A Double Dissociation Between Striate and Extrastriate Visual Cortex for Pattern Motion Perception Revealed Using rTMS

Benjamin Thompson,[1,2]* **Craig Aaen-Stockdale,**[2] **Lisa Koski,**[3] **and Robert F. Hess**[2]

[1]*Department of Optometry and Vision Science, University of Auckland, New Zealand*
[2]*McGill Vision Research, Department of Ophthalmology, McGill University, Montréal, Canada*
[3]*Transcranial Magnetic Stimulation Laboratory, Division of Experimental Medicine,*
McGill University, Montréal, Quebec, Canada

◆ ══════════════════ ◆

Abstract: The neural mechanisms underlying the integration and segregation of motion signals are often studied using plaid stimuli. These stimuli consist of two spatially coincident dynamic gratings of differing orientations, which are either perceived to move in two unique directions or are integrated by the visual system to elicit the percept of a checkerboard moving in a single direction. Computations pertaining to the motion of the individual component gratings are thought to take place in striate cortex (V1) whereas motion integration is thought to involve neurons in dorsal stream extrastriate visual areas, particularly V5/MT. By combining a psychophysical task that employed plaid stimuli with 1 Hz offline repetitive transcranial magnetic stimulation (rTMS), we demonstrated a double dissociation between striate and extrastriate visual cortex in terms of their contributions to motion integration. rTMS over striate cortex increased coherent motion percepts whereas rTMS over extrastriate cortex had the opposite effect. These effects were robust directly after the stimulation administration and gradually returned to baseline within 15 minutes. This double dissociation is consistent with previous patient data and the recent hypothesis that both coherent and transparent motion percepts are supported by the visual system simultaneously and compete for perceptual dominance. *Hum Brain Mapp 30:3115–3126, 2009.* © 2009 Wiley-Liss, Inc.

Key words: component motion; pattern motion; plaids; rTMS; V1; V5/MT; fMRI

◆ ══════════════════ ◆

INTRODUCTION

During natural viewing the human visual system must combine multiple spatially distributed motion signals into coherent forms. This requires both integration and segregation mechanisms [Braddick, 1993]. Integration mechanisms combine individual local motions with a common origin to produce the percept of a coherent dynamic surface or form. Segregation mechanisms prevent the combination of local motion signals with distinct origins thereby preventing over integration of visual information. Given the fundamental importance of such mechanisms to visual per-

ception, the cortical basis of motion integration and segregation has attracted considerable interest, see Born and Bradley [2005] and Orban [2008] for reviews.

One of the most commonly used stimuli for investigating integration and segregation mechanisms in the mammalian visual cortex is the plaid [Adelson and Movshon, 1982]. Plaid stimuli are constructed from a pair of gratings moving in different directions. When the two gratings are combined (i.e. superimposed) one of two percepts can occur. Either the two component gratings appear to slide over one another in their respective directions producing a "transparent" percept, or the two gratings appear to bind together into a checkerboard pattern, which is perceived to move in a single "coherent" direction, distinct from either of the two component directions. Following the nomenclature common to this field of research, the former case will be referred to as component motion and the latter case as pattern motion [Adelson and Movshon, 1982; Rodman and Albright, 1989]. The conditions favoring the perception of either component or pattern motion have been well studied psychophysically [Delicato and Derrington, 2005]; for example, the greater the difference in spatial frequency between the two components, the less pattern motion will be perceived [Kim and Wilson, 1993; Smith, 1992].

