virtual boxes. On any trial, the target or distractors could appear randomly in any one of these boxes. Stimuli were randomly displaced by ±3 pixels in horizontal and/or vertical directions.

Subjects were required to report the presence/absence of a target by pressing one of two buttons on a button box. Speed and accuracy were stressed in the instructions to the subject. The target was present on 50% of the trials. On each trial, the subject was presented with a 500 ms alerting tone accompanied by a fixation spot in the centre of the monitor, which disappeared at the end of the tone. The search array was presented for 1500 ms or until the subject made

a response. Inter-trial interval was 4 s, determined by the recharging requirements of the TMS machine.

Stimuli were displayed against a black background. Stimulus arrays were as follows:

Movement/form conjunction (Fig. 1)	
Target	Downwards moving white cross (X); 1.1° line length, 0.2° line thickness, moving at 2.1°/s
Distractors	Stationary white cross (X); 1.1° line length, 0.2° line thickness Moving white horizontal (—); 1.1° line length, 0.2° line thickness, moving at 2.1°/s
Easy colour/form conjunction (Fig. 1)	
Target	Stationary green cross (X); 1.1° line length, 0.2° line thickness
Distractors	Stationary red cross (X); 1.1° line length, 0.2° line thickness Stationary green horizontal (—); 1.1° line length, 0.2° line thickness
Hard colour/form conjunction (Fig. 1)	
Target	Stationary red slash (/); 1.1° line length, 0.2° line thickness
Distractors	Stationary green slash (/); 1.1° line length, 0.2° line thickness Stationary red backslash (\); 1.1° line length, 0.2° line thickness

2.4. Procedure

One group of six subjects were set the easy colour conjunction (ECC) task and the motion conjunction (MC) task.

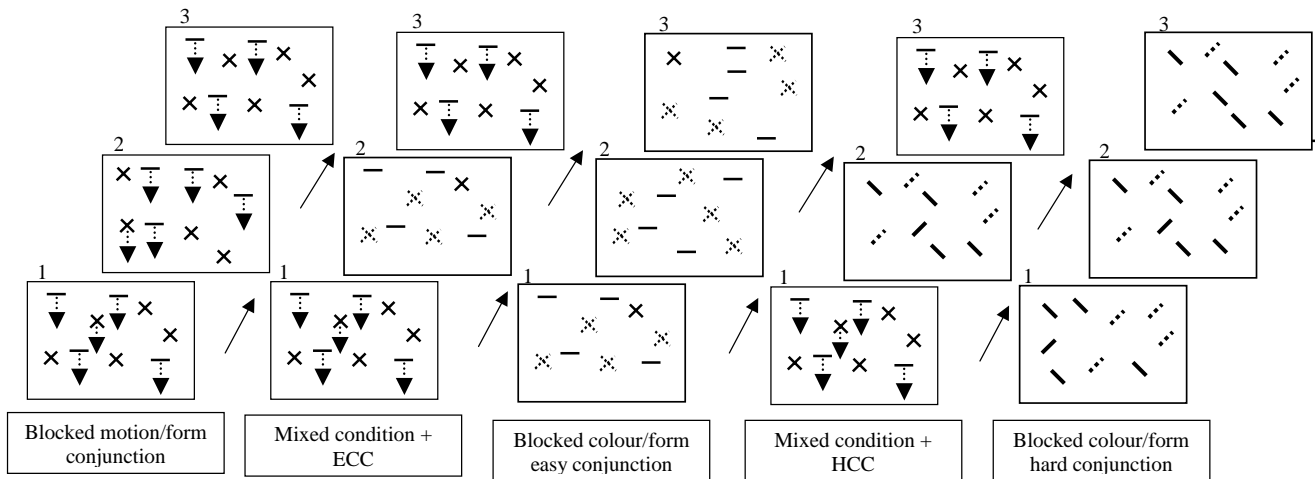


Fig. 1. Blocked and mixed experimental designs. The moving/form conjunction stimulus array consists of a moving cross target, with stationary crosses and moving horizontal lines as distractors. The stationary colour/form conjunction stimulus consists of a green stationary cross (solid lines) as target, with green horizontal lines (solid lines) and red crosses (dashed) as distractors. Target absent trials are also represented.

The other group of subjects completed the hard colour conjunction (HCC) task and the motion conjunction task.

