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The role of V5/MT+ in the control of catching movements: an rTMS study

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Abstract

Milner and Goodale [Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: Oxford University Press] described a model which distinguishes between two visual streams in the brain. It is claimed that the ventral stream serves object recognition (i.e. vision for perception), and the dorsal streams provides visual information for the guidance of action (i.e. vision for action). This model is supported by evidence from the domain of spatial vision, but it remains unclear how motion vision fits into that model. More specifically, it is unclear how the motion complex V5/MT contributes to vision for perception and vision for action. We addressed this question in an earlier study with the V5-lesioned patient LM [Schenk, T., Mai, N., Ditterich, J., & Zihl, J. (2000). Can a motion-blind patient reach for moving objects? *European Journal of Neuroscience, 12*, 3351–3360]. We found that she is not only impaired in perceptual tasks but also in catching, suggesting a role for V5/MT+ in vision for both perception and action. However, LM's lesion goes beyond V5/MT+ into more dorsal regions. It is thus possible, that the catching deficit was not produced by damage to V5/MT+ itself. In this case, one would expect that selective interference with V5/MT+ would have no effect on catching. In the present study we tested this prediction by applying rTMS over V5/MT+ of the left hemisphere while healthy subjects were either performing a catching or a reaching task. We found that V5-TMS reduced the speed of the catching but not the reaching response. These results confirm that V5/MT+ is not only involved in perceptual but also in visuomotor tasks.
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1. Introduction

Ungerleider and Haxby (1994) and Ungerleider and Mishkin (1982) suggested that the various areas of the visual brain could be separated into two visual streams, which are anatomically and functionally distinct. Both of these streams originate in the primary visual cortex, but then part company and go either towards the temporal cortex in the case of the ventral stream, or towards the parietal cortex, in the case of the dorsal stream. Ungerleider and Mishkin (1982) assumed that the ventral stream is primarily concerned with visual attributes that allow the identification of objects (e.g. colour and form), whereas the dorsal stream is concerned with visuo-spatial aspects (e.g. position and motion), and allows the localization of visual objects. More recently, Goodale and Milner (1992) and Milner and Goodale (1993) suggested a functional re-interpretation of the original two-stream hypothesis. They argue that the functional distinction between the two streams is not primarily based on the type of visual attributes, which are processed in these two streams (i.e. colour/form in ventral stream versus position and motion in the dorsal stream), but on the behavioural or cognitive function for which the visual information is used. More particularly they suggest that visual information which is used for object identification and scene identification, i.e. vision for perception, is processed in the ventral stream, whereas visual information used for the control of motor behaviour, i.e. vision for action, is processed in the dorsal stream. This model by Milner and Goodale received much support from neuropsychological and experimental studies (see Milner & Goodale, 1995). However, most of its evidence comes from experiments on intrinsic physical attributes such as form, size, and orientation perception (Norman, 2002). Other visual attributes (e.g. motion and depth perception) have been examined much less in this context, and it therefore remains unclear how these aspects of processing fit into the model (Goodale, 1993).

In the case of motion vision it is certainly conceivable that the distinction between vision for perception and ac-

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tion also applies, since it is obvious that motion vision is relevant for both object recognition and visuomotor control. For example, object recognition requires figure-ground segregation, for which motion is an important cue (Anstis, 1978; Sekuler et al., 1990). Similarly, visuomotor control tasks also include catching behaviour, and we would expect that successful catching behaviour is not possible without motion vision. Even manual movements towards stationary targets might involve motion vision, namely for the visual monitoring of the moving hand (Paillard, 1996). The question thus arises whether there are distinct brain areas processing visual motion information either for perceptual or visuomotor tasks. Functional imaging studies have shown that there is a whole set of motion-related areas in the human brain (Culham, He, Dukelow, & Verstraten, 2001). For most of those areas very little is known about their functional contribution, and therefore it is too early to decide whether this set of motion-related areas can be subdivided into a perceptual and a visuomotor stream.

However, one of those brain areas, namely the motion complex V5/MT+, has been examined much more extensively, and it is clear that this area makes an important contribution to a number of aspects of motion perception. For example it has been found that the preferred speed range of cells in V5/MT+ (Lagae, Raiguel, & Orban, 1993; Maunsell & Van Essen, 1983; Mikami, Newsome, & Wurtz, 1986; Rodman & Albright, 1987) correlates closely with psychophysical performance in speed-discrimination tasks (McKee, 1981; Orban, de Wolf, & Maes, 1984; Orban, Van Calenbergh, De Bruyn, & Maes, 1985), suggesting that V5/MT+ is the essential mechanism underlying this performance. This conclusion is confirmed by studies that show a degradation of speed discrimination after damage to V5 (Hess, Baker, & Zihl, 1989; Orban, Saunders, & Vandenbussche, 1995; Plant & Nakayama, 1993; Zihl, von Cramon, & Mai, 1983; Zihl, von Cramon, Mai, & Schmid, 1991). Similarly, for the perception of direction in global motion stimuli it has been found that activity in V5/MT+ is closely related to performance. In fact, it could be demonstrated that a bias in perceived direction can be induced by stimulating direction-specific cells in V5/MT+ (Salzman & Britten, 1990). Furthermore, it was found that damage to V5/MT+ leads to a performance drop in tasks involving the identification of direction in global motion stimuli (Baker, Hess, & Zihl, 1991; Newsome & Paré, 1988; Plant & Nakayama, 1993; Plant, Laxer, Barbaro, Schiffman, & Nakayama, 1993; Schenk & Zihl, 1997; Vaina, Cowey, Eskew, LeMay, & Kemper, 2001). It is thus well established that V5/MT+ plays an essential role in a variety of perceptual tasks.

