

Double Dissociation of V1 and V5/MT activity in Visual Awareness

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The critical time windows of the contribution of V1 and V5/MT to visual awareness of moving visual stimuli were compared by administering transcranial magnetic stimulation (TMS) to V1 or V5/MT in various time intervals from stimulus offset during performance of a simple motion detection task. Our results show a double dissociation in which the critical period of V1 both predates and postdates that of V5/MT, and where stimulation of either V1 at V5/MT's critical period or V5/MT at V1's critical period does not impair performance. These findings demonstrate the importance of back-projections from V5/MT to V1 in awareness of real motion stimuli.

Keywords: awareness, back-projections, motion detection, transcranial magnetic stimulation, V1, V5/MT

Introduction

The contribution of the primary visual cortex (V1) to visual awareness is a question that has raised much recent controversy. On some views V1 activity is not needed for awareness, which can arise simply as a result of activity in feature-specialized neurons in extrastriate cortex, with any integration of activation across visual areas being post-conscious. In this view, for example, activity in movement-specialized extrastriate area V5/MT is necessary and sufficient for awareness or 'microconsciousness' of visual motion (Zeki and Bartels, 1999). On other views V1 cannot participate in phenomenal vision because it is not directly connected with the frontal lobe (e.g. Crick and Koch, 1995).

By contrast, however, the phenomenon of blindsight, namely, the manifestation of some visual processing despite the total loss of visual awareness caused by damage to V1 (e.g. Weiskrantz, 1986, 1997; Cowey and Stoerig, 1991), appears to suggest a role for V1 in awareness. There is also a growing body of literature which suggests that activity in V1 correlates with awareness. Super *et al.* (2001), for example, have found that neurons in V1 are selectively suppressed when a monkey does not perceive a visual stimulus. Functional neuroimaging with human subjects has revealed that activity in early visual cortex, and in particular V1, is predictive of whether or not a subject will perceive a stimulus (Ress and Heeger, 2003). Indeed, even in the absence of a visual stimulus, if a subject makes a false alarm response, activity in V1 resembles that seen on trials in which the subject was presented with and saw a stimulus. There is ample evidence of back-projections from higher visual areas to V1 (Lamme *et al.*, 2000; Bullier, 2001; Hupe *et al.*, 2001; Hochstein and Ahissar, 2002; Foxe and Simpson, 2002; Juan and Walsh, 2003). However, while several studies show either V1 to be important for awareness (e.g. Cowey and Walsh, 2000; Ress and Heeger, 2003) or back-projections to be important for some aspects of visual perception (e.g. figure-ground segregation;

Hupe *et al.*, 2001; Angelucci *et al.*, 2002), it has not been directly demonstrated that it is the recursive neural network between the extrastriate and striate cortex that is necessary for human visual awareness. The studies mentioned above do not establish whether it is the feedback or the feed-forward sweep of information that is the critical factor. An encouraging result was found in a transcranial magnetic stimulation (TMS) study in humans which showed that when TMS over V5/MT is delivered at intensities sufficient to induce perception of moving phosphenes, a subsequent TMS pulse (that is subthreshold for eliciting phosphenes) delivered over V1, 5–45 ms after V5/MT stimulation, can degrade or remove the sensation of moving phosphenes (Pascual-Leone and Walsh, 2001).

Although this finding suggests that back-projections to V1 play a role in induced perception of moving phosphenes, it falls short of demonstrating a role for back-projections to V1 in normal visual awareness of real motion because no feed-forward sweep was possible in the absence of external visual stimuli, as is the case when a real motion stimulus is present. What is required to establish the case of recurrent neural networks in visual awareness is a temporal dissociation between the contributions of extrastriate and striate cortex (see Pollen, 2003).