In the baseline blocked condition, two blocks of 60 trials were presented, one with either colour/form conjunction arrays and the other with the motion/form array. In the TMS blocked condition, these blocks, now of 100 trials, were each administered with a single pulse of TMS at 0, 50, 100, 150, and 200 ms post-stimulus onset. In the baseline mixed condition, 120 trials were presented in which both colour/form conjunction arrays and motion/form conjunction arrays were mixed. In the TMS mixed condition, 200 trials were presented. Single pulse TMS was again applied at 0, 50, 100, 150, and 200 ms post-stimulus onset. The baseline condition had three set sizes with 4, 8, and 16 distractors. In the TMS condition, one set size (eight distractors) was used to match conditions in the previous report (Walsh et al., 1998). Reaction times were normalised with respect to the baseline condition (eight distractors set size).

During TMS, the coil was placed tangential to the surface of the skull and the centre of the figure of eight coil was positioned approximately 3–4 cm above the mastoid inion line and 5–6 cm lateral to the mid-sagittal plane, in accordance with co-ordinates used by others (e.g. Hotson, Braun, Herzberg, & Boman, 1994; Walsh et al., 1998). Stimulation was always applied to the left hemisphere. In previous experiments, left hemisphere stimulation has proved sufficient to impair perception in bilaterally presented moving arrays. A typical TMS session lasted between 20 and 30 min.

3. Results

This experiment sought to probe the differential effects of TMS over V5 in colour conjunction tasks when the task is presented in a blocked design, or mixed in presentation with a motion conjunction task.

Two colour/form conjunction tasks of different levels of difficulty were used, the baseline properties of which can be seen in Table 1. The hard colour conjunction task has

a serial slope (e.g. 24.1 ms per item in the blocked design, target-present responses), whereas the easy colour conjunction task has a parallel search function (e.g. –2.9 ms per item in the blocked design, target-present responses). A two-factor mixed design ANOVA (distractors \times task) illustrates the difference in difficulty between these tasks due to the significant interaction between distractors and task ($F_{(4,20)} = 28.404$, $P < 0.001$). The slope is marginally steeper in the motion conjunction task when in a mixed design with the HCC task (Table 1). Also, motion conjunction reaction times are slower in this case than when mixed with the ECC task, indicating some cost of processing when mixed with the harder task even in the baseline condition (see Table 2).

TMS reaction times were collapsed across stimulation time as stimulation time had a non-differential effect on reaction time ($F_{(4,19)} = 0.083$, $P = 0.986$). Table 3 shows the TMS effect on each task, normalised with respect to baseline (no TMS) reaction times. In the target-absent condition, TMS has a greater effect in the MC task when these trials are mixed with HCC as opposed to ECC. Error rates shown in Tables 2 and 3 are negligible, averaging less than 3%.

The effects of TMS over V5 on each of the tasks is graphically represented in Fig. 2A and B as a %difference in reaction time with TMS with respect to baseline scores. TMS causes a deficit in reaction time in the MC target-present responses (Fig. 2A) in blocked and both mixed designs. On MC target-absent responses, TMS causes a deficit in reaction times in the blocked design and when MC is mixed with HCC, but has no effect when MC is mixed with ECC.

In contrast, for target-present responses, TMS causes a facilitation of performance in the blocked design in both ECC and HCC. For target-absent responses, there only seems to be a trend towards facilitation although variance is quite high particularly in the case of HCC. When ECC and HCC tasks are mixed with MC, there is little or no effect on reaction times with TMS over V5 in either target-present or target-absent responses.

Table 1
Slope and intercept data for each condition in the baseline (no TMS) condition

	Target present		Target absent			
	Blocked	Mixed	Blocked	Mixed		
Easy						
Colour/form slope (ms/item)	–2.9	0.48	0.3	18.2		
Colour/form intercept (ms)	454	610	472	577		
Hard						
Colour/form slope (ms/item)	24.1	36.0	49.4	50.1		
Colour/form intercept (ms)	750	824	862	715		
		+ECC	+HCC	+ECC	+HCC	
Moving/form slope (ms/item)	38.1	41.9	42.3	41.9	42.3	44.5
Moving/form intercept (ms)	315	400	448	380	582	661

Note that one of the colour/form conjunction tasks was easy and performed in a parallel manner with negative or negligible slopes. The motion conjunction task yields a slightly steeper slope and higher intercept when mixed with the harder colour conjunction (HCC) task than the easy colour conjunction (ECC) task.