However, V5/MT+'s role in visuomotor tasks is still unclear. We addressed this question in a recent study with the motion-blind patient LM (Schenk, Mai, Ditterich, & Zihl, 2000). LM's brain damage includes V5/MT+ in both hemispheres, and consequently her ability to perceive visual motion is severely impaired (Zihl et al., 1983, 1991). In our study, we found that she is also impaired in a catching task (Schenk, Mai, et al., 2000). This seems to suggest that V5/MT+ contributes both to perceptual and visuomotor tasks. There is, however, a problem with this conclusion in that LM's lesions go beyond V5/MT+ and extend into surrounding areas (Shipp, de Jong, Zihl, Frackowiak, & Zeki, 1994). The lesions extend dorsally to the intraparietal sulcus, infringing on area 39 at least in her right hemisphere. Her lesions might therefore also include the superior temporal sulcus and the motion-responsive areas in the intraparietal sulcus. These regions have been found in functional imaging studies to respond selectively to visual motion stimuli (Culham et al., 2001).

Given the extent of LM's lesion, it is therefore quite possible that areas other than V5/MT+ are responsible for her deficits. With respect to the perceptual deficits, LM's results have been confirmed by various studies that used transcranial magnetic stimulation (TMS) to induce transient disruptions in V5/MT+. These TMS studies showed that a selective disruption of V5/MT+ produces deficits in the perception of visual motion that are similar to LM's deficits (Beckers & Hömberg, 1992; Beckers & Zeki, 1995; Walsh, Ellison, Battelli, & Cowey, 1998). However, similar TMS studies using visuomotor tasks have not yet been conducted, and it is, therefore, unknown whether a selective disruption of V5/MT+ would also suffice to produce a visuomotor deficit.

It was the aim of the present study to examine this question. We compared the effects of repetitive TMS (rTMS) over V5/MT+ with the effects obtained after stimulation over a control site (vertex) or a site that is approximately 2 cm dorsal to V5/MT+. Two visuomotor tasks were used: a catching task using a moving target object, and a standard reach-to-grasp task with a stationary target object. We expected that if V5 is involved in visuomotor processing, TMS over V5 should interfere with the subjects' ability to predict the course of the target's movement, and thereby impair their catching performance.

2. Methods

2.1. TMS stimulation

We used a MagStim 200 Super Rapid Stimulator with a figure of eight coil (diameter 90 mm; Magstim, Whitland, Dyffed, Wales, UK), which was placed tangential to the surface of the skull with the coil handle pointing backwards at approximately 45° to the spinal cord. The coil was held to the skull by the experimenter using the right hand to hold the coil, and the left hand to stabilize the head against the coil. A head and chin rest was used to minimize head movements during the experiment. After each trial the position of the coil was checked. In three subjects head movements during the experiments were measured and found to be negligible. For these head movement measurements, we used a 3D movement registration system which uses ultrasonic markers. This system is described in more detail below. One marker (coil-marker)

was placed at the centre of the coil, the other marker (reference marker) was placed at the centre of the dorsal surface of the skull (i.e. vertex). We recorded head movements for both the catching and the reach-to-grasp task. Three subjects and 10 trials per subject and task were recorded. To assess the extent of coil-displacement during the period of TMS stimulation, we determined the maximum value of change in the distance between the coil- and the reference marker during the 500 ms Stimulation period. The average value of maximal displacement was less than 0.7 mm (SD: 0.16) during the catching task, and less than 0.8 mm (SD: 0.29) during the reach-to-grasp task.

Repetitive pulse TMS (rTMS) was delivered at 10 Hz for 500 ms at 65% of stimulator output (corresponding to 1.3 T or 110% of the average TMS motor thresholds of our subjects), beginning at the onset of the trial, which was indicated by the opening of the LC shutter glasses (see below).

We stimulated at three different sites: V5, vertex, and a site which was approximately 2 cm dorsal to V5 (dorsal site, DS). To stimulate V5 the centre of the coil is typically positioned 3 cm above the mastoid-inion line and 5 cm lateral to the midline in the sagittal plane (Walsh et al., 1998). However, since it is known that the locus of V5 varies between individuals (Watson et al., 1993), we used the perception of TMS-induced moving phosphenes to confirm the correct position for stimulation in each individual (Stewart, Battelli, Walsh, & Cowey, 1999). The chosen position was typically near the conventional coordinates V5 stimulation (see above). However, deviations of up to 1.5 cm in either direction were found. In five out of six subjects the position of V5 could also be checked anatomically. For those subjects structural MRI scans were available, and it was confirmed with a frameless stereotaxic system (Brainsight^{TM}, Rogue Research, Montreal, Canada) that the chosen stimulation site was near the anatomical landmark for V5 (Dumoulin et al., 2000), namely the intersection of the ascending limb and the posterior continuation of the inferior temporal sulcus. V5 was stimulated unilaterally on the left hemisphere, because previous TMS studies found effects across both hemifields when stimulating over the left hemisphere (Stewart, Ellison, Walsh, & Cowey, 2001). Left hemisphere stimulation, thereby, produces perceptual deficits that are similar to the deficits observed in patient LM (Walsh et al., 1998).