Physiological studies into plaid perception in the monkey have revealed the existence of two types of motion responsive cells that can be categorized as component or pattern selective [Majaj et al., 2007; Movshon et al., 1985; Rodman and Albright, 1989; Rust et al., 2006]. Component motion cells have direction-selective receptive fields that respond only to the individual components that make up a coherent plaid. The second, less common type of receptive field is tuned to the pattern direction of the plaid regardless of the relative directions of the components. Hierarchical two-stage models have been proposed, suggesting that component motion is computed in striate cortex which then leads to pattern motion computation in the extrastriate middle temporal area (area MT, the human homologue of which is known as V5) [Movshon et al., 1985; Rust et al., 2006; Simoncelli and Heeger, 1998]. MT is further along the motion processing hierarchy than V1 and is known to be highly specialized for motion perception [Born and Bradley, 2005]. Evidence for such a processing hierarchy was provided by studies demonstrating a lack of pattern motion responses in V1 [Movshon and Newsome, 1996] and a subset of neurons (∼15%) that were pattern selective in MT [Movshon et al., 1985]. While the relative distribution of pattern cells within the visual cortex does support this general idea, it seems that there is not such a clear cut segregation of labor between visual areas as previously thought. Pattern cells have been reported in striate cortex (V1) of the awake monkey (9%) [Guo et al., 2004], although the same experiment conducted on anesthetized animals (monkeys and cats) supported previous reports demonstrating an absence of pattern cells, thus highlighting the potential importance of feedback from other neural areas. In addition, investigations into the receptive fields of V1 neurons in the monkey have suggested that properties such as end-stopping [Pack et al., 2003] and broad tuning, which would enable feature tracking [Tinsley et al., 2003], may allow V1 to contribute directly to pattern motion perception. Pattern cells have also been reported in monkey V3, an extrastriate visual area intermediate in the visual processing hierarchy between V1 and MT [Gegenfurtner et al., 1997]. In V3 ∼8% of neurons showed pattern selectivity, similar to unanesthetized V1 [Guo et al., 2004], but less than MT [Movshon et al., 1985]. A similar distribution of pattern cells can be inferred in the cortex of the human from neuroimaging studies demonstrating responses characteristic of pattern motion in both V3/V3A and V5 [Castelo-Branco et al., 2002; Huk and Heeger, 2002; Wenderoth et al., 1999] with a gradual increase in such responses from V1 up to V5 [Huk and Heeger, 2002]. Finally, pattern motion responses have been found in subcortical visual areas, including the superior colliculus [Zhao et al., 2005] of the cat, and the pulvinar of both cats [Merabet et al., 1998] and humans [Villeneuve et al., 2005]. It is clear therefore that the neural representation of pattern motion may recruit multiple brain areas including striate and extrastriate visual cortex as well as subcortical areas.

It has recently been proposed that, when viewing plaid stimuli, pattern and component motion may compete for perceptual dominance [Hupe and Rubin, 2003, 2004]. This hypothesis was supported by measurements of the inherent bistability present in plaid patterns when viewed for extended periods of time [Hupe and Rubin, 2003, 2004; Sheppard and Pettigrew, 2006; Thompson et al., 2008a]. A competition between two rival percepts could also shed light on findings from patient studies that, like the presence of pattern cells outside of MT, cannot easily be explained by a rigidly hierarchical model assuming component motion processing in V1 and subsequent pattern motion processing in MT. Victor and Conte [1994] report a patient with occipital lesions affecting striate cortex who showed superior direction discrimination for plaids than their components. In addition, Clifford and Vaina [1999] reported a range of patients who had lesions affecting either striate or extrastriate cortex. Depending on the location of the lesion, striate or extrastriate, patients tended to perceive more component or pattern motion, respectively, than controls. The extrastriate results can be easily explained by a strict hierarchical model assuming lesions affecting MT/V5, whereas the effects of the striate lesions cannot. These clinical findings are more consistent with active competition between component and pattern percepts. This could entail a competition for perceptual dominance between neuronal populations that rely predominantly on input from component selective cells and neuronal populations that rely predominantly on input from pattern motion cells.

Given the inherent bistability of plaid percepts, plaid stimuli are well suited to a study attempting to directly manipulate the conscious perceptual experience of an observer. Accordingly, we used plaid stimuli combined with