Table 2
Mean reaction times and error numbers as a function of distractor display size in the baseline (no TMS) condition

	Four distractors		Eight distractors			Sixteen distractors			
	Blocked	Mixed	Blocked	Mixed		Blocked	Mixed		
Present responses task									
Easy colour conjunction									
Mean reaction time (ms)	442	612	430	603		408	618		
Mean error	0	0.50	0	0.33		0.83	0.50		
Hard colour conjunction									
Mean reaction time (ms)	846	968	929	968		1136	1400		
Mean error	0.16	0	0	0.83		0.83	0.16		
		Mixed		Mixed			Mixed		
		+ECC	+HCC	+ECC	+HCC		+ECC	+HCC	
Motion conjunction									
Mean reaction time (ms)	467	567	609	578	655	786	924	1074	1117
Mean error	0.83	0.83	0	0	0.66	0.50	0.16	1.16	0.33
Absent responses task									
Easy colour conjunction									
Mean reaction time (ms)	473	650		495	697		477	868	
Mean error	0.50	0.33		0.16	0.16		0	0.66	
Hard colour conjunction									
Mean reaction time (ms)	1059	915		1192	1116		1652	1517	
Mean error	0	0		0.16	0.5		0	0.33	
		Mixed		Mixed			Mixed		
		+ECC	+HCC	+ECC	+HCC		+ECC	+HCC	
Motion conjunction									
Mean reaction time (ms)	548	751	839	690	890	1017	1050	1259	1373
Mean error	0.16	0	0	0	0.66	0.50	0.16	0	0.33

It can be seen here also that mixing the motion conjunction with the hard colour conjunction (HCC) task yields higher reaction times than when it is mixed with an easy colour conjunction (ECC) task.

In order to statistically investigate the data fully, a four-factor mixed ANOVA was carried out with an $A \times B \times C \times (D)$ design; i.e. design [blocked/mixed] \times task [MC/HCC/ECC] \times presence of target [present/absent] \times (TMS[no TMS/TMS] within subject factor). Results of this analysis are shown in Table 4. There was no significant main effect for TMS which is not surprising given the dif-

ferent directions of TMS effects shown in Fig. 2. However, there were significant interactions between TMS and task, and TMS, task and design. A significant main effect was found for presence of target, design and task. Due to a significant interaction between presence of target and task, the data was further analysed separately for target-present and target absent-responses.

Table 3
Normalised reaction times and mean error number in the TMS condition

TMS effects	Motion conjunction			Easy colour conjunction		Hard colour conjunction	
	Blocked	Mixed		Blocked	Mixed	Blocked	Mixed
		+ECC	+HCC				
Present							
Normalised reaction time	1.188	1.198	1.23	0.818	1.068	0.799	1.029
Mean error	1.66	2.90	2.45	2.16	2.66	1.83	1.33
Absent							
Normalised reaction time	1.170	1.000	1.18	0.952	1.004	0.735	1.071
Mean error	1.00	2.16	1.21	1.33	1.00	0.66	0.16

Again, results are shown for the motion conjunction task when it was mixed with the easy colour conjunction task (ECC) and the hard colour conjunction task (HCC).