Our second stimulation site was at the vertex. Location of the vertex was determined by finding the intersection of the mid sagittal plane (defined by the nasion to inion line) and the mid coronal plane (defined by the line between the intertrachial notches of the ears). This location corresponds to the position Cz of the 10–20 International EEG system. Stimulation over the vertex provides a good control condition since it evokes all of the unspecific TMS-effects (e.g. noise and tickling sensation), without inducing currents in specific brain areas. In addition we introduced a second control condition to determine the spatial specificity of any effects, which might be found after V5 stimulation. For this purpose we chose a control site that was near to V5, but clearly outside of its borders. To determine the position for this control site, we first localized the V5 site, and then moved the coil dorsally along the surface of the skull until moving phosphenes could no longer be induced. The position of this site (dorsal site, DS) was on average 1.8 cm dorsal (SD: 0.4) to the position of V5.

2.2. Subjects

Six subjects (aged 21–38, three female, three male) participated in this study. All subjects were right-handed, had normal vision, and reported an absence of epilepsy in their family medical history. They consented to take part in the study after they had received information about safety issues relating to TMS and rTMS. Local ethical committee approval was granted for all procedures.

2.3. Tasks and procedures

Two visuomotor tasks were used. The first task was a catching task using a target object that moved away from the subject either to the right or to the left (see Fig. 1A). Two different speed conditions were used (object speed = 0.25 or 0.50 m/s). The parameters of the catching task were the same as those used in the experiment with LM (Schenk, Mai, et al., 2000). The second task was a reach-to-grasp task, in which the target object was stationary (see Fig. 1B). The spatial measurements for the trajectories in the catching task, and the positions of the object in the reach-to-grasp task are presented in Fig. 1. The two tasks were similar with respect to the demands on the motor system, but quite different with respect to their demands on the visual system. In both tasks, subjects had to produce rapid grasping movements. However, only in the catching task, the subject had to take visual information about the target's movement into account. Since V5 is primarily involved in the coding of visual motion, it was expected that V5-specific effects should be found primarily in the catching task.

In both tasks, subjects were instructed to use their right hand. To ensure that the temporal parameters of the subjects' responses were comparable in the two tasks, subjects were asked in both tasks to move as fast as possible. To prevent head movements the subject's head was constrained by a head and chin rest. Ear plugs suppressed the noise coming from the TMS coil and the moving object. At the start of each trial, the subject's right hand rested on a plate (start switch) in front of the body. Subjects wore LC shutter glasses (Plato System, Translucent Technologies, Toronto, Canada), which opened at the beginning of the trial. At the same time the rTMS-sequence was triggered, and in the case of the catching task the object started to move. The LC shutter glasses stayed either open for 100 ms (observation time, OT = 100 ms) or for 800 ms (OT = 800 ms). With an OT of 100 ms, subjects saw the start of the trial, but not the movement of their hand. With an OT of 800 ms, subjects saw the object for the entire duration of the trial, and could also observe the movement of their hand. In the case of LM, we had found that the duration

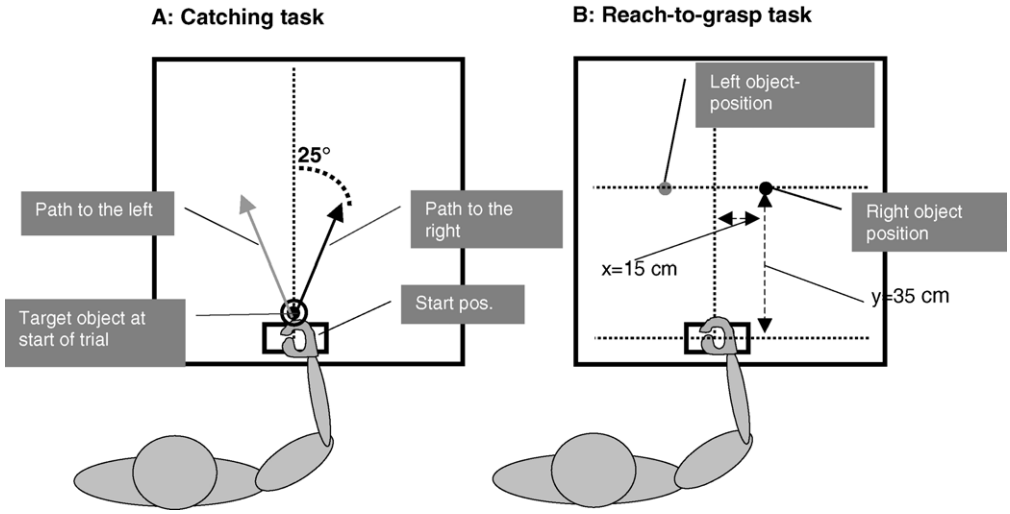

Fig. 1. Set-up for the catching (A) and the reach-to-grasp task (B).

of the OT had a significant effect on her performance. LM caught significantly more objects if she could observe the object for a longer period, and if she could see her hand (Schenk, Mai, et al., 2000).