In the present study we administered TMS over V1 or V5/MT in different time windows during performance of a motion detection task in order to trace the flow of information that gives rise to awareness. Three accounts make different predictions about the location and timing of TMS effects over striate and extrastriate areas. According to the 'microconsciousness' account (Zeki and Bartels, 1999), activity in any secondary visual area is sufficient to generate a conscious visual percept without requiring any feedback activity in V1. In motion detection this account has led to suggestions that activation of V5/MT is sufficient for motion awareness (Barbur *et al.*, 1993): once motion information has reached V5/MT, V1 is no longer necessary for motion detection. This view predicts that TMS over V1 should only lead to disruption during feed-forward activity, and hence the critical time window of disruption by TMS over V5/MT should post-date that of disruptions caused by applying TMS over V1.

It is also possible that the activity between V1 and extrastriate cortex needs to be in synchrony for awareness to arise. The prediction from this synchronous activity theory is that the phenomenal experience of a particular attribute requires near-simultaneously experienced percepts in a number of cortical areas involved in the processing of that stimulus (Pollen, 1999). Thus TMS disruptions of motion detection should be affected by applying TMS over either V1 or V5 at similar times after stimulus onset.

If back-projections from V5/MT to V1 are necessary for motion awareness, however, TMS applied over V1 should

disrupt motion detection at a later point in time than V5/MT stimulation, in addition to an earlier time window reflecting the role of V1 feed-forward projections. As mentioned earlier, one previous study suggested that TMS over V1 following TMS over V5 disrupts induced perception of moving phosphenes (Pascual-Leone and Walsh, 2001). However, the method of inducing moving phosphenes by TMS over V5/MT necessitated stimulation of V5/MT before V1, and thus precluded comparison of the critical time windows for activity in V1 and V5/MT in awareness of motion. Nor did it allow any clear conclusion about the role of back-projections to V1 in awareness of real motion rather than induced phosphene motion. This is important because of the possibility that interactions are different in the absence of a V1 input from the retina (Covey and Walsh, 2000). Here, in three experiments, we control for the spatial localization, the temporal specificity and the task specificity of TMS effects to test these three competing predictions and to probe the timing of interactions between human V5/MT and V1.

Materials and Methods

Experiment 1

Participants

Seven participants, five of whom were naive to the objective of the study, took part in experiment 1. The two other participants were authors J.S. and V.W., and they were naive to the timing of stimulation in each TMS block. All experiments were undertaken with the understanding and written consent of each subject. Subjects were treated in accordance with the Declaration of Helsinki.

Stimuli

The stimuli were presented on a 19" (800 × 600 pixels) monitor. Viewing distance was 100 cm. Each trial began with a fixation point appearing in the middle of the screen for 500 ms. The motion stimulus consisted of 80 yellow dots (1 pixel each) placed at random positions within an imaginary square subtending $0.72 \times 0.72^\circ$ of visual angle moving coherently either right or left on a black background. The displacement of the dots on motion trials was one pixel per frame. On 'no motion' trials, the dots were stationary. Stimuli were presented for either 48 or 64 ms, with the motion stimulus consisting of either three or four frames lasting for 16 ms each (see Fig. 1).

Location of Stimulation

TMS was administered with a Magstim Super Rapid stimulator (Magstim Company, UK). The coil was a 70 mm figure-eight coil, held with the handle pointing directly upwards. V1 and V5/MT were localized using a functional method in which the center of the coil is placed on the surface of the skull such that the stimulation elicits phosphenes that

intrude on the center of the visual field, i.e. the target location (for a discussion of this method, see Walsh and Pascual-Leone, 2003). For V1, the starting point of stimulation was 2 cm dorsal from theinion. The coil was then moved slightly to find a region from which the clearest phosphenes could be obtained, ending up in an average coil position for V1 stimulation 2.0 cm dorsal and 0.5 cm lateral from theinion. Initially, the intensity of stimulation was 70% of TMS output, and it was increased if participants failed to perceive any phosphenes. It should be noted that although such occipital stimulation will clearly disrupt V1, it may have also affected areas close to V1, including V2. However, because perception of phosphenes is not possible without activity in V1 (Covey and Walsh, 2000; Pascual-Leone and Walsh, 2001), and V1 is the likeliest site of stimulation (Kammer *et al.*, 2001), it is parsimonious to attribute the effects in our study to V1 stimulation (see also Campana *et al.*, 2002).