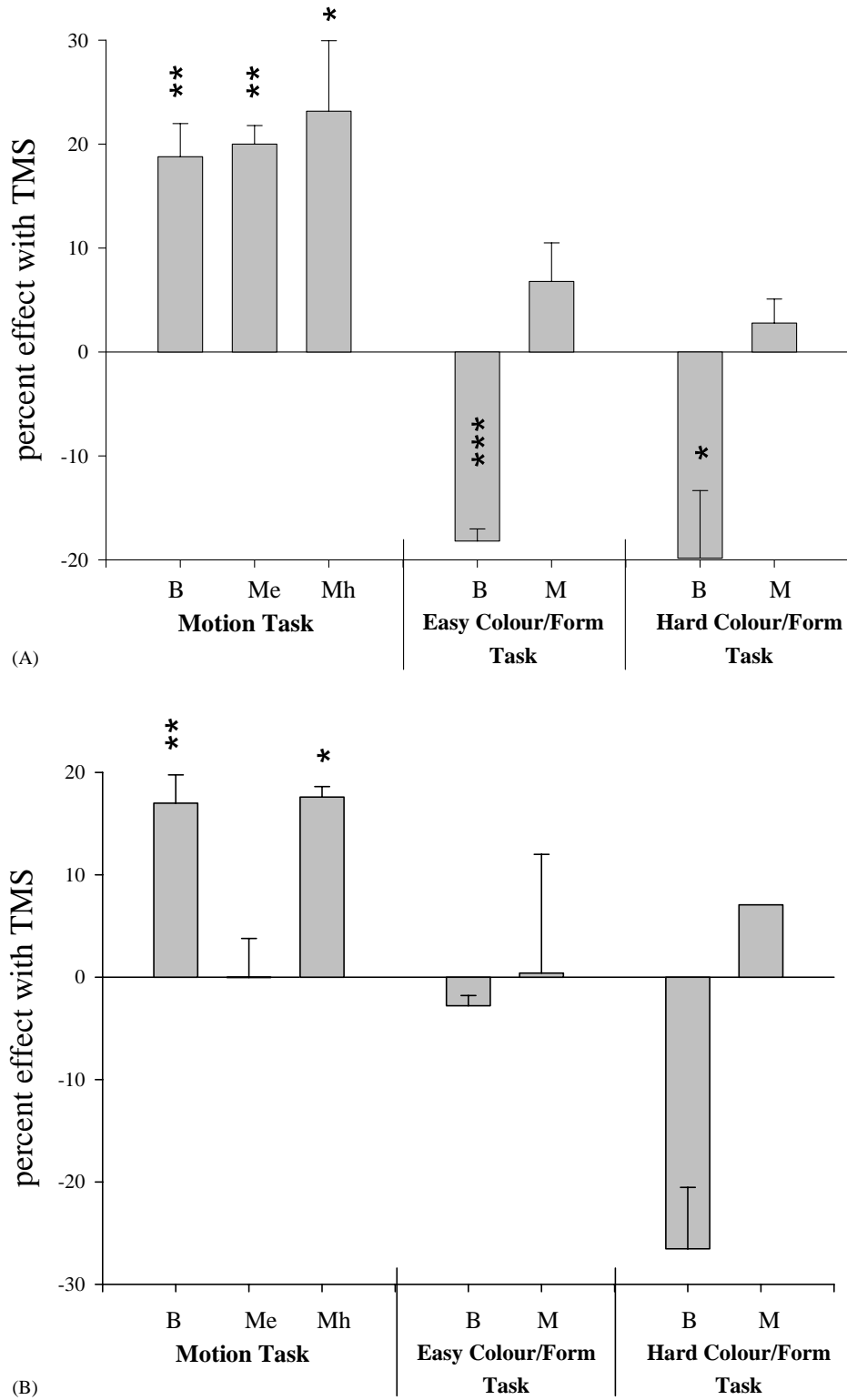


Fig. 2. Percentage reaction time deficit in TMS trials with respect to baseline reaction times for blocked and mixed trials in motion/form and colour/form (easy and hard) conjunctions for target-present responses (A) and target-absent responses (B). Significance is denoted by (***) $P < 0.001$ and (**) $P < 0.01$ (B: blocked; M: mixed; Me: mixed motion and easy colour/form conjunction task; Mh: mixed motion and hard colour/form conjunction task).

Table 4
Results of the four-factor mixed ANOVA with TMS as the repeated measure

Main effects	
TMS	$F_{(1,30)} = 0.001, P > 0.05$
Presence	$F_{(1,30)} = 33.700, P = 0.000$
Design	$F_{(1,30)} = 6.400, P = 0.017$
Task	$F_{(3,30)} = 12.763, P = 0.000$
Interactions (only significant interactions reported)	
TMS × task	$F_{(3,30)} = 4.896, P = 0.007$
Presence × task	$F_{(3,30)} = 4.055, P = 0.016$
TMS × task × design	$F_{(2,30)} = 4.738, P = 0.016$

3.1. Target-present responses

A three-factor mixed ANOVA with an $A \times B \times (C)$ design was carried out, i.e. design × task × (TMS). No main effect for TMS was found ($F_{(1,30)} = 0.144, P > 0.05$) due to the multi-directional TMS effects but both task ($F_{(3,30)} = 7.861, P = 0.001$) and design ($F_{(1,30)} = 6.353, P = 0.017$) had a significant effect on reaction time. There was a significant interaction between TMS and task ($F_{(3,30)} = 3.890, P = 0.018$).