offline repetitive transcranial magnetic stimulation (rTMS) to assess whether modifying activity in the cortical regions generally thought to be primarily responsible for component and pattern motion perception processing in humans could influence the way in which plaid stimuli were perceived. TMS is a method that uses magnetic fields to stimulate the human cortex through the scalp and can be used to demonstrate a causal link between a neural region and a particular perceptual process [Pascual-Leone et al., 1999]. When a train of TMS pulses is applied repeatedly over the same area for an extended period of time, a technique termed offline rTMS, there is a lasting effect on the excitability of the stimulated cortex that endures for a period of time after the stimulation has ceased [Walsh and Pascual-Leone, 2003]. By applying TMS pulses at a frequency of 1 Hz it is possible to induce a temporary reduction of excitability in the stimulated region of cortex as measured by the relative strength of TMS stimulation required to elicit a certain cortical response pre- and post-rTMS stimulation [Fitzgerald et al., 2006]. This effect has been demonstrated specifically in visual cortex [Brighina et al., 2002; Fierro et al., 2005]. Offline 1 Hz rTMS has also been used to demonstrate that striate cortex is involved in the dichoptic (separate stimuli to each eye) combination of two components into a plaid percept [Saint-Amour et al., 2005]. For the current study we based our use of rTMS on previous behavioral findings indicative of rTMS having a transient disruptive effect on the function of the stimulated cortical area [Rafal, 2001]. Since the effects of rTMS on neural activity are now known to result from an interaction between both stimulation frequency and the initial cortical activation state of the stimulated area [Lang et al., 2004; Siebner et al., 2004; Silvanto et al., 2007a; Silvanto et al., 2007b; Silvanto and Pascual-Leone, 2008], we employed 1 Hz rTMS under the assumption that the initial cortical activation state was stable and consistent across all subjects. We used rTMS to alter function in either striate (V1) or extrastriate cortical areas (V3/V5) specialized for motion perception as localized by the induction of moving phosphenes [Campana et al., 2002; Marg and Rudiak, 1994; Pascual-Leone and Walsh, 2001; Silvanto et al., 2005b; Stewart et al., 1999]. We then measured the effect of this stimulation on the perception of plaid stimuli constructed from components that differed in their spatial frequencies. We found a strong interaction between the area targeted with rTMS (striate or extrastriate) and the change in percept relative to baseline. Consistent with patient data [Clifford and Vaina, 1999; Victor and Conte, 1994], disrupting the function of striate cortex increased pattern motion percepts whereas disrupting extrastriate cortex increased component motion percepts.

METHODS

Participants

Seventeen participants took part in this study. All had normal vision or wore their prescribed correction, and had
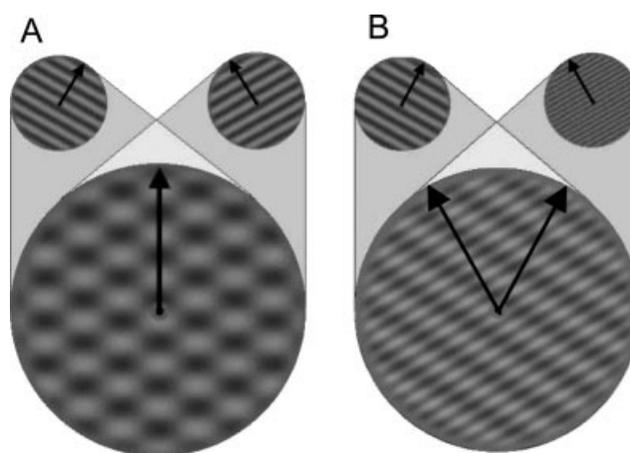

Figure 1.
A schematic representation of the plaid stimuli. In **A**, the two components have the same spatial frequency (1 c/d) which, when combined, give the percept of pattern motion in a vertical direction. In **B**, the two components have an unmatched spatial frequency which would tend to give the percept of component motion.

normal neurological function. All psychophysical and magnetic stimulation procedures conformed to institutional ethic guidelines and were approved by the institutional Research Ethics Board.

Stimuli

Plaid stimuli (Figure 1) were presented within an 8° diameter circular aperture surrounded by mean luminance grey (51.3 cd/m²). A mean luminance circular region in the centre of the aperture was included to assist stable fixation on a black fixation point located in the very centre of the display. The blank region in the centre of the aperture was 0.5° of visual angle in diameter.

Plaids were constructed from two sinusoidal gratings oriented 60° on either side of vertical. Both gratings drifted diagonally upwards at 3° per second and the resulting plaid had a contrast of 30%. Within every plaid one component was always held constant at a spatial frequency of 1 cpd and the second component had a spatial frequency which could range from 0.25 cpd to 4 cpd in steps of 0.25 cpd. The veridical direction of pattern motion under these presentation conditions is vertical. Plaids were created offline by generating the two components individually (at 15% contrast) and then summing them together. The stimuli were then presented as a sequence of frames using the psychophysics toolbox [Brainard, 1997; Pelli, 1997].