For V5/MT, the starting location for stimulation was 2 cm dorsal and 4 cm lateral from theinion. The coil was then moved slightly to find a region from which moving phosphenes could be induced (the reliability of this method in locating V5/MT has been demonstrated by Stewart *et al.*, 1999), giving an average coil position 3.1 cm dorsal and 5.1 cm lateral from theinion. V5/MT in the left hemisphere was stimulated in all participants because it has consistently been found to produce phosphenes more reliably than the right hemisphere (Beckers and Hömberg, 1992; Stewart *et al.*, 1999; Antal *et al.*, 2001). Due to the size of the cortical surface area covered by the figure-of-eight coil, it is likely that the satellites of V5/MT (e.g. MST) are also affected by this stimulation (see Fig. 2 for stimulation sites).

For the experimental blocks in both experiments, the intensity of TMS was decreased to 60%, at which none of the participants reported phosphenes during the experimental blocks.

Stimulation Onsets

There were six TMS conditions with double-pulse TMS applied at either 60 and 80 ms, 80 and 100 ms or 100 and 120 ms from stimulus offset over V1 or V5/MT (124 and 144 ms, 144 and 164 ms or 164 and 184 ms from stimulus onset for five participants; 108 and 128 ms, 128 and 148 ms and 148 and 168 ms for two participants). Double pulses of TMS were applied in order to make use of the summation properties of TMS pulses — double-pulse TMS gives larger effects than single-pulse TMS (as one would expect) but still allows good temporal resolution defined by the temporal distance between the two pulses (see Walsh and Pascual-Leone, 2003). These stimulation onsets are consistent with experiments that have used TMS to address the timing of V5/MT activity in tasks involving moving random-dot patterns. For instance, Hotson and Anand (1998) and Anand *et al.* (1999) disrupted direction discrimination of a moving random-dot pattern by administering single-pulse TMS over V5/MT between 100 and 175 ms from stimulus onset. Disruption of motion speed judgements as a result of V1 stimulation within this time window has also been observed (Matthews *et al.*, 2001).

Procedure

The participants' task was to report whether or not they detected motion in the display. Each of the TMS conditions was run in one block

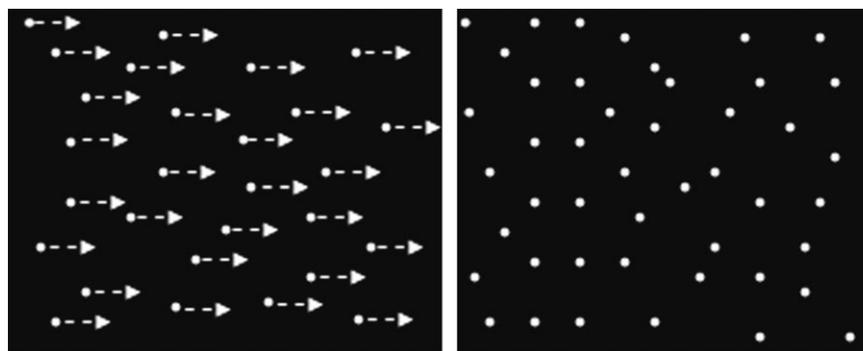


Figure 1. An example of motion stimulus used in experiments 1 and 3 (left). The arrows illustrate motion to the right. On motion present trials, all dots moved either to the left or to the right. On motion absent trials, all dots were stationary. The right panel shows an example of the stationary stimulus in the 'present' trials of experiment 2. The figure shows a path-like pattern amongst randomly distributed dots. On absent trials, all dots were distributed randomly. Both stimuli consisted of 80 dots.