The effect of TMS in each task must be investigated, as the significant interaction between TMS and task suggests a differing main effect for TMS dependant on task. To investigate the significance of each TMS effect, TMS reaction times were normalised with respect to their own baselines for each subject and corrected one-sample *t*-tests (one-tailed) were carried out. This revealed that TMS had a significant effect on MC in the blocked and mixed (+HCC and +ECC) conditions, and that TMS significantly facilitated reaction times in both colour conjunction blocked conditions, but not mixed conditions (see Table 5 for full results).

To investigate the source of the interaction effect, the differential effect of TMS across tasks was investigated by performing a two-factor ANOVA on normalised TMS effects between task and design. Task had a significant effect on TMS effect ($F_{(3,28)} = 17.863, P < 0.001$) as did design ($F_{(1,28)} = 3.890, P = 0.018$). There was also a significant interaction between task and design ($F_{(2,28)} = 4.313,$

$P = 0.023$). Post hoc Bonferroni tests show that the TMS effect in the blocked MC task is significantly different to that in the blocked ECC ($P < 0.001$) and blocked HCC ($P < 0.001$) tasks. Interestingly, there is a significant difference between the TMS effect seen in the blocked ECC and mixed ECC conditions ($P = 0.029$). The difference between blocked and mixed HCC TMS effect only just approaches significance ($P = 0.061$) due to greater variance in the data. The TMS effect on the blocked and two mixed conditions in the MC task are not significantly different from each other.

3.2. Target-absent responses

A three-factor mixed ANOVA with an $A \times B \times (C)$ design was carried out, i.e. design × task × (TMS). Again, no main effect for TMS was found ($F_{(1,30)} = 0.139, P > 0.05$) but there was a main effect for task ($F_{(3,30)} = 15.156, P < 0.001$) and design ($F_{(1,30)} = 5.023, P = 0.033$). There was a significant interaction between TMS and task ($F_{(3,30)} = 3.615, P = 0.024$) and also for TMS × task × design ($F_{(2,30)} = 6.526, P = 0.004$).

Due to the fact that task has a significant interaction with TMS, a series of one-sample *t*-tests (one-tailed) were carried out to analyse the TMS effect for each task. They revealed that TMS had a significant effect on MC in the blocked condition ($t_{(4)} = 5.516, P = 0.002$) and when MC was mixed with HCC trials ($t_{(4)} = 2.511, P = 0.033$) (see Table 5 for full results). There was no significant facilitation of reaction time with TMS in the ECC or HCC task.

The interaction effects were again investigated using normalised TMS reaction times with respect to their own baselines for each subject. The differential effect of TMS over tasks was investigated using a two-factor ANOVA (task × design). It showed a main effect for task ($F_{(3,28)} = 4.185, P = 0.014$) and a significant interaction between task and design ($F_{(2,30)} = 8.109, P = 0.002$). Post hoc Bonferroni tests showed that there were significant differences between TMS effects in the blocked HCC and mixed HCC ($P = 0.017$) conditions and blocked MC, mixed MC (+HCC) and HCC ($P = 0.001$ in both cases).

4. Discussion

The main finding of this experiment was a difference between the effect of TMS over V5 when subjects either did or did not know the visual stimulus type to be presented on each trial. When subjects were presented with a block of trials in which colour and form processing but not motion analysis was required, TMS over V5 facilitated performance. However, when subjects had no foreknowledge of the discrimination, the facilitation disappeared. The second finding of the experiment was that TMS effects on motion search are robust for target-present trials irrespective of blocked or mixed trials. In target-absent trials, deficits in

Table 5
Full statistical outcome of one-sample *t*-tests using normalised TMS reaction times (with respect to baseline reaction times)

	Target present		Target absent	
	$t_{(4)}$	P	$t_{(4)}$	P
Blocked MC	5.288	0.003	5.516	0.002
Mixed MC (+ECC)	9.759	<0.001	-0.557	0.303
Mixed MC (+HCC)	3.384	0.014	2.511	0.033
Blocked ECC	-13.797	0.000	-2.039	0.055
Mixed ECC	1.638	0.088	0.356	0.370
Blocked HCC	-2.803	0.024	-2.034	0.056
Mixed HCC	1.072	0.172	1.054	0.176

reaction time in motion trials with TMS over V5 are only demonstrated in the blocked condition and when motion trials are mixed with trials requiring a serial search.