Psychophysical Procedure

Participants were introduced to the plaid stimulus by viewing several long duration (120 seconds) plaids and

reporting their percepts to the experimenter. This introductory session continued until the participant was confident with the distinction between pattern ("coherent") and component ("transparent") plaid stimuli. Stimuli were presented on a 22-inch Sony Trinitron monitor at a resolution of 1,024 × 768 pixels with a 60-Hz refresh rate. Participants sat 100 cm from the display and were asked to fixate on a dot in the centre of the screen. Stimuli were viewed monocularly with the dominant eye since a previous study found that viewing plaids binocularly seemed to protect against the effects of rTMS over primary visual cortex [Saint-Amour et al., 2005]. Plaid stimuli were presented for 1 second and there was a minimum of 2 seconds between each stimulus presentation in order to prevent a buildup of adaptation. An ISI of 2 seconds was used as pilot observations indicated no buildup of adaptation at this interstimulus interval and it was brief enough to allow a sufficient number of trials to be presented within a 4.5-minute block. Each spatial frequency combination was presented 22 times, with the constant spatial frequency component (1 cpd) oriented clockwise of vertical for 11 of these trials and counter-clockwise from vertical for the remaining 11 trials. The parameters used for the plaids were chosen with reference to Hupe and Rubin [2003] who found that sinusoidal plaids (as used in this study) did not have a bias toward either coherency or transparency in the first epoch before perceptual alternations began, whereas rectangular wave plaids (with a duty cycle different from 50%) were always seen as coherent in the first epoch. In addition, 1 second was the duration within which the first percept was reported for Hupe and Rubin's [2003] subjects and the first switch in percept never occurred until 1.7 seconds after stimulus onset. Using sinusoidal plaids with a 1-second presentation time, we could therefore be relatively confident that any alterations induced in the perception of these stimuli were due to our rTMS manipulations rather than an inherent short-duration bistability in the stimulus.

Following a previous study of plaid perception [Thompson et al., 2008a], participants were asked to perform two tasks. Firstly they were asked to indicate, using a button press, whether they perceived the plaid as transparent (component percept) or coherent (pattern percept). If the plaid was perceived as transparent the next trial was presented after a 2-second intertrial interval. However, if coherent motion was perceived, participants were then required to indicate in which direction they saw the plaid move. A vertical line was presented on the screen running from the fixation point to the edge of the presentation aperture. Participants used two keys to pivot the line around the fixation point until it lay along the motion direction they had perceived. A key press confirmed the direction selection and the next stimulus was displayed 2 seconds later. Perceived direction data were used to verify a report of coherent motion since we did not want to rely solely on subjective report for this measure. If a pattern motion response was reported but the perceived

direction was greater than 15° from vertical (halfway between the vertical pattern motion direction and the two component motion directions), the response was reclassified as component. This correction was important as it provided an objective criterion for ensuring that both components had fully cohered before a pattern motion percept could be accepted. Such a dissociation between perceived direction and perceptual report was of interest, but such an effect could have been due to a range of rTMS effects such as rTMS selectively effecting contrast sensitivity to higher spatial frequency patterns [Thompson et al., 2008b]. We therefore used this conservative correction to account for such possibilities. In the final dataset, only 4% of responses required correction and the pattern of corrections did not differ reliably between conditions.

Once psychophysical measurements of perceived coherence had been made, three spatial frequency combinations were selected for each participant, one that yielded coherent percepts on approximately 80% of trials, one yielding coherent percepts on 50% of trials, and one yielding coherent percepts on 20% of trials. These three spatial frequency combinations were then used as the stimuli in the subsequent TMS experimental sessions. Three different spatial frequency combinations with a variety of percepts were presented during the TMS session so that participants saw a variety of stimuli and would therefore be discouraged from adopting a stereotyped response.

During the rTMS session, participants completed three blocks of measurements before rTMS (pre-rTMS blocks) and after each of the two rTMS sessions (post-rTMS blocks). Pre-TMS blocks were combined to provide a baseline measure of performance. Post-rTMS blocks were analyzed independently and designated as Time 1, Time 2, and Time 3 to measure the duration of any rTMS-induced changes in the way in which the plaids were perceived. Each block contained 24 measurements of each of the three spatial frequency combinations, with the constant spatial frequency component (1 cpd) oriented clockwise of vertical for 12 of these trials and counter-clockwise from vertical for the remaining 12 trials. During a block, stimulus order was randomized. Blocks lasted approximately 4.5 minutes although the exact duration of a block varied slightly depending on the response time of the participant.