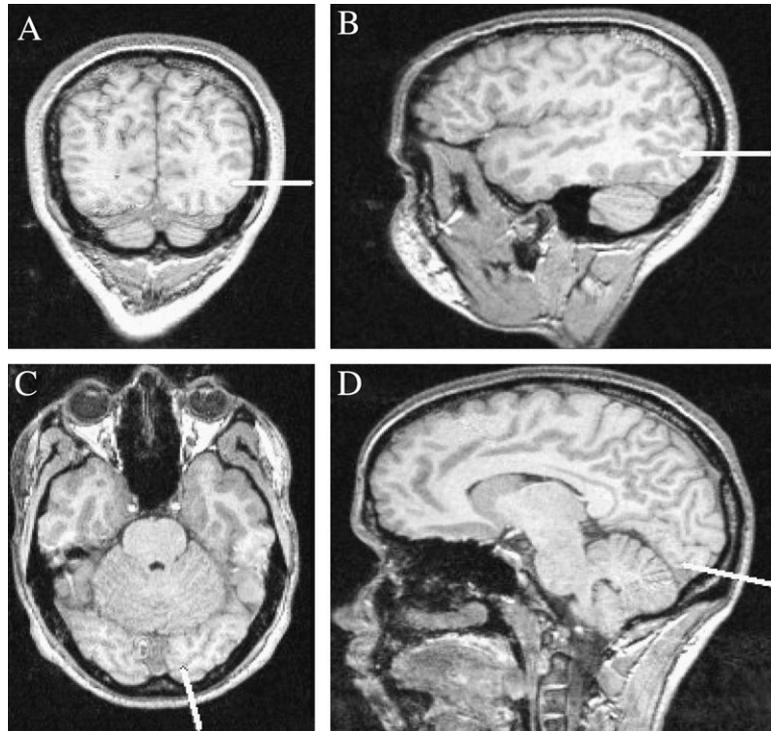


Figure 2. Coil locations for V5/MT (A, transverse view; B, sagittal view) and V1 (C, transverse view; D, sagittal view) stimulation on MRI image of one participant. The white lines represent the TMS trajectory. Note that left and right are reversed.

of 75 trials each, 50 were motion trials (25 left movement, 25 right movement) and 25 no motion trials. All types of trials were intermixed randomly within a block. The order of blocks was counterbalanced across subjects. Two baseline conditions with no TMS were also run, one before and one after the TMS blocks. In order to obtain a stable level of performance, two practice blocks preceded the experiment. If performance in these blocks exceeded a d' value of 2.5, the task was made more difficult by removing one frame from the stimulus. If performance was below a d' value of 1, the task was made easier by adding a frame. Five participants performed the motion task with four frames (stimulus duration 64 ms), two with three (48 ms). Note that even though the absolute time windows of V1 and V5/MT activity varied across these subjects (as TMS was applied after a fixed time after stimulus offset rather than stimulus onset) the relative time windows of V1 and V5 are the same across all subjects.

Experiment 2

Participants

Seven participants took part in experiments 2, six of whom had participated in experiment 1. Five of the participants were naive to the objective of the study.

Stimulus

The stimulus consisted of two vertical columns, each consisting of six dots (1 pixel each), extending 0.72° of visual angle vertically, separated by a distance of 5 pixels (see Fig. 1, right). This path-like pattern appeared at one of four possible horizontal locations within the same imaginary square as that used in experiment 1. Sixty-eight noise dots were distributed randomly in the other positions of the imaginary square to complete the number of dots to 80 (as in experiment 1). On 'absent' trials all dots were distributed randomly. The stimuli were presented for either 48 or 64 ms. For the six participants who had taken part in experiment 1, stimulus duration was same as in that experiment. In all other aspects the stimulus and viewing conditions were identical to that of experiment 1.

Location and Onsets of Stimulation

For the six participants who took part in experiment 2, V1 and V5/MT coordinates that were determined in experiment 1 were used. For the additional participant the localization was carried out using the procedure described in experiment 1 (see Fig. 2). Stimulation was carried out as described in experiment 1. TMS onsets were identical to those in experiment 1.