An explanation for the main finding may involve two phenomena known to involve extrastriate cortex—priming and attribute competition. Priming refers to the fact that reaction times to find a target are faster when the same target was present on the preceding trial. Two studies have recently shown that extrastriate areas V4 and TEO are important sites for visual object or attribute priming (Bar & Biederman, 1998; Walsh, LeMare, Blaimire, & Cowey, 2000). Also, psychological studies suggest that in the movement domain, area V5 occupies a similar role to these areas (Magnussen & Greenlee, 1999; Raymond, O'Donnell, & Tipper, 1998). For our argument however, the critical point is that V4 and TEO are known to be important for colour and form priming (Raymond et al., 1998) and V5 for motion priming, as we have recently shown (Campana, Cowey, & Walsh, 2002). There are also several convincing accounts of competition between stimuli within receptive fields of areas V5 (Treue & Maunsell, 1996), V4, and IT (Desimone & Duncan, 1995; Moran & Desimone, 1985). These accounts of competition are limited to single stimulus domains (motion versus motion, colour versus colour, etc.), but it is a small step to suggest that competition may also exist between different visual attributes (and therefore between specified visual areas). This is particularly pertinent to situations where a perceptual decision is required or the stimuli potentially occupy the same regions of visual space. In light of the above facts and the extensive anatomical connections between areas V4 and V5 (Fellman & van Essen, 1991), our results suggest the following interpretation. When subjects receive magnetic stimulation over area V5, a degree of neural noise is introduced in the motion processing system (cf. Walsh & Cowey, 1998; Walsh & Cowey, 2000). This neural noise will not only affect V5 processing but may also have consequences for processing in areas connected with V5. In this case, we propose that V4 and V5 compete for processing resources to maximise the analysis of their own favoured attributes. These resources can access to other visual areas (e.g. STS or posterior parietal cortex or even back projections to V1, Pascual-Leone & Walsh, 2001), access to blood supply or access to regions of cortex responsible for generating motor responses. Adding noise to the V5 system will therefore reduce any competitive or inhibitory influence it has on V4, resulting in an increased efficiency in V4 processing as seen in the reaction time enhancement. The failure of TMS over V5 to enhance reaction time to colour and form in the mixed condition suggest that, in this task at least, disruption of V5 is alone insufficient to 'liberate' V4 and that V4 can only benefit if the type of stimulus to be presented is predictable.

There are two strong predictions from this competition-based account of our data. The converse results should be obtained if TMS were applied to V4—colour/form processing should be impaired and motion processing enhanced.

Our second prediction is that the responses of single units in V4 or V5 should depend not only on competing stimuli within the receptive field but also on competing stimuli in different stimulus domains. That activity in visual areas is selectively enhanced by expectation of a stimulus has been shown in brain imaging studies (Kastner, DeWeered, Desimone, & Ungerleider, 1998; Shulman et al., 1999).

The second finding, that the effects are more robust for blocked trials, also yields to an explanation based on known facts about the visual system. TMS effects on motion search are robust for target-present and target-absent in the blocked condition. When motion trials are mixed with easy colour/form trials, TMS deficits are seen for target-present but not target-absent trials. It has recently been shown that V5 is important in monkeys in holding representations of targets defined by direction of motion (Rudolph & Pasternak, 1999). When no target is present or when the direction of non-targets needs to be computed, it may be the case that other areas sensitive to direction of motion can filter distractors. There are several reasonable candidates for this kind of role—V3, V3A, posterior parietal cortex, even V2, and, if the stimuli are slow enough, V4.

However, using the harder conjunction-type trials, there is a deficit in reaction time for motion target-absent responses. This may be due to the greater processing load required by the harder colour/form conjunction task; a higher load in a competing area may be considered as higher competition against V5 and therefore yielding a greater combined effect of TMS over V5 and competition with it (Rees, Frith, & Lavie, 1997). In such a case, TMS will have an effect on motion target-absent trials.

The proposed explanations for these findings provide a novel way of looking at the functions of lateral connectivity within extrastriate cortex. The most common proposal is that lateral connections may facilitate binding of features in space or time, but a competitive account may also provide an alternative to the temptation to look outside the visual areas for explanations of stimulus processing that involves anything more complex than detection or discrimination. A more complex factor could be the difference in memory load for mixed trials, i.e. two targets to be remembered rather than one. However, the direction of the deficits and enhancements would be difficult to explain in terms of memory and it is unlikely that memory affects would be differential with respect to stimulus type since both had to be remembered. Although it is common to invoke top-down inputs from prefrontal cortex or posterior parietal cortex in the explanation of differential processing, it could be perhaps that much more of the battle is fought at earlier levels of cortex.

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