In each condition 40 trials were presented. The three different TMS conditions (V5, vertex, DS) and the two different visual conditions (100 ms versus 800 ms) were presented in separate blocks. Each block was presented twice; blocks for the different conditions were presented in an interleaved order. The order of the blocks and thus the order of the TMS and visual conditions were counterbalanced across the subjects. Within each block, different types of trials were randomly mixed. In the case of the catching task the trials differed with respect to the direction and speed of the target. In the case of the reach-to-grasp task the trials differed with respect to the position of the object. The two tasks were presented in two separate sessions. At the start of each experimental session, the skull positions for the TMS were determined, and the task was practised for 15 min (40 trials). Each session lasted for approximately 90 min. A short break of approximately 10 min was provided after the first half of the session.

2.4. Apparatus

In this section, we provide a description of the machine that was used to generate the object motion, and the devices used to record the temporal and spatial aspects of the manual response.

2.4.1. System to generate 2D motion of real objects (servo-object-controller, SOC)

This system uses two motor-driven linear axes to move a target object within a horizontal area that covers an area of 1 m^2. The linear axes are covered by a metal plate. Magnets transfer the movement of the linear axes to an object carrier that sits on the surface of the metal plate. The target object itself (small cylinder: weight 15 g, height 6 cm, diameter 4 cm) also contains a weak magnet and sits on the object carrier. This system is controlled by a PC, which also triggers all other events (e.g. opening and closing of LC shutter glasses, start of rTMS-sequence). A detailed description of that system has been provided elsewhere (Schenk, Philipp, et al., 2000).

2.4.2. Measuring the manual response

At the start of each trial subjects rested their hand on a start button which was on the table in front of the centre of their body (see Fig. 1A and B). This start button contained an electronic switch which signalled the beginning of the manual response. The end of the manual response was indicated by another switch that was contained within the target object. As soon as the subject grasped the object the switch within the object was released, and a signal was transmitted to the PC.

In addition a 3D movement registration device was used to record the trajectory of the arm and fingers during the subject's manual response. This registration device employs ultrasonic loudspeakers as markers and a panel with embedded microphones as receivers for the ultrasonic signals. This system (CMS 70, Fa. Zebris, Germany) has a spatial resolution of 0.1 mm and achieves a sampling frequency of 50 Hz when three markers are used. We used three markers to measure both the hand's transport to the target (marker on the wrist, above the styloid process of the ulna) and the opening and closing of the fingers during the grasp (markers on the nails of the index finger and the thumb).

2.5. Data analysis and statistics

Our choice of performance measures was partly based on the results from our study with LM, and partly on the results from other TMS studies, and included measures of accuracy and movement timing. Accuracy was measured by comput-

ing the percentage of trials (%error) in which the subject could catch or grasp the target object. A grasp was only considered to be successful, if the subject could lift the object from the object carrier without dropping it. In our study with LM, we found that her success rate in the catching task was significantly lower than that of healthy subjects. But even in those trials in which LM was able to catch the target object, her performance was not normal. In particular, we found that her reaching speed was lower and more variable than that of healthy subjects (Schenk, Mai, et al., 2000). We therefore decided to compute average *reaching speed* (*RS*) and *peak reaching speed* (V_{max}) as a further performance measure in the present study. We also measured the *relative time when the peak velocity occurred* ($T_{V_{max}}$; this variable is computed in the following way: [time of peak velocity/time of reaching movement] × 100). This variable is often used to assess the relative duration of the acceleration and deceleration phase of the reaching movements. It has been found that the deceleration phase is selectively prolonged in the absence of visual feedback from the moving hand (for a review, see Churchill, Hopkins, Roenqvist, & Vogt, 2000). This suggests that the relative duration of the deceleration phase, and accordingly $\%T_{V_{max}}$ could be used to check for TMS-induced changes in the use of visual feedback from the moving hand. Our last performance measure was reaction time. *Reaction time* (*RT*) is a measure that is frequently used in TMS studies, because it provides a sensitive indication of TMS-induced processing delays.

A further index, that expressed the amplitude of the TMS-effect, was computed for variables that proved to be significantly affected by TMS in one or more conditions. To calculate this index, called %TMS-effect, the following formula was used: $\%\text{TMS-effect}_{PM}(i) = (PM_v - PM_i) \times 100/\text{mean}(PM_v, PM_i)$. In this formula PM stands for a performance measure (i.e. %error, RS or RT), *i* indicates the TMS-site for which %TMS-effect was computed (i.e. either V5 or DS), and subscript v indicates that vertex was used as the reference condition. This index expresses the TMS-effect relative to the performance in the control condition (i.e. vertex) as a normalized percentage-difference.

For the computation of %errors all trials were used. For the computation of the kinematic measures (i.e. RS, V_{max}, $\%T_{V_{max}}$, and RT) some trials had to be discarded, namely those trials in which the subject did not grasp or catch the object, or which contained recording artefacts. However, 94% of the trials could be used. Before reaching speed could be computed, the recording traces had to be filtered using a non-parametric regression method (Marquardt & Mai, 1994). The results from the catching and reach-to-grasp tasks were analysed separately. For the catching task, an ANOVA with the three within-subject factors *TMS* (V5, vertex, DS), *observation time* (100, 800 ms), and *motion direction* (leftward, rightward) was conducted. A similar ANOVA was used for the results from the reach-to-grasp task. Instead of the factor motion direction, the factor *object position* (left, right) was employed. Bonferroni-corrections were used for post-hoc comparisons. A significance-threshold of 5% was adopted.

3. Results

3.1. Task 1: catching task

The factor TMS-site had a significant effect on average reaching speed (RS, $F(2/10) = 9.98$, $P < 0.004$), and peak reaching speed (V_{max}, $F(2/10) = 14.91$, $P < 0.001$). Post-hoc comparisons confirmed that V5 stimulation produced a reduction in RS and V_{max} when compared to stimulation at either of the two control sites (see also Table 1). It should be noted that the factor TMS-site had no effect on %error or on RT.

The factor observation time had a significant effect on %error ($F(1/10) = 7.98$, $P < 0.37$), and RT ($F(1/10) = 18.18$, $P < 0.008$), but not on RS, V_{max}, or $\%T_{V_{max}}$. Shorter observation times led to higher error rates (at 100 ms (mean, S.D.): 6.17%, 2.76; at 800 ms: 1.73%, 1.92), and shorter reaction times (at 100 ms (mean, SD): 182.89 ms, 53.29; at 800 ms: 188.94 ms, 49.36). These effects of observation time are probably best explained if one assumes that subjects produce their best performance when they are able to view the target for more than 100 ms. If subjects are deprived of this option,

Table 1
Catching task: effect of TMS-site

Observation time	TMS	Errors (%)		RT (ms)		RS (m/s)		V_{max} (m/s)		$\%T_{V_{max}}$	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
100.00	V5	6.25	2.31	181.45	50.49	1.11	0.41	1.86	0.18	51.36	7.39
	Vertex	6.24	2.76	179.59	56.43	1.31	0.41	2.01	0.12	51.20	10.45
	DS	6.01	4.06	187.77	52.18	1.32	0.55	2.01	1.82	51.06	7.78
800.00	V5	1.29	1.50	178.94	42.04	0.99	0.29	1.83	1.84	46.14	6.18
	Vertex	1.07	1.92	187.53	50.90	1.13	0.32	1.95	1.60	46.63	9.55
	DS	2.84	2.96	199.72	52.29	1.18	0.34	1.93	1.37	48.04	8.94

Note: These values represent the mean and standard deviations across the group of subjects. As can be seen, the absolute values for RS vary considerably between subjects. Regardless of this variability in RS, the effect of TMS-site on RS was quite consistent. To see this, it is necessary to compute the difference of RS in the different TMS conditions for each subject separately. This has been done to compute %TMS-effect. Fig. 2, which presents the values for the variable %TMS-effect, therefore provides a much more accurate picture of the effect of TMS-site on performance.

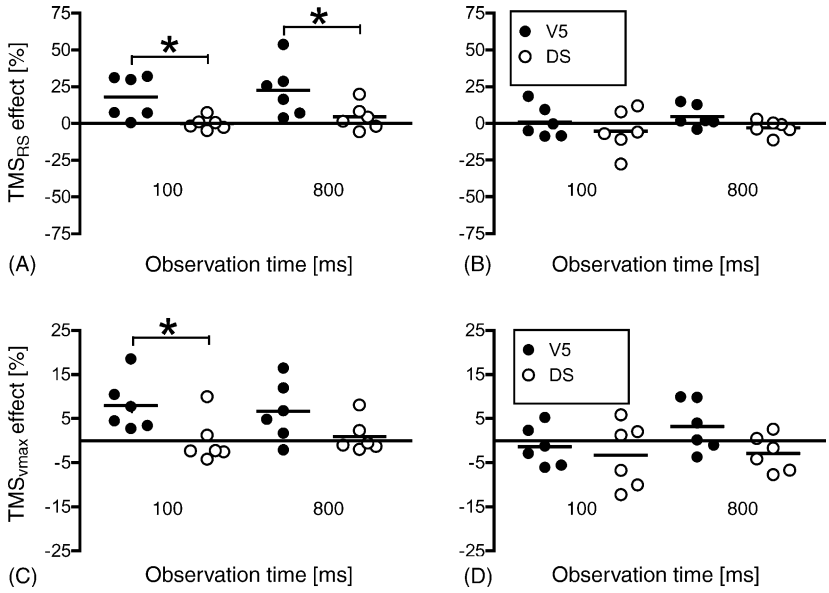

Fig. 2. Comparing the %TMS-effect for stimulation at V5 and DS. A definition of the variable $\%TMS_{RS}$ and $\%TMS_{V_{max}}$ effect is provided in Section 2. (A) and (B) $\%TMS_{RS}$ effect for catching (A) and reach-to-grasp task (B). (C) and (D) $\%TMS_{V_{max}}$ effect for catching (C) and reach-to-grasp task (D).

the accuracy of their movements will suffer (i.e. higher error rates), but at the same time they will be able to initiate their response earlier (i.e. reduced RTs). An alternative explanation could be that subjects launched their reaching movements faster when they anticipated an early closure of the glasses (i.e. OT = 100 ms). In this case, we could also expect that accuracy would drop as a consequence of the well-known speed-accuracy trade-off. Therefore, this explanation would also be consistent with the observed effect of observation time on RTs and error rates. The factor observation time did not modulate the effect of TMS (i.e. no interaction between the factors TMS-site and OT for any of the dependent measures). This result contrasts with the significant effect of OT on LM's catching performance. On the basis of LM's results it might have been expected that TMS stimulation of V5 would lead to more pronounced deficits when the observation time was restricted to 100 ms. The fact that we did not find this effect in this study suggests interesting differences in the behavioural consequences of TMS and lesions. We will explore the reasons for these differences in Section 4.

The factor motion direction did not produce any significant effects, nor were there any significant interaction effects involving the factor motion direction. In particular, the lack of an interaction between the factors TMS-site and motion direction might be unexpected given the fact that we stimulated unilaterally over the left hemisphere. One might therefore have expected to see more pronounced V5-TMS-effects with objects moving to the contralateral hemispace, i.e. the right hemispace. We will return to this issue in Section 4. The results are summarized in Table 1.

To see whether the effect of the factor TMS-site on average and peak reaching speed was specific to stimulation of V5, we conducted a further analysis in which we used $\%TMS_{RS}$ and $\%TMS_{V_{max}}$ (see Section 2, for a definition of %TMS-effect) as the dependent variables for a repeated measures ANOVA with the factors TMS-site (V5 versus DS) and observation time (100 versus 800 ms). A significant effect of factor TMS-site was obtained for both $\%TMS_{RS}$ ($F(1/5) = 10.46$, $P < 0.023$) and $\%TMS_{V_{max}}$ ($F(1/5) = 28.94$, $P < 0.003$). This confirms that the reduction in reaching speed was significantly more pronounced after V5 stimulation than after DS-stimulation. Moreover, one-sample *t*-tests showed that the %TMS-effect differed significantly from zero only in the case of V5 [for H_0 $\%TMS_{RS}(V5) = 0$, $P < 0.03$; for H_0 $\%TMS_{V_{max}}(V5) = 0$, $P < 0.025$], but not in the case of DS-stimulation. The %TMS-effects for the two sites and the two observation times are presented in Fig. 2A. No significant effect of factor observation time, and no interaction effect (TMS-site × observation time) was found.

3.2. Task 2: reaching for a stationary object

The factor TMS-site had no significant effect (see Table 2 and Fig. 2B). Observation time had a significant effect on $\%T_{V_{max}}$ ($F(1/5) = 21.609$, $P < 0.006$), reflecting the fact that peak reaching speed occurred in an earlier portion of the movement, when observation was shorter [$\%T_{V_{max}}$ (means, S.D.) OT = 100: 30.48%, 4.08; OT = 800: 33.51, 4.02]. This means that the deceleration phase was comparatively prolonged in the short-observation time condition. Since the short-observation time condition corresponds to an open-loop condition (i.e. condition where subjects were unable to see their reaching movements), this finding is consistent with that of earlier studies where it was shown that the withdrawal of visual feedback leads to a prolonged duration of the deceler-

Table 2
Reach-to-grasp task: effect of TMS-site

Observation time	TMS	RT (ms)		RS (m/s)		V_{max} (m/s)		$\%T_{V_{max}}$	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
100.00	V5	192.76	50.89	1.06	0.27	1.80	0.25	29.62	4.34
	Vertex	199.94	40.91	1.11	0.18	1.77	0.22	30.55	4.19
	DS	194.28	38.93	1.06	0.22	1.82	0.19	31.28	4.40
800.00	V5	177.54	52.52	1.13	0.32	1.82	0.34	33.07	4.42
	Vertex	188.67	44.11	1.21	0.30	1.87	0.31	33.50	3.75
	DS	185.62	36.80	1.17	0.28	1.92	0.29	33.95	4.40

Table 3
Reach-to-grasp task: effect of object position and observation time

Observation time	Object position	RT (ms)		RS (m/s)	
		Mean	S.D.	Mean	S.D.
100.00	Right	182.91	35.12	1.21	0.25
	Left	208.41	45.50	0.94	0.18
800.00	Right	178.63	46.35	1.30	0.35
	Left	189.26	39.86	1.03	0.26

ation phase (Churchill et al., 2000). Otherwise no significant effects of observation time were obtained.

The factor object position had a significant effect on RT ($F(1/5) = 10.16$, $P < 0.024$), and RS ($F(1/5) = 44.19$, $P < 0.001$). Subjects responded earlier and faster to objects on their right than to objects on their left side [RT (mean, S.D.), right pos.: 180.77 ms, 40.73; left pos.: 198.33 ms, 42.68; RS (mean, S.D.), right pos.: 1.26 m/s, 0.30; left pos.: 0.99 m/s, 0.22, see also Table 3]. We assume that this effect of object position reflects the fact that the head rest slightly hampered movements of the (right) hand towards positions in the left hemispace.

Furthermore, a significant interaction between the factors object position and observation time was found for RT ($F(1/5) = 7.97$, $P < 0.037$). This interaction reflects the fact that RTs for movements towards the leftward position are even more prolonged when the observation time is reduced to 100 ms (see Table 3). We can only speculate why this is the case. We assume that most subjects are even more hesitant to start their movement in the short-observation time condition, because in this condition, they cannot see their response, and therefore subjects might feel that the risk of colliding with the head rest is further increased.

4. Discussion

The results from this TMS study suggest that it is indeed the disruption of processing in V5/MT+ and not the disruption of more dorsal areas that was responsible for LM's catching deficits. By using rTMS we could show that selective interference with V5/MT+ is sufficient to cause a reduction in catching speed. Moreover, we found that stimulation in nearby dorsal regions does not affect catching performance. These findings broadly confirm the findings obtained in our earlier study with the motion-blind patient LM (Schenk, Mai, et al., 2000), and suggest that V5/MT+ is not only involved in purely perceptual but also in visuomotor tasks. One might therefore conclude that V5/MT+ provides visual motion input to both the ventral and the dorsal visual streams.

However, there were also some differences in the findings obtained in the patient and with TMS. The most obvious difference relates to the effect of observation time. LM's performance but not the performance of the healthy subjects was significantly affected by the duration of the observation interval. Her catching performance dropped to subnormal levels if the duration of the observation interval was less than 400 ms (Schenk, Mai, et al., 2000). Accordingly, one might have expected that the effect of V5-TMS would be more pronounced for shorter observation times. However, such an interaction between TMS and observation time was not found. At this stage we can only speculate why this difference occurs. We think the most likely explanation is that LM's dependence on long observation times reflects a compensatory strategy, which she acquired to use her intact spatial vision in order to compensate for her loss of motion vision. Long observation times allowed her to use the length of the path travelled by the moving object during the observation period to estimate the velocity of that object. It is likely that such a compensatory strategy only evolves over time and only in response to the experience of behavioural problems. In the TMS study, subjects had neither the time nor the need to develop a compensatory strategy, since the effect of TMS was only transient and did not produce a dramatic drop in performance.

This leads on to the second difference between the findings in LM and in our TMS study. Whereas LM's deficits were reflected in a decrease in catching speed and in an increase in catching errors, the TMS deficits were only reflected in a decrease in catching speed. This seems to suggest that a catching deficit induced by V5-TMS is much more subtle than a deficit that is caused by a lesion to this area. This is probably not surprising if one considers the fact that rTMS only induces a transient increase of noise in the affected area (Walsh & Rushworth, 1999), and therefore does not faithfully mimic the total disruption of information flow that results from structural brain damage.

Another reason why LM's deficit is more pronounced than the deficit found after V5-TMS might be that the spatial extent

of LM's lesion certainly exceeded the extent of the area which was affected in our rTMS study. Moreover, LM's lesion was bilateral, whereas the stimulation in the present study was only unilateral. Any of these factors could explain why LM's deficit was more pronounced than the deficit which we observed after V5-TMS.

It is in fact rather surprising that the TMS-induced deficits were found equally for objects travelling to both the right and the left hemispace despite the TMS stimulation being restricted to the left hemisphere. This is surprising since we know from electrophysiological (Maunsell & Van Essen, 1987; Van Essen, 1985; Zeki, 1974, 1980) and lesion studies (Newsome & Paré, 1988; Plant & Nakayama, 1993; Plant et al., 1993; Schenk & Zihl, 1997; Vaina et al., 2001) that V5 on each hemisphere contains only a representation of the contralateral visual field. Accordingly one would expect that unilateral TMS of V5 should lead to strictly contralateral deficits. Although some studies confirmed this expectation (Beckers & Hömberg, 1992; Beckers & Zeki, 1995; Stewart et al., 1999), others found whole-field deficits after unilateral TMS (Hotson, Braun, Herzberg, & Boman, 1994; Walsh et al., 1998). One way of explaining such whole-field deficits after unilateral stimulation is by assuming that unilateral TMS disrupts not only the processing in the underlying cortical area but also affects the activity in connected brain areas in the same but also the opposite brain hemisphere (including the area which is homotopic to the stimulated area). In fact, it has been shown in a number of studies that TMS-induced activity is transferred to such connected areas, including the homotopic area of the contralateral hemisphere (Cracco, Amassian, Maccabee, & Cracco, 1989; Ilmoniemi et al., 1997; Komssi et al., 2002; Paus et al., 1997). However, in a combined TMS-ERP study, it was found that although stimulation over left motor cortex induced activity in right-hemispheric sensorimotor areas, this activity was much smaller than the activity in the left hemisphere (Nikulin, Kicicacute, Kahkonen, & Ilmoniemi, 2003). It is therefore quite likely that the induced activity in the opposite hemisphere is too small to cause any disruption of processing and thus too small to cause any performance deficits. The same might be true for area V5. This means that the transfer of activity to the opposite hemisphere offers a possible, but at the moment not very plausible explanation for the observed whole-field deficits after unilateral V5 stimulation.

At least in our study a more plausible explanation for the lack of hemispace differences has to do with fact that subjects in our experiments were free to move their eyes. Since the object always started from a central position, it is quite likely that subjects directed their eyes first towards that central start position, and then followed the object with their eyes during the object's movement to the right or left. In this case the object's image would always be near the centre of the visual field, and consequently no hemispace differences should be expected.

Finally, we would like to return to the effect of V5-TMS on catching performance, and ask more specifically what aspect of the visuomotor processing has been disrupted by interfering with V5/MT+. In principle there are two sources of visual motion during the catching task, which might have been affected by the interference with the processing in the visual motion area V5/MT+. The first and more obvious source is the moving target object; the second source is the movement of the hand during the catching response.

There are three arguments which suggest that it is not the interference with the perception of the moving hand (i.e. on-line visual feedback) that caused the catching deficits. First, if the disruption of visual feedback were to blame for the catching deficits, then similar deficits should have been found in the reach-to-grasp task. This, however, was not the case. Secondly, we would expect that the deficits would only be found when visual feedback is provided. But in fact the TMS-induced catching deficits were also found in the 100 ms condition; yet during that condition on-line visual feedback was not available. Thirdly, we showed recently that visual feedback is not used in the control of catching behaviour (Schenk, Mair, & Zihl, 2003). It would therefore be difficult to explain the TMS-induced changes in catching behaviour, if TMS interferes primarily with the use of visual feedback. Furthermore, it is possible to examine the time-course of the reaching movement to look for changes which might betray effects of TMS on the use of visual feedback. Changes in the time-course have been described in a number of studies in which the effect of visual feedback was examined. In particular, it was found that the deceleration phase is relatively prolonged when visual feedback is withdrawn (for a review, see Churchill et al., 2000). Thus, if we had found a TMS-induced increase in the deceleration phase, this might indicate that the TMS has interfered with the use of visual feedback. However, no such TMS-induced prolongation of the deceleration phase was found. Taken together, our findings suggest that it is not interference with the use of on-line visual feedback, but with the perception of the target's movement that is responsible for the observed V5-TMS-effects.

More specifically, we would like to suggest that it is the degradation of information on the target's speed and not its movement direction that caused the TMS-induced changes in catching speed. This reduction in catching speed most probably reflects an underestimation of the speed of the target object that is induced by interference with V5. Such an underestimation of the speed of visual targets after damage to V5 has been found both for patient LM (Hess et al., 1989; Zihl et al., 1991) and for patients who suffered unilateral damage to V5 (Plant & Nakayama, 1993). Moreover, evidence from neurophysiological and behavioural studies suggests that V5 plays a unique role in velocity perception, whereas V5's contribution to the identification of unambiguous motion direction is much less essential. The range of velocities that are represented in V5 (Lagae et al., 1993; Maunsell & Van Essen, 1983; Mikami et al., 1986; Rodman & Albright, 1987; Van Essen, 1985) extends to much higher values than that for cells in either V1 (Newsome, Mikami, & Wurtz, 1986; Orban, Kennedy, & Bullier, 1986) or V3 (Felleman & Van

Essen, 1987). This means that since disruption of V5 disables the cell-population that codes higher velocities, such velocities are instead coded in lower-velocity cells in V1 or V3, and consequently velocity is underestimated. In contrast faithful direction discrimination can be found not just in V5, but in many more visual areas including V1 and V3 (Van Essen, 1985). Accordingly, disruption of V5 will not lead to a significant deficit in the identification of the direction of a single moving object. This has been confirmed in lesion studies (Baker et al., 1991; Hess et al., 1989; Shipp et al., 1994). We would not expect, therefore, that V5-TMS would cause deficits in the identification of the direction of the target object in our catching task. However, it should be noted that for other types of direction-discrimination tasks, which involve ambiguous stimuli (e.g. random kinematograms or so-called moving plaid patterns), V5 seems to make a unique contribution. This has been found in single-unit studies (Movshon, Adelson, Gizzi, & Newsome, 1985; Salzman & Britten, 1990; Snowden, Treue, & Andersen, 1992), and has been confirmed in lesion (Baker et al., 1991; Marcar, Zihl, & Cowey, 1997) and TMS studies (Beckers & Hömberg, 1992; Beckers & Zeki, 1995).

5. Conclusions

The results from this study confirm that V5/MT+ plays a role not just in perceptual but also in visuomotor tasks that require the processing of visual motion information. It is interesting that although anatomically V5/MT+ is often regarded as part of the dorsal stream, most of the functional studies have focussed on V5's role in purely perceptual tasks. Our results confirm that V5/MT+ also plays a role in vision for action, and thus seems to contribute to both dorsal- and ventral-stream functions. V5's functional contribution to the two streams is consistent with the well-established anatomical fact that V5 projects to areas within both the dorsal and the ventral streams (Felleman & Van Essen, 1991).

Thus, mostly this TMS-study confirms the findings from our earlier study with patient LM. There are, however, also informative differences between the two studies. Most importantly, the dependence on extended observation times that was found in patient LM was not found as a consequence of disrupting V5/MT+ by TMS. It seems that this dependence is only found in the context of a chronic V5 deficit, and is therefore probably not a direct effect of a V5 impairment, but an indirect effect of the long-term adaptation to the motion-blindness resulting from a chronic V5 lesion. This study along with similar studies (Walsh et al., 1998) suggests that the comparison between the effects of TMS and lesions may provide a method to discriminate between the direct behavioural consequences of a lesion that reflect the loss of a specific brain mechanism, and the indirect consequences, which result from neural or behavioural changes that take place in response to the lost brain capacity.

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