Procedure

The participants' task was to report whether or not they detected the presence of the path-like pattern. Each of the TMS conditions was run in one block of 60 trials (40 'present' trials and 20 no motion trials intermixed randomly). The order of blocks was counterbalanced across subjects. Two baseline conditions with no TMS were also run, one before and one after the TMS blocks. In order to obtain a stable level of performance, two practice blocks preceded the experiment. If performance in these blocks exceeded a d' value of 2.5, the task was made more difficult by adding 10 noise dots to the display. If performance was below a d' value of 1, the task was made easier by decreasing the number of noise dots by 10.

Experiment 3

Participants

Seven participants, four of whom had taken part in experiments 1 and 2, took part in experiment 3. Five of the subjects were naive to the objective of the study.

Stimulus

The stimulus was identical to that in experiment 1. For the four participants who had taken part in experiments 1 and 2, stimulus duration was kept constant.

Stimulation Location and Onsets

V1 and V5/MT were localized using the technique described in experiment 1. For the four participants who had taken part in

experiment 1, coordinates from experiment 1 were used. Double pulses of TMS were applied over V1 or V5/MT at four different time windows: 40 and 60 ms, 120 and 140 ms, 140 and 160 ms and 160 and 180 ms from stimulus offset. Other aspects of stimulation were carried out as described in experiment 1. The order of sessions was counterbalanced across participants.

Procedure

The experiment was run in two sessions, the order of which was counterbalanced across participants. One session consisted of the 40–60 ms TMS condition and the no TMS condition, the second consisted of the three late TMS time windows (120–140, 140–160 and 160–180 ms) and the no TMS condition. In each session the no TMS condition was run in two blocks, one before and one after the TMS blocks. In all other aspects the procedure was identical to that in experiment 1.

Results

Experiment 1

This experiment showed that V5/MT has an early critical time window for motion detection followed by a later critical time window for V1. Figure 3 shows motion detection performance (d') as a function of the TMS condition averaged across the seven participants. A within-subjects analysis of variance (ANOVA) indicated a significant interaction between site and time [$F(4,24) = 10.805, P = 0.0001; SEM = 0.115$]. Sidak-adjusted paired-sample t -tests revealed that V5/MT stimulation at the first (60–80 ms) time window produced a significant disruption in motion detection by comparison with no TMS condition [$t(6) = 7.821; P = 0.001; SEM = 0.095$], and by comparison with the second (80–100 ms) time window [$t(6) = 6.231; P = 0.002; SEM = 0.116$] and the third (100–120 ms) time window [$t(6) = 4.557; P = 0.012; SEM = 0.147$]. As can be seen in Figure 3, the effect of V5/MT stimulation on motion detection did not differ from the no TMS condition at the second or the third time window.

In contrast, V1 stimulation produced a disruption in motion detection at the second (80–100 ms) time window relative to the no TMS condition [$t(6) = 3.952; P = 0.022; SEM = 0.178$], to the first (60–80 ms) time window [$t(6) = 4.921; P = 0.008; SEM = 0.141$] and the second time window [100–120 ms, $t(6) = 1.3.651;$

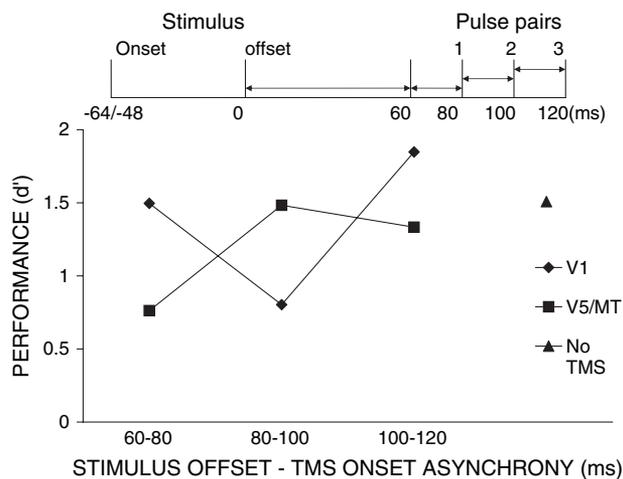


Figure 3. Timeline of an experimental trial and the mean performance (d') of the seven subjects at each stimulus offset — TMS onset asynchrony in the motion detection task. Each trial began with a 500 ms fixation point, which was followed by the test stimulus with a duration of either 48 or 64 ms, depending on the participant's ability. TMS was applied after the offset of the stimulus at intervals indicated in the methods.

$P = 0.032; SEM = 0.286$]. As can be seen in Figure 3, V1 TMS did not disrupt motion detection performance at the first (60–80 ms) or the third (100–120 ms) time window compared with the no TMS condition. At the critical time windows the effect of V5/MT stimulation (in the first time window) and V1 stimulation (in the second time window) were comparable [$t(6) = 0.265; P = 0.800; SEM = 0.153$].

Experiment 2

The pattern of results in experiment 1 suggests that back-projections from V5/MT to V1 play a role in awareness of real motion. However, an alternative explanation of these results is that TMS disrupted awareness in general, rather than motion specifically. TMS can have the effect of degrading the visibility of stimuli of short durations (Amassian *et al.*, 1989; Kammer and Nusseck, 1998). It is therefore possible that at the critical time windows TMS merely made the dots (both moving and stationary) less visible. It is also possible that the V5/MT stimulation disrupted positional information which may have compromised motion perception (McGraw *et al.*, 2004). To examine directly whether the TMS effects in experiment 1 are selective to motion, experiment 2 involved the detection of a stationary pattern that was constructed from dots of the same size and contrast as in experiment 1 and required relative location perception to perform the task accurately.

Figure 4 shows pattern detection performance (d') as a function of the TMS condition averaged across the seven participants. As can be seen in Figure 4, there was no effect of TMS on the detection task. This was confirmed by a within-subjects ANOVA, which showed no interaction between stimulation site and time window [$F(4,24) = 0.258; P = 0.902; SEM = 0.106$] and no main effects of stimulation site [$F(2,12) = 0.327; P = 0.727; SEM = 0.161$] and stimulation onset [$F(2,12) = 0.300; P = 0.746; SEM = 0.121$]. These results rule out any non-specific accounts for the TMS effects on motion detection (e.g. in terms of general effects of masking, or a failure to detect the dots).

In addition, we examined phosphenes sensitivity in our subjects when stimulated in darkness at the intensity (60%) and frequency (double pulse) used in the experiment, and when they were looking for phosphenes rather than the visual

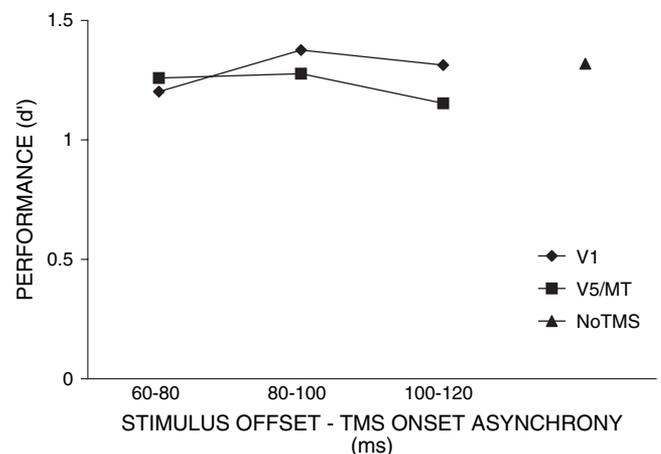


Figure 4. The mean performance (d') of the seven subjects at each stimulus offset — TMS onset asynchrony in experiment 2, showing that the effective time window for interference with motion stimuli has no effect on the detection of stationary pattern stimuli.

stimulus. For four of the seven participants of experiment 1 (three of whom also took part in experiment 2), this stimulation was below the threshold for eliciting phosphenes. The three participants who did report an occasional appearance of phosphenes on some trials took part in both experiments 1 and 2. Thus, as all participants displayed the same temporal relationship of V5/MT and V1 activity, the pattern of results obtained here cannot be explained in terms of masking by phosphenes. It is important to note that phosphenes are only perceived reliably when subjects are looking for them. Stimulation above the phosphene threshold while subjects are performing a visual task does not usually induce phosphene perception (see Stewart *et al.*, 1999; Walsh and Pascual-Leone, 2003).

Experiment 3

The stimulation time windows in experiment 1 were chosen to reveal feedback connections from V5/MT to V1 that are likely to occur relatively late in processing. In order to determine whether back-projections from V5/MT to V1 play a role in awareness of motion stimuli in the presence of V1 feed-forward activity, the objective of experiment 3 was to investigate whether the motion task used in experiment 1 is dependent on the feed-forward projections from V1 to V5/MT. As V5/MT stimulation disrupted motion detection at the 60–80 ms time window, stimulation of V1 at the immediately preceding time window (40–60 ms) should impair motion detection by disrupting the feed-forward projections from V1 to V5/MT. Secondly, to confirm the specificity of the time windows of experiment 1, V1 and V5/MT were also stimulated at three time windows that postdate the time windows of experiment 1.

This experiment showed that an early V1 time window, consistent with feed-forward activity, is critical for awareness of visual motion. At the 40–60 ms stimulation time window a within-subjects ANOVA indicated a significant effect [$F(2,12) = 15.993$; $P = 0.0001$; SEM = 0.007 (Figure 5)]. Sidak-adjusted paired-sample *t*-tests revealed that V1 stimulation at this time window produced a disruption in motion detection (mean $d' = 1.4$) compared with the No TMS condition (mean $d' = 2.0$)

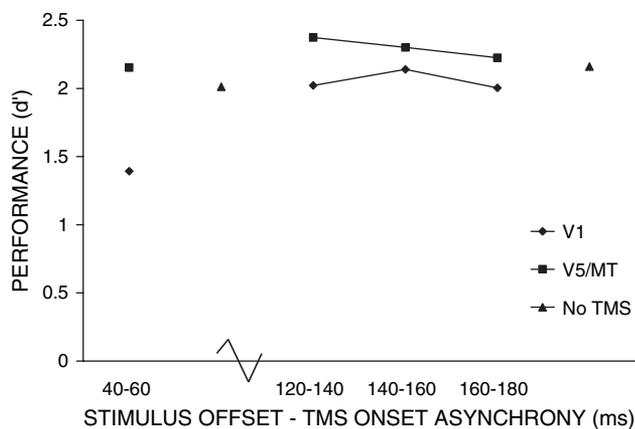


Figure 5. The mean performance (d') of the seven subjects at each stimulus offset — TMS onset asynchrony in experiment 3. As the 'early' (40–60 ms) and 'late' (120–140, 140–160 and 160–180 ms) TMS conditions were run in separate sessions, subjects' performances in the No TMS condition are presented separately: left and right triangles represent early and late No TMS controls respectively. The 'early' V1 time window is critical for awareness of visual motion.

[$t(6) = 4.701$; $P = 0.01$; SEM = 0.133] and the V5/MT condition (mean $d' = 2.2$) [$t(6) = 4.971$; $P = 0.008$; SEM = 0.157], whereas the V5/MT condition did not differ significantly from the No TMS condition [$t(6) = 1.033$; $P = 0.715$; SEM = 0.147]. This V1 effect at the 40–60 ms time window is likely to reflect a disruption to the feed-forward activity in V1, as it occurs immediately before the V5/MT critical time period in experiment 1 (at 60–80 ms) and V1 is the major source of V5/MT input (Maunsell and Van Essen, 1983a, b).

Late time windows were run in a separate session. Mean d' for the No TMS condition in this session was 2.2. Mean d' values for V1 TMS were: 2.0 for the 120–140 ms onset, 2.1 for the 140–160 ms onset and 2.0 for the 160–180 ms onset; for V5/MT TMS mean d' values were: 2.4 for the 120–140 ms onset, 2.3 for the 140–160 ms onset and 2.2 for the 160–180 ms onset. A within-subjects ANOVA indicated an absence of a site by stimulation onset interaction [$F(4,24) = 0.613$; $P = 0.657$; SEM = 0.143], as well as an absence of main effects of site [$F(2,12) = 1.420$; $P = 0.280$; SEM = 0.491] and stimulation onset [$F(2,12) = 1.523$; $P = 0.257$; SEM = 0.153].

Discussion

The present results show two critical periods of V1 activity, one preceding (at 40–60 ms from stimulus offset) the V5/MT critical period (which occurred at 60–80 ms from stimulus offset) and another postdating (at 80–100 ms from stimulus offset) the V5/MT critical period. Importantly, stimulation of V5/MT at the critical periods of V1 or of V1 at the critical period of V5/MT had no effect on participants' performance. This double dissociation of critical periods suggests that although V5/MT obtains visual information through V1 feed-forward activity (reflected in the early V1 critical period predating that of V5/MT), back-projections from V5/MT to V1 remain critical for awareness of motion, as demonstrated by the presence of the late V1 critical period postdating that of V5/MT.

The lack of V5/MT effect at 80–100 ms or at any of the later time periods is important in indicating that once V1 has received the back-projections, activity in V5/MT is no longer necessary for motion awareness (see Fig. 3), and that the late V1 effect cannot be attributed to another cycle of feed-forward activity (as this would imply the presence of a further V5/MT critical period). This double dissociation between the critical time windows of V5/MT and the late period of V1 activity in motion detection demonstrates the importance of back-projections in normal vision and shows that the role of V1 extends beyond the feed-forward sweep.

Our results clearly demonstrate that integrity of the early V1 feed-forward activity does not obviate the need for the late V1 activity. Moreover, stimulation of V1 during this later phase of activity is not only capable of disrupting the sensation of phosphenes (as previously reported in Pascual-Leone and Walsh, 2001), it can also impair detection of a real motion stimulus, to the same degree as V5/MT stimulation, as assessed psychophysically in the present experiment. To the best of our knowledge these findings are the first to show that V1 activity at a later period than V5/MT's activity is necessary for detection of real motion in humans.

These findings are inconsistent with the view that activity in an extrastriate area selective for a particular attribute is sufficient for awareness of that attribute (Zeki and Bartels, 1999). They also argue against the possibility that perceiving a

visual stimulus requires simultaneous activity in all visual areas involved in processing of that stimulus (see Pollen, 1999, 2003) — although whether synchronous activity is more important when more than one attribute is present, e.g. in binding when being aware of the colour and movement of a stimulus, is still a good question to be examined.

A number of theoretical frameworks have made a distinction between feed-forward and feedback activity in the visual system and, consistent with our findings, it has been suggested that these two processes reflect a qualitative difference between unconscious and conscious vision (Lamme, 2001). Other theories have emphasized the role that feedback activity plays in computing local details in images that cannot be computed by the large receptive fields of extrastriate neurons (Bullier, 2001; Hochstein and Ahissar, 2002). In these models, awareness of global representations of the visual field, provided by extrastriate areas, precedes awareness of local details computed in V1 (for a discussion of what is termed 'the grain problem', see Pollen, 1999). Our task may have required computation of local details in V1 as the motion was across very short distances (each dot moved only one pixel between the frames). Our findings clearly demonstrate that back-projections to V1 are essential to visual awareness of motion. We are now engaged in establishing the extent to which this principal generalizes to interactions between other cortical areas and V1.

Notes

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