TMS

The TMS component of the experiment was separated into two separate sessions; a screening session and a testing session. The purpose of the screening session was to locate the correct cranial target area for rTMS administration using phosphene perception as a functional marker for striate and motion-sensitive extrastriate cortex stimulation [Silvanto et al., 2005a] and then to acquire a threshold measurement of stimulation intensity subsequently used to calibrate stimulation for the testing session [Machii et al., 2006]. TMS was administered using a MagStim Rapid2 biphasic stimulator and a MagStim figure-8 air-cooled coil

(active surface of 2 × 70 mm). During rTMS administration the BrainSight Frameless® stereotaxic system was used to monitor coil position.

Screening Session

Participants wore a swimming cap and light-proof goggles [Deblieck et al., 2008]. Two grids were drawn on the swimming cap; one 4 × 4 cm grid, the lower right corner of which was centered on a point 2 cm above the inion, and one 5 × 5 cm grid centered on a point 3 cm above the inion and 4 cm laterally to the left. The first grid was used to localize left striate cortex (V1) and the second motion-sensitive regions of left extrastriate cortex (V3/V5). Striate[1] localization was performed first. Participants were asked to keep their eyes open and to attend to the whole visual field. The coil was positioned in the bottom right hand corner of the striate cortex grid with the handle pointing directly upwards parallel to the participant's spine. Single pulses of stimulation were administered with a minimum separation of 5 seconds at this grid position whilst stimulation intensity was gradually increased from 40% to 100% maximum stimulator output (MSO) to allow the participant to become accustomed to the sensation of the stimulation. Once stimulation intensity reached 100% MSO (or the observer's tolerance threshold) each point of the grid was stimulated and participants were asked to report any visual percepts. Phosphene reports were verified in two ways. First, the coil was moved laterally to ensure that the phosphene moved contralaterally in the visual field [Kammer et al., 2005]. Second pulses were administered to the top of the head (point CZ) to ensure that no phosphenes were reported. All participants who reported phosphenes passed this verification test. Once a verified phosphene was acquired, the coil was moved around the grid until a strong and reliable phosphene was induced in a relatively central portion of the visual field as reported by the participant.

Once an occipital stimulation position had been selected, the coil was moved to the second grid and each point was stimulated at 100% MSO or tolerance threshold at least three times until the participant reported a moving phosphene. Once a moving phosphene had been reported, the coil was moved both on and between the grid points surrounding this region and participants were asked to compare pairs of phosphenes, reporting which appeared to have the most motion. A process of elimination followed until the position that elicited the strongest sensation of motion was determined. Once a moving phosphene "hot

---

[1]Although that stimulation in the occipital region is likely to recruit areas other than striate cortex and should more accurately be referred to as early visual cortex stimulation, for simplicity we will use the term striate cortex. In addition there is a reasonable argument to be made in support of striate cortex being the primary target of such stimulation (see Saint-Amour et al., 2005).

spot" was identified, the coil was held in this position and stimulation intensity was reduced in small steps (1% MSO), until 5/10 pulses elicited a moving phosphene percept. During this process participants reported one of three response options: no percept, a static phosphene or a moving phosphene. The static phosphene option was included because in some cases when stimulation intensity was close to threshold, a phosphene would be reported but would be perceived as static. Static and no-phosphene reports were taken as null responses. This moving phosphene threshold was used to calibrate rTMS intensity over both extrastriate and striate stimulation sites in the subsequent testing session. If no moving phosphenes were reported after each point on the extrastriate grid had been stimulated three times, participants were given a 10-minute break and then the stimulation was repeated, the participant was excluded from the study if successful functional localization of motion-sensitive regions of extrastriate cortex had not been achieved at the end of the second attempt.

Testing Session

Striate and extrastriate cortex stimulation was conducted in the same testing session, with stimulation sessions separated by 30 minutes since 15 minutes is generally considered to be the duration of rTMS effects elicited by similar stimulation parameters [Grossman et al., 2005]. The order of stimulation was counter balanced across participants. For the first stimulation session the relevant stimulation location was reconfirmed with a single pulse of TMS at 100% MSO or tolerance threshold whereby a phosphene with the same characteristics as those reported in the screening session was sought. If the phosphene had not been reproducible between sessions, the participant would have been excluded; however, this did not occur for our sample. One hertz rTMS was then delivered at moving phosphene threshold for 10 minutes. This process was repeated for the second stimulation session.

fMRI Localization of Extrastriate Stimulation Sites

In 6 of the 11 participants that took part in the full study we localized motion-sensitive extrastriate areas using an fMRI protocol known to activate areas V5 and V3/V3a [Dumoulin et al., 2000]. This data was not used to guide the rTMS during the study, but rather as a post-hoc experiment to identify the extrastriate visual areas that produced optimal moving phosphenes in our sample. The visual stimulus used to localize motion-sensitive extrastriate areas, which has been described in detail previously [Dumoulin et al., 2000], consisted of a low-contrast (3%) checkerboard pattern which was either refreshed with a new randomly generated pattern every 0.5 seconds (temporal frequency of ~2 Hz), or for the baseline condition remained stationary. For both conditions participants fix-

ated on a central black dot and performed a contrast discrimination task. Eighteen-second blocks of dynamic checkerboards were interleaved with 18-second baseline blocks. Each scanning run contained 10 repetitions of dynamic checkerboard and baseline blocks. Stimuli were square, subtended 15° and were back projected onto a screen fixed to the scanner bore. Participants viewed the stimuli through a mirror mounted above their eyes.

Functional and anatomical data were acquired using a Siemens 1.5T Sonata scanner. Anatomical images were acquired using a head coil (circularly polarized transmit and receive) and a T1 weighted sequence (TR 22 ms; TE 10 ms; flip angle 30°), which provided 180 sagittal slices of 256×256 mm^3 image voxels. Functional scans were acquired using a surface coil (circularly polarized, receive only) positioned beneath the occipital pole. The acquisition of functional images was preceded by an anatomical sequence acquired using the surface coil for use in subsequent alignment of functional and anatomical data. The surface coil anatomical scan was the same as the head-coil sequence except that $80 \times 256 \times 256$ sagittal images of slice thickness 2 mm were acquired. Functional scans were multislice T2*-weighted, gradient-echo, planar images (GE-EPI, TR 3.0 seconds, TE 51 ms, flip angle 90°). Each image volume consisted of 30 slices positioned orthogonally to the calcarine sulcus. The field of view was 256×256 mm, the matrix size was 64×64 with a thickness of 4 mm giving voxel sizes of $4 \times 4 \times 4$ mm. During a functional run 128 volumes were acquired at a TR of 3 seconds, the first eight of which were discarded before analysis. Each participant completed six functional runs within their scanning session.

Data were analyzed using the commercially available BrainVoyger analysis package. Head-coil anatomical images were registered to Talairach space [Talairach and Tournoux, 1988]. Functional data were motion corrected and highpass filtered using routines within BrainVoyager, registered to the anatomical images and transformed to Talairach space. Multiple runs were combined to allow for a contrast between dynamic presentations and baseline to be calculated. The resulting maps of t statistics were visualized overlaid on each participant's anatomical data and thresholded for multiple comparisons using an FDR correction ($q < 0.01$) [Benjamini and Hochberg, 1995]. Bilateral motion-sensitive extrastriate visual regions including area V5 were clearly identifiable in all six participants as a cluster of strong activation in the correct anatomical position [Dumoulin et al., 2000].

To compare the location of the functionally localized motion-sensitive areas with the scalp position that elicited moving phosphenes, high-resolution mesh representations of each participant's head (in native space) were constructed in BrainVoyager. For each participant, the TMS stimulation site used for extrastriate stimulation was marked on the mesh by converting the scalp measurements made during moving phosphene localization to the $1 \times 1 \times 1$ mm coordinate system used in BrainVoyager.

The stimulation site was marked on the anatomical scan and transformed to Talairach space for comparison with the functional data.

RESULTS

Of the 17 participants enrolled, 5 did not perceive moving phosphenes and were excluded from the rest of the study. In addition, one participant did not tolerate repetitive stimulation at moving phosphene threshold and was excluded from the study[2]. Therefore $n = 11$ for the experimental phase of the study; six participants had extrastriate cortex stimulation first and five participants had striate cortex stimulation first. Striate cortex coil positions were fairly consistent across participants with an average position of 2.4 cm (SD 0.7 cm) above the inion and 0.7 cm (SD 0.7 cm) to the left of the inion. Phosphenes most commonly fell in the lower portion of the visual field. Extrastriate cortex coil positions were more variable with an average location of 3.4 cm (SD 0.6) above the inion and 5.2 cm (SD 1.1) to the left of the inion in good agreement with previously reported V5 stimulation sites [Beckers and Homberg, 1992; Beckers and Zeki, 1995; Hotson et al., 1994; Hotson and Anand, 1999; Sack et al., 2006; Stewart et al., 1999]. The average moving phosphene threshold was 89% MSO (SD 8). Each block of psychophysical measurements lasted an average of 277 seconds (SE ±11) for the pre-TMS baseline measurements. Post-rTMS blocks were slightly shorter lasting an average of 272 seconds (SE ±8). Although the difference between pre- and post-rTMS block duration was significant, ($t(10) = 4.14$, $P = 0.002$), there was no difference between the length of blocks post-rTMS, for the two conditions (post-V1 stimulation and post-V5 stimulation) ($t(10) = 1.49$, $P = 0.17$) confirming that small but reliable changes in response time cannot explain the results presented below.

The effects of rTMS were quantified by normalizing the proportion of coherent percepts reported in each of the post-rTMS blocks (Time 1, Time 2 and Time 3) to each participant's baseline measure. The baseline was the proportion of coherent responses averaged across the three pre-TMS blocks. Each spatial frequency combination had a separate baseline. Normalization was achieved by subtracting the baseline from the proportion of pattern motion responses for each block of post-rTMS measurements. After normalization there was no effect of spatial frequency either when considering the whole dataset ($F(2,20) = 0.17$, $P = 0.8$) or the data from the two separate stimulation sites (striate; $F(2,20) = 0.42$, $P = 0.63$, extrastriate; $F(2,10)$
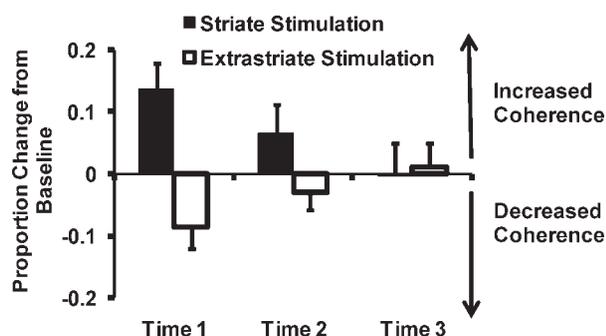
Figure 2.

The difference in the proportion of pattern motion responses relative to baseline 0–4.5 minutes after cessation of rTMS (Time 1), 4.5–9 minutes post-rTMS (Time 2) and 9–13.5 minutes post-rTMS (Time 3). Bars showing positive values indicate an increase in pattern motion responses whereas bars showing negative values indicate a reduction in pattern motion responses. Error bars show ±1 SEM, n = 11.

= 0.82, P = 0.45). We therefore averaged across the three different spatial frequency combinations for subsequent analysis.

The average proportion of pattern motion responses in the pre-rTMS baseline across participants was 0.51 (SD 0.08) indicating that the correct range of spatial frequency combinations were selected on a participant by participant basis to give a balanced range of pattern and component motion percepts.

As can be seen in Figure 2, there was a clear double dissociation between the effects of striate stimulation and those of extrastriate stimulation on plaid perception. rTMS over striate cortex increased the proportion of coherent motion responses immediately after stimulation. This effect then fell off over time indicating that it was indeed an rTMS-related effect. The opposite pattern was found for extrastriate stimulation whereby immediately after stimulation the proportion of pattern motion responses fell below baseline and gradually recovered over the succes-

sive two measurement blocks. This differential effect of rTMS over striate and extrastriate cortex on the perception of pattern motion relative to baseline was significant (significant interaction between stimulation site [striate vs. extrastriate] and time after stimulation [Time 1 vs. Time2 vs. Time 3], repeated measures ANOVA, $F(2,19) = 12.81$, $P = 0.00073$, degrees of freedom adjusted for sphericity using the conservative Greenhouse-Geisser correction). Paired samples t-tests were used to test the difference between striate and extrastriate stimulation at each timepoint (due to multiple comparisons the Bonferroni corrected significance level of $P = 0.017$ was adopted