

Does interhemispheric competition mediate motion-induced blindness? A transcranial magnetic stimulation study

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Abstract. Motion-induced blindness (MIB) is a phenomenon, perhaps related to perceptual rivalry, where stationary targets disappear and reappear in a cyclic mode when viewed against a background (mask) of coherent, apparent 3-D motion. Since MIB has recently been shown to share similar temporal properties with binocular rivalry, we probed the appearance–disappearance cycle of MIB using unilateral, single-pulse transcranial magnetic stimulation (TMS)—a manipulation that has previously been shown to influence binocular rivalry. Effects were seen for both hemispheres when the timing of TMS was determined prospectively on the basis of a given subject's appearance–disappearance cycle, so that it occurred on average around 300 ms before the time of perceptual switch. Magnetic stimulation of either hemisphere shortened the time to switch from appearance to disappearance and vice versa. However, TMS of left posterior parietal cortex more selectively shortened the disappearance time of the targets if delivered in phase with the disappearance cycle, but lengthened it if TMS was delivered in the appearance phase after the perceptual switch. Opposite effects were seen in the right hemisphere, although less marked than the left-hemisphere effects. As well as sharing temporal characteristics with binocular rivalry, MIB therefore seems to share a similar underlying mechanism of interhemispheric modulation. Interhemispheric switching may thus provide a common temporal framework for uniting the diverse, multilevel phenomena of perceptual rivalry.

1 Introduction

Motion-induced blindness (MIB) belongs to a class of stimuli known as 'visual-disappearance' phenomena, during which apparently salient stimuli cease to be perceived under normal (monocular) viewing conditions. In MIB, the cyclic disappearance and reappearance of bright, stationary targets is brought about by a coherently moving cloud (or mask) of dots, with the effect enhanced by the degree to which target and mask are contrasting in apparent depth, colour, and motion. Bonnef et al (2001), in their description of MIB, also demonstrated that it is subject to Gestalt rules and therefore is not likely to be explicable entirely by peripheral sensory mechanisms. For example, if the targets have different orientations or colours, they are much less likely to disappear at the same time than if they can be grouped perceptually by orientation or colour. Non-sensory attentional mechanisms have instead been suggested to underlie the phenomenon, supported by clinical cases of parietal lesions, where patients experience explicit erasing or disappearance of salient stimuli, otherwise known as 'visual extinction' (Driver et al 2001; Marzi et al 2001; for review, see Marshall and Fink 2001). As several regions within the parietal cortex have been implicated in visuospatial attention, we suggest that visual-disappearance phenomena may incorporate aspects of attentional switching or gating mechanisms.

Binocular rivalry is another form of visual disappearance, whereby orthogonal contours are presented simultaneously to opposite eyes and perceived in alternation. For example, horizontal lines may be presented to the right eye, while vertical lines are simultaneously shown to the left eye; the subject then alternates between these two percepts. Miller et al (2000) argued that an interhemispheric switch may mediate the

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perceptual alternations observed in binocular rivalry. As both MIB and binocular rivalry are visual-disappearance phenomena, it was of interest to determine whether the perceptual phases of MIB might also be influenced by hemispheric asymmetries. This question was highlighted recently by the finding that the dynamics of both MIB and binocular rivalry are very similar in the same subject despite the wide variation between subjects (Carter and Pettigrew 2003). The details of these temporal similarities are compelling in a special case where both phenomena are measured under the influence of psychotomimetic drugs. The striking correspondence between precise details of the bizarre interval histograms in each case raises the possibility of a shared underlying oscillatory mechanism or 'switch'. Intervening in such a fast-switching mechanism is not straightforward experimentally, but Miller et al (2000) were able to show that the precise timing of single-pulse (disruptive) TMS could successfully alter binocular rivalry, if delivered at the appropriate phase of the perceptual switch and to the appropriate hemisphere. Here, we sought to investigate whether unilateral, single-pulse TMS would also produce a phase-specific, hemisphere-specific disruption of MIB.

Phase-specific disruptions of MIB stimulus were produced by TMS of left and right posterior parietal areas, with the disappearance phase being more effectively shortened by in-phase left-hemisphere TMS, and opposite but weaker effects in the right hemisphere. Interhemispheric switching may thus provide a common temporal framework for uniting the diverse, multilevel phenomena of perceptual rivalry.

2 Materials and methods

2.1 Pilot experiments

Eight subjects viewed the version of MIB with three yellow discs, kindly supplied by Yoram Bonne that can be viewed at www.uq.edu.au/nuq/jack/rivalry.html. It was demonstrated that the duration of the appearance–disappearance cycle could be predicted from the binocular-rivalry cycle ($r = 0.62$, $p = \leq 0.0001$). Similarly, the time spent in the disappearance phase correlated with the time subjects observed horizontal gratings in binocular rivalry ($r = 0.53$, $p = 0.01$). A horizontal bias in binocular rivalry reflects more activation in the left hemisphere than in the right hemisphere (Carter and Pettigrew 2003; Miller et al 2000), suggesting that the disappearance of the yellow discs might be preferentially associated with left-hemisphere activity; we tested this hypothesis using TMS synchronous with the perceptual switch (indicated by a key press).

It was shown that left-hemisphere TMS reduced the duration of the disappearance phase to a greater extent than right-hemisphere stimulation with an averaged hemispheric difference of 1.5 (figure 1A), while right-hemisphere TMS induced the reverse phase dominance with an averaged difference of 0.2 (figure 1B, repeated-measures ANOVA, $p = 0.004$). The right-hemisphere appearance-phase effect was more difficult to obtain, reflected in the greater fluctuation of difference values amongst subjects compared with left-hemisphere TMS. Difficulties in altering right-hemisphere function were also observed in binocular-rivalry experiments, where disruption via caloric stimulation or TMS (again synchronous with the perceptual switch) did not produce consistent results (Miller et al 2000). In view of the evidence that the right hemisphere may use shorter time 'blocks' than the left during rivalry (O'Shea and Corballis 2001), we adopted an approach that relied upon the regularity of the cycle of disappearance and reappearance of MIB to deliver TMS pulses in more precise relation to the switch.

2.2 Subjects

Six male and seven female right-handed subjects, aged 18–55 years, and naïve to the experimental hypothesis, were studied both on the binocular-rivalry apparatus already described (Pettigrew and Miller 1998) and on MIB. All subjects gave their written informed consent and completed a medical-history questionnaire for TMS. The study

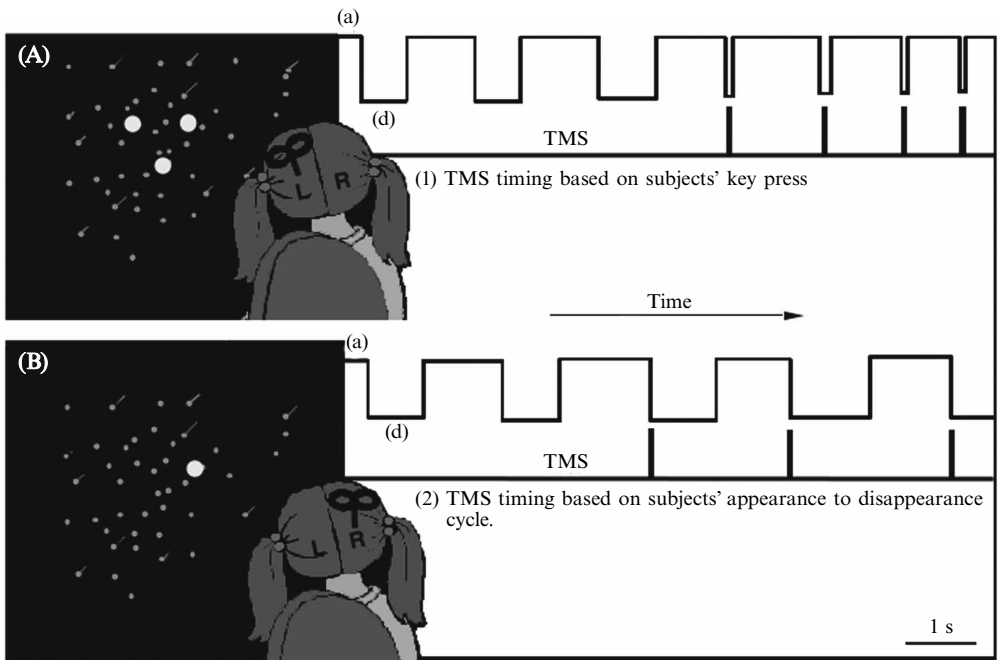


Figure 1. Differential hemispheric effects of TMS on MIB. The subject steadily views the display (A) by fixating the top-right yellow disc and reports the disappearance of either or both of the other two yellow discs (B). All three yellow discs are stationary, while the blue dots swirl in apparent 3-D motion. Single-pulse TMS is delivered to the parietal region of each hemisphere. The timing of the TMS pulse is determined in two different ways: (1) by the subjects' key press [as shown in this example where there are delays associated both with the subject's recognition of the phase shift, where (a) is appearance and (d) disappearance, and the reaction time to key press] and (2) in advance, based on the observed rhythm of each subject's cycle of appearance and disappearance. The rhythm of this cycle is sufficiently regular that a high proportion of preprogrammed pulses can be timed to occur precisely at the phase change of the perceptual switch, or even preceding it. Note that the disappearance phase (d) is disrupted when TMS is delivered to the left hemisphere following a key press, but not by TMS delivered to the right hemisphere. In experiments with preprogrammed pulses where TMS was more precisely coupled to the phase change, we saw elongation of the appearance phase when TMS disrupted right-hemisphere function. A colour version of this figure can be viewed on the *Perception* website at <http://www.perceptionweb.com/misc/p5088/>.

was approved by the University of Queensland Behavioural and Social Sciences Ethical Review Committee.

2.3 Visual stimuli

The MIB stimulus used in the pilot studies was displayed on a 266 MHz Power Macintosh G3 computer with a Mitsubishi Diamond Pro 67TXV colour monitor (resolution 1024×768 pixels, refresh rate 75 Hz, 15 ms frame rate). Each run gathered intervals over 30 min in twelve trials divided into three blocks, to allow rests between, as described earlier (Miller et al 2000, www.bireme.com.au). The display measured $15 \text{ cm} \times 15 \text{ cm}$ and was viewed at 1.5–2.0 m so that the yellow discs subtended around 0.3–0.5 deg. The subject was asked to steadily fixate the top-right yellow disc (blinks and eye movements can cause a premature reappearance of the disappearing discs) and to signal if either of the other discs disappeared by pressing 'B' on the keyboard. The subject was asked to press 'V' if either of these two discs (ie not the subject of fixation) became visible again. All subjects found the task straightforward and provided data with little training. The average disappearance times of our subjects are slightly shorter than

those of Bonneh et al (2001) on the same apparatus, perhaps because our subjects fixated one of the discs rather than the blue, moving part of the display. We adopted our strategy because this gave much more regular cycles than when the moving part of the display was used for fixation. Also, our pilot studies revealed no change in the hemispheric-phase specific effect when the hemifield of fixation was varied.

2.4 Transcranial magnetic stimulation (TMS)

The coil was a 70 mm, figure-of-eight connected to a single-pulse transcranial magnetic stimulator (MagStim 200); trigger timing was controlled with MacProbe (Aristometrics, Castro Valley, CA, USA). Stimulus intensity varied from 50% to 70% and was determined by reference to the motor-cortex threshold. Previous studies showed effective disruption of visual perception at similar outputs (Beckers and Zeki 1995; Hotson and Anand 1999; Miller et al 2000). A calibrated latex cap was used to facilitate the placement of the coil in the same anatomical position for all subjects. The vertex (or top centre) of the cap was aligned with the vertex of the subject. The vertex of each subject was determined with the nasion-inion line (the distance between the nasal bone and inion) and the inter-aural line (the distance from the midpoint of one tragus, over the dorsal surface of the skull to the other tragus midpoint). The point at which the nasion-inion line and the inter-aural line intersected was the vertex of the skull.

TMS was applied to the posterior parietal cortex at coordinates 9 cm dorsal of the inion and 6 cm lateral of the mid-sagittal line, which is thought to correspond to the intraparietal sulcus/superior parietal lobe (Bjoertomt et al 2002; Walsh et al 1999). The coil was held tangential to the skull with the handle pointing towards the back of the skull (Walsh et al 1999). The accuracy of target cortical site location can only be inferred from the references studies, as access to brain imaging technology was not available for this study. More generally, the scalp coordinates used in this study correspond with the P3 and P4 locations of the international 10–20 system used in EEG studies. EEG activity associated with these sites is thought to correspond with parietal function, close to the IPS (Homan et al 1987; Jack et al 1990). There is also the issue of the spread of TMS effects to adjacent cortical areas (Ilmoniemi et al 1997; Pascual-Leone and Meador 1998; Paus et al 1997). This was greatly reduced by the use of a figure-of-eight coil which produces a more focal area of stimulation. Nonetheless, there remains the possibility that the function of cortical areas, other than the targets, may have been disrupted by TMS. The exact anatomical location of the posterior parietal cortex, and the spread of TMS effects are issues which are applicable whenever reference is made to the site of TMS delivery.

2.5 Procedure

The experiment involved three blocks consisting of four trials each, where data were collected for a total of 10 min per block. The baseline cycle of each subject was determined in the first block during which no TMS occurred. We could then anticipate the subject's key press by preprogramming the TMS pulse on the basis of the subject's baseline appearance–disappearance cycle, whose regularity lent itself to this approach (figure 2).

In practice, the preprogrammed TMS pulses occurred at various times just before, precisely at, and just after the phase. In this way we could test the phase specificity of the TMS, both before and after the phase shift in the subject's perception. For the remaining two experimental blocks, TMS was triggered to occur 300 ms before the end of each phase (see figure 3). TMS was semi-randomly delivered to both hemispheres, alternating between the disappearance and reappearance phases. For example, in one block, TMS was delivered during the disappearance phase first to the left hemisphere for two trials, then to the right hemisphere. In the next block, the same order of hemisphere stimulation occurred, except that TMS was delivered during the appearance phase.

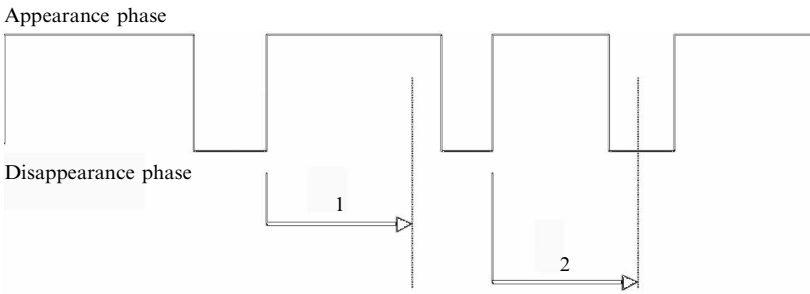


Figure 2. Diagram of preprogramming of TMS pulses. Note that the quasi-regularity of the cyclic disappearances in MIB allow for a prior estimate of the mean phase duration of the appearance phase. By triggering a TMS pulse with a delay after the perceptual switch that corresponds to the mean phase duration (see examples 1 and 2) it is possible to probe the effect of TMS around the time of the next switch if enough trials are collected. In the actual experiment, a delay was used that was the mean phase duration minus 300 ms, to increase the number of TMS pulses that fell just before the switch. In practice, a TMS pulse was programmed to be triggered only every three switches to reduce the possibility of long-term effects and to optimise the comfort of the subject.

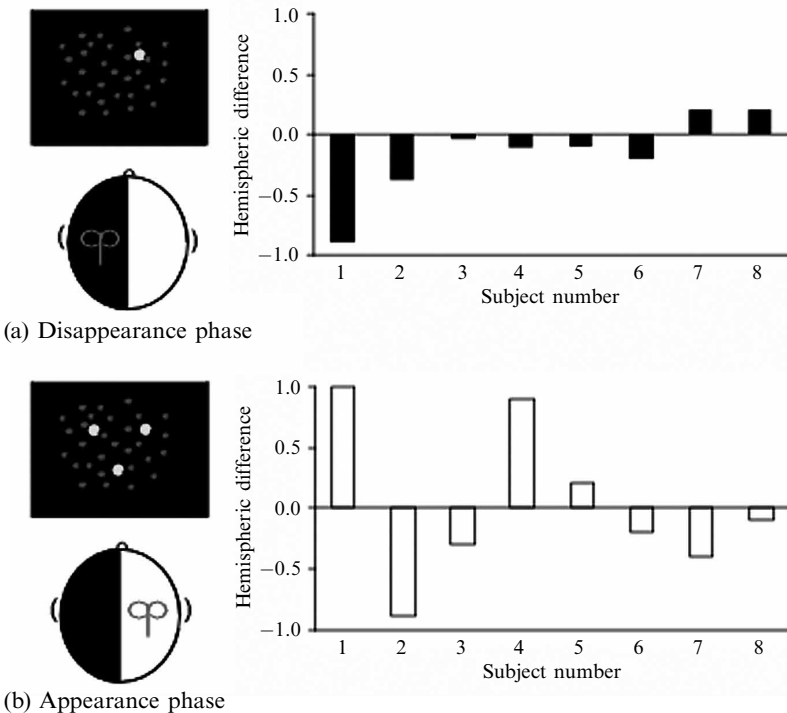


Figure 3. Pilot data showing the hemispheric effects of TMS on the duration of the appearance and disappearance phases. (a) Shows the hemispheric difference following TMS (red coil) of the left hemisphere (black) during the disappearance phase. The graph (black bars) shows the difference between left and right-hemisphere TMS (left disappearance time minus right disappearance time), thus a negative value indicates that left-hemisphere magnetic stimulation induced a shorter disappearance time compared with right-hemisphere stimulation. (b) Shows the results for the opposite (appearance) phase during TMS of the right hemisphere (white). The graph (white bars) indicates the hemispheric difference (right appearance time minus left appearance time), where a negative value indicates that right-hemisphere TMS shortened appearance time to a greater extent than left-hemisphere stimulation. Also, note that right-hemisphere TMS yielded greater fluctuation in difference scores resulting in a less consistent effect compared with left magnetic stimulation. A colour version of this figure can be viewed on the *Perception* website at <http://www.perceptionweb.com/misc/p5088/>.

3 Results

Although TMS was timed to occur 300 ms before the end of the phase switch, in practice the preprogrammed TMS pulses occurred at various times just before, precisely at, and just after the phase switch. As a result, we obtained a spectrum of TMS delivery times (figure 4). Although this range appears rather wide, from approximately 6 s before the switch to 12 s after it, the vast majority of trials (1606 of 1831, 88%) landed within ± 1.25 s of the phase switch. Consequently, we targeted trials within this time range. The graph also shows the larger degree of scatter associated with data for the appearance phase compared with those for the disappearance phase, which parallels the pilot findings of more fluctuation following right-hemisphere stimulation.

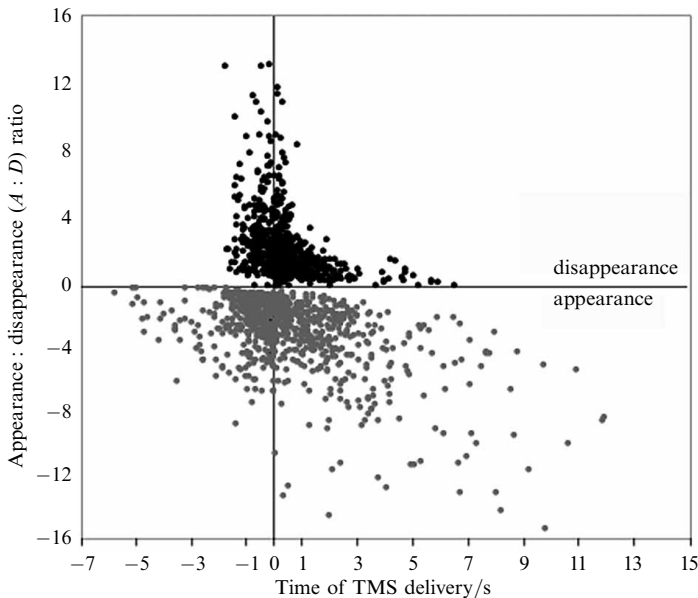


Figure 4. All appearance and disappearance data ($n = 1831$ trials) depicting the effects of TMS on the $A : D$ ratio. Each point represents the ratio of the two perceptual phases occurring around the time of a perceptual switch (0 s). Timing of each pulse is shown in relation to the perceptual switch. TMS pulses were preprogrammed to occur 300 ms prior to the predicted phase shift for each subject, based upon a prior study of each subject's cycle. In practice, this meant that pulses were distributed around the time of the phase shift, with some pulses preceding it. However, the vast majority of trials (88%) fell within ± 1.25 s of the perceptual switch. Note that the appearance-phase TMS data show more scatter than the disappearance-phase data, consistent with previous observations of less robust results following right-hemisphere TMS or caloric stimulation.

The overall effect of TMS on either phase was disruptive, regardless of the hemisphere stimulated. Thus, whichever phase was targeted by TMS, its duration was shortened and the subject's perception biased to the opposite phase. Table 1 lists data within the target time range (± 1.25 s of the phase switch), without considering the time or hemisphere of TMS delivery. Following TMS, the duration of the appearance phase (A) compared with baseline (duration with no stimulation) is shortened in 11 of 13 subjects, and reduced for the disappearance phase (D) in 9 of 13 subjects.

The target time range (± 1.25 s) was divided into ten time groups which are shown in table 2.

The $A : D$ ratio was determined for each TMS trial, and the difference between this ratio and that obtained for the baseline was calculated, yielding the $A : D$ baseline difference. A positive difference would reflect a bias toward the appearance phase; a negative difference would indicate a disappearance-phase bias.

Table 1. Difference between the baseline and TMS appearance and disappearance-phase durations averaged across both hemispheres, indicating that the overall effect of TMS was disruptive regardless of the time or hemisphere of TMS delivery. The data are from the target-time range of ± 1.25 s of the phase switch. A negative difference score indicates TMS shortened the phase in comparison with the baseline. The durations are shortened in 11 of 13 subjects (appearance) and 9 of 13 subjects (disappearance).

Phase	Subject	Baseline duration/s	TMS duration/s	Difference/s
Appearance	1	3.09	1.90	-1.18
	2	5.97	6.59	+0.62
	3	1.87	1.49	-0.37
	4	3.25	2.62	-0.63
	5	3.16	2.84	-0.31
	6	2.48	1.68	-0.81
	7	3.20	2.24	-0.96
	8	2.82	2.80	-0.02
	9	2.97	2.37	-0.60
	10	4.28	5.00	+0.72
	11	2.33	2.25	-0.07
	12	3.59	2.73	-0.86
	13	5.32	4.31	-1.01
Disappearance	1	1.30	1.38	+0.08
	2	1.96	1.37	-0.59
	3	2.27	1.75	-0.5
	4	2.42	1.96	-0.5
	5	3.33	3.00	-0.3
	6	1.80	1.72	-0.1
	7	1.92	1.73	-0.2
	8	1.78	1.61	-0.2
	9	0.97	1.14	+0.2
	10	2.56	3.06	+0.5
	11	1.37	1.55	+0.2
	12	2.02	1.78	-0.2
	13	1.68	1.51	-0.2

Table 2. The ten time groups into which the target time (-0.125 to 1.25 s) was divided. The groups are constructed so that running averages are obtained, in order to acquire a smoother representation of the perceptual cycles, especially close to the switch.

Time group	Time range/s
1	1.25–1.0
2	1.125–0.875
3	1.0–0.75
4	0.875–0.625
5	0.75–0.5
6	0.625–0.375
7	0.5–0.25
8	0.375–0.125
9	0.25–0
10	-0.125–0.125

Note: Group 10 indicates ± 0.125 s of the switch.

The ratio difference obtained following stimulation of both hemispheres was compared over all time groups for each perceptual phase by using linear regression. All factors were significant: (i) hemisphere of TMS ($p = 0.0247$), (ii) MIB phase ($p < 0.0001$), and (iii) time group ($p < 0.0001$). The analysis showed that left-hemisphere

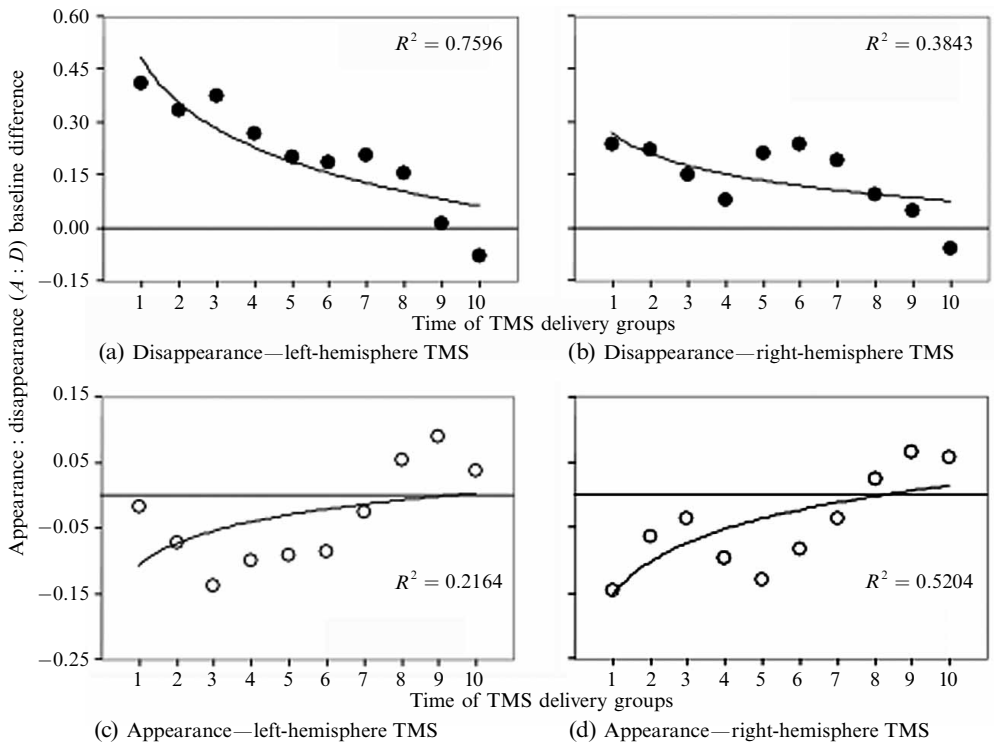


Figure 5. Comparison of disappearance phase (solid circles) and appearance phase (open circles) following TMS of the left and right hemispheres. The y -axis depicts the mean difference between the baseline cycle rate and the $A : D$ ratio. A stronger correlation between the $A : D$ baseline difference and time of TMS delivery follows the hemispheric-phase specific effect. Specifically (a) shows that for the disappearance phase left-hemisphere TMS is more strongly correlated with TMS delivery time ($R^2 = 0.7596$) than (b) right-hemisphere stimulation ($R^2 = 0.3843$). The appearance phase has a stronger correlation between (d) right-hemisphere TMS and delivery time ($R^2 = 0.5204$) compared with (c) left-hemisphere stimulation ($R^2 = 0.2164$).

TMS during the disappearance phase had a stronger correlation ($R^2 = 0.7596$, figure 5a) compared with right-hemisphere stimulation ($R^2 = 0.3843$, figure 5b). Accordingly, 58% of the variability in ratio difference could be predicted from the time of TMS delivery to the left hemisphere. The appearance phase showed the opposite hemispheric effect with right-hemisphere TMS having a larger correlation ($R^2 = 0.5204$, 27%, figure 5d) than left-hemisphere stimulation ($R^2 = 0.2164$, figure 5c). The results indicate that a greater proportion of the variability in ratio difference could be predicted from left-hemisphere TMS during the disappearance phase (58%) than from right-hemisphere TMS during the appearance phase (27%).

Each time group was examined for hemispheric asymmetries (figure 6). Tukey's 'honestly significant difference' test revealed that, for time groups 1–4 (1.25 s to 0.625 s inclusive), TMS delivered to the left hemisphere shortened the disappearance time to a greater extent than right-hemisphere stimulation (time groups 1–3, $p < 0.01$; time group 4, $p < 0.05$). A right-hemispheric bias for the appearance phase occurred in time group 4 (0.625 s to 0.875 s, $p < 0.05$); indicating that TMS delivery must occur in a smaller time window compared with the left hemisphere. The size of the hemispheric difference was much greater for the disappearance phase, where the ratio increased by +1.57 (averaged over time groups 1–4). As the ratio increased, this indicates that the disappearance phase was shortened. The right-hemispheric bias for the appearance phase was reflected in a negative ratio difference of -0.6 . In this case, the ratio decreased,

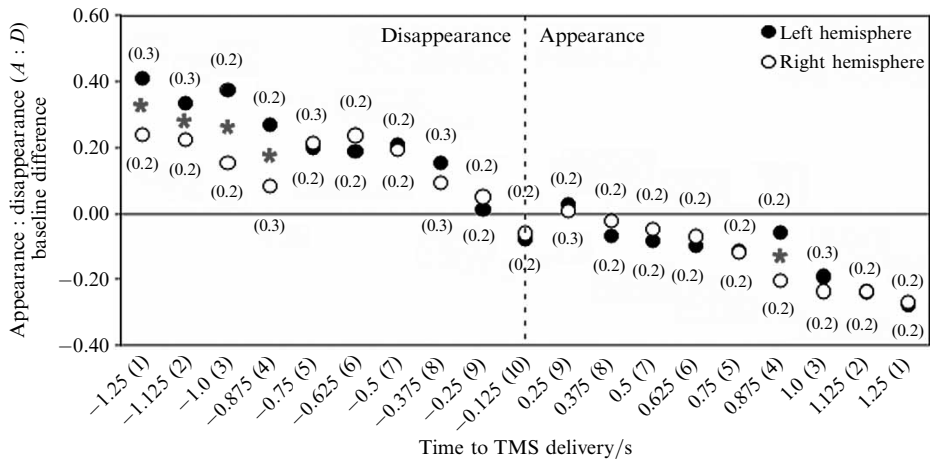


Figure 6. Comparison of hemispheric asymmetries observed for each TMS time group during both the disappearance and appearance phase. The y -axis depicts the mean difference between the baseline cycle rate and the $A : D$ ratio. Time group 10 approximates the perceptual switch, and time groups preceding the switch (negative values) are contained in the disappearance phase, while those after the switch (positive values) are within the appearance phase. Note that the negative and positive values are arbitrarily set, and simply provide a means of delineating between the disappearance and appearance phases. The averaged difference for the disappearance phase (+1.57) was much greater than for appearance (-0.6). Importantly, the positive increase for the disappearance phase (+1.57) indicates that left-hemisphere TMS shortened disappearance and lengthened appearance to a greater degree than right-hemisphere TMS. The negative difference for appearance (-0.6) reflects greater shortening of the appearance phase and lengthening of disappearance following right-hemisphere TMS. These results show the reciprocal nature of the perceptual phase changes. Note the smaller time window required to induce hemispheric asymmetry for appearance-phase stimulation (250 ms) compared with disappearance-phase stimulation (625 ms); the asterisk indicates significant difference between hemispheres (time groups 1–3, $p < 0.01$; time group 4, $p < 0.05$). SD is shown in parentheses. A colour version of this figure can be viewed on the *Perception* website at <http://www.perceptionweb.com/misc/p5088/>.

thus reflecting shortening of the appearance phase, and lengthening of disappearance—an important result that confirms the reciprocal nature of the phase changes that can be produced by the appropriate combination of phase and hemisphere.

4 Discussion

We have demonstrated that TMS of either hemisphere can disrupt the appearance and disappearance phases of MIB. However, the analysis revealed that left-hemisphere TMS can more selectively disrupt the disappearance phase of MIB. The effect of right-hemisphere TMS was to disrupt the appearance phase of the illusion to a greater extent than the disappearance phase. Initially one might be tempted to assume that our results are the consequence of an asymmetric stimulus presentation, whereby the fixation point is in the right hemifield and the yellow dots in the left. However, our results are directly opposite of a contralateral hemisphere-hemifield representation. If this were the case, then one would predict that TMS of the *right* hemisphere should result in the disappearance of the yellow dots (which are in the left hemifield). Furthermore, the left-hemisphere bias for suppression or disappearance has been observed in other studies which did not selectively stimulate the two hemifields (eg Miller et al 2000). Also, recall that in our pilot studies hemispheric phase specificity persisted regardless of hemifield of fixation.

Given a reported preference of the left hemisphere for motion processing (eg Beckers and Homberg 1992; Corbetta et al 1991; Pike and Polich 1988; Sunaert et al 1999; Zeki 1991), it is possible that the left-hemisphere effect was due to specific disruption of motion processing. This deserves further study and consequently disruption of MIB requires further investigation, by, for example, applying TMS to area MT while subjects observe the MIB stimulus. Theoretically, interference with area-MT function should disrupt perception of the moving global sphere as motion processing, and specifically 3-D motion (Bradley et al 1998; Maunsell and Van Essen 1983; Siegel and Andersen 1988) has been shown to involve area MT. In preliminary experiments, TMS of area MT gave consistent effects on MIB (A P Funk, unpublished).

On the other hand, since opposite effects were seen in the right hemisphere, a more general hypothesis would involve the contrasting cognitive styles of the two hemispheres, which compete with each other along the same cognitive dimension. The notion of complementary cognitive styles has been compellingly illustrated by Ramachandran (1994) in anosognosia patients, who formulated a left-sided 'general' with a specific plan and a tendency to ignore (deny) discrepancies compared with the more veridical 'devil's advocate' on the right—that serves to highlight discrepancies rather than deny them. Ramachandran's hypothesis may reflect the hemisphere phase specificity reported in the current study, whereby left-hemisphere TMS resulted in the disruption of the 'denial' process and consequently the disappearance phase. Right-hemisphere stimulation would have interfered with the 'comparator' function, resulting in the disruption of the veridical appearance phase. As the appearance phase was the correct veridical perception, this may have been why the right hemisphere was more difficult to disrupt overall.

Although the anosognosia patients in Ramachandran's study showed rather extreme behaviours, this is indicative of the level of damage sustained to their cortex. In this study, cortical processing was disrupted briefly and temporarily, perhaps being more indicative of the switching and 'denial' processes that occur during normal visual perception. Given that the natural visual world is full of perceptual ambiguities (Purves et al 1999), cyclic fluctuations may be a more common feature of visual perception than previously realised, perhaps because a significant fraction of the cycle escapes attention in 'denial'.

Recent evidence for interhemispheric competition between homologous cortical areas includes: (i) TMS studies of Broca's area in aphasic patients whose function is paradoxically improved by disrupting the right cortex, contralateral to the lesion (Naeser et al 2002); (ii) TMS studies of parietal areas where attention is paradoxically improved in the hemifield ipsilateral to the disrupted cortex (Hilgetag et al 2001); (iii) TMS studies of extinction after parietal lesions where function is improved by disruption of the intact side of the brain (Oliveri et al 2000). All of these studies are difficult to understand in terms of traditional ideas that homologous cortical regions cooperate with each other across the midline. Yet they follow directly from the model presented by Ramachandran (1994), and are further supported here, where there is interhemispheric modulation between homologous cortical regions on each side, whose functions will therefore be complementary.

There is the possibility that attentional switching mechanisms may also be involved in the hemispheric phase specific effects observed in this study. The greater effect found for the left-hemisphere disappearance bias may reflect the role this hemisphere has in the switching of attention. Recall that Bonneh et al (2001) suggested that MIB may allow the observation of the attentional switch between objects, because of its configuration which allows one to become conscious that a stimulus has just been 'denied'. Human-brain imaging evidence suggests that parietal regions are preferentially involved

in attentional switching tasks (Corbetta et al 2000; Hopfinger et al 2000; Wojciulik and Kanwisher 1999), and that these may be more active in the left hemisphere (Dove et al 2000; Rushworth et al 2001; Sohn et al 2000). Perhaps the more pronounced left posterior parietal TMS effect found in the current study reflects disruption of the attentional switching mechanism. Alternatively, it could be argued that the disruption of the right hemisphere was more difficult to achieve owing to its involvement in visuospatial attention. However, the timing data of the current study suggest that the smaller time window required to disrupt right-hemisphere function is more likely the source of the weaker right-hemisphere appearance-phase effect. Further investigation into whether and how attention and perceptual switching interact would be important to establish the underlying neural mechanisms of visual perception.

4.1 *Alternative explanation for TMS effects on MIB? Eye-movement artifact?*

Since the disappearance phase of MIB can be terminated by saccadic eye movements and other transient stimuli, it might be argued that our left-hemisphere TMS effects are mediated indirectly by transients, such as a saccade, associated with the TMS pulse. This explanation is unlikely, as right-hemisphere TMS does not shorten the disappearance phase to the same extent as left-hemisphere stimulation, even though it is exposed to the same transient stimuli. The asymmetry between the effects of right-hemisphere and left-hemisphere TMS argues against any indirect explanation that would be shared in both cases, such as the induction of saccades via TMS. In addition, studies have demonstrated that TMS of the parietal region does not evoke eye movements (Muri et al 1999; Wessel and Kompf 1991) and that the parietal region is independent of eye-movement processes (fMRI: Connolly et al 2002; Le et al 1998; Wojciulik and Kanwisher 1999; PET: Coull et al 1996). However, other TMS studies have shown alteration of saccade latency (Kapoula et al 2001) and disruption (Van Donkelaar et al 2000; Van Donkelaar and Muri 2002; Leff et al 2001), the timing of which was in the order of 100 ms or thereabouts, often before saccade onset. The effective TMS time reported in the current study was between 1.25 s and 0.625 s; well outside of the time range required to disrupt saccades.

Instead, it seems likely that this asymmetry in effect on MIB is a result of asymmetry between the two sides of the brain. This conclusion is further reinforced by the fact that TMS, as well as producing a shortened disappearance phase, can also produce a lengthening of the disappearance phase when applied at the appropriate combination of phase and hemisphere. Such a lengthening is difficult to explain by any indirect effect of TMS. The lengthening of the disappearance phase seen in figure 6 when the TMS pulse is applied to the left hemisphere during the appearance phase, or when TMS is delivered to the right hemisphere during the disappearance phase, is more parsimoniously explained by its effect on interhemispheric balance. This explanation is further supported when taken together with the demonstration that MIB shares a timing mechanism with binocular rivalry, which may function through interhemispheric modulation, the evidence of which comes from several sources, including caloric vestibular stimulation as well as TMS.

4.2 *Timing effects of TMS*

Clear effects on perceptual rivalry, of intervening with right-hemisphere function, are difficult to obtain. In the case of binocular rivalry, right-hemisphere TMS had more variable, weaker, and generally less-significant effects compared to left-hemisphere TMS, in most subjects (Miller et al 2000). In the present study, we saw significant right-hemisphere effects, although not as prominent as those on the left hemisphere. We attribute this improvement in right-hemisphere effects to refinements in the timing of the TMS pulse in relation to the perceptual switch. The timing data showed that the right-hemisphere effect was restricted to a smaller time window (250 ms) compared

with the left hemisphere (625 ms) (see figure 6). This supports the findings of O'Shea and Corballis (2001) that the right hemisphere uses 'shorter' time blocks during rivalry. Perhaps further refinement of the spatial location, as well as the timing, of the TMS pulse will see even more control of right-hemisphere function.

The strongest hemispheric TMS effects for the disappearance phase were observed in the 1 s range (time groups 1–3, figure 6). This corresponds with the rhythmic 1 s timing observed in a subject who had taken the hallucinogen LSD 10 h before being tested with binocular rivalry and MIB (Carter and Pettigrew 2003). Although any conclusions drawn from this can only be speculative at this point, it is possible that these results reflect the consequences of exogenous disruption of the oscillation process associated with perceptual rivalry, the rhythmicity of which falls into 1 s harmonic intervals.

4.3 Conclusion

The observations, taken together with the similarity of timing mechanisms in binocular rivalry and MIB, suggest that MIB may be a special, asymmetrical case of perceptual rivalry where different interpretations of the same stimulus are adopted by different hemispheres. The right hemisphere seems to adopt a veridical representation with appropriate weight given to all physical stimuli present, even the stationary yellow discs that are so distinct from the swirling blue motion. In contrast, the left hemisphere adopts an interpretation that rejects the discrepant discs because they cannot be incorporated into the coherent percept of motion and different colour. The consequence of the left-hemisphere process is that the discrepant targets become invisible for a time, until the right hemisphere dominates the balance of activation. In Ramachandran's (1994) formulation, the pattern-seeking left hemisphere is likely to adopt an interpretation or hypothesis that is internally consistent, and then to deny discrepancies that do not fit with that interpretation. If our interpretation is correct, as well as the complex attributes studied by Ramachandran, left-hemisphere denial may also involve the disappearance of much simpler visual percepts, as in MIB. The findings also raise the possibility that the cyclic nature of rivalry may be more general to visual perception and not confined to symmetrical, mutually exclusive percepts, such as the Necker cube and binocular rivalry. Given the widespread occurrence of inescapable ambiguities in the natural visual world (eg Purves et al 1999; Purves and Lotto 2002), the strong similarities between MIB and more well-recognised rivalries suggest that cyclic perceptual fluctuations may be a more general feature of visual perception than is commonly realised. In addition, these findings, in support of an interhemispheric switching model, enable the multilevel phenomena of perceptual rivalry (Blake and Logothetis 2002) to be unified in a shared temporal framework despite the diversity in the quality of the alternating percepts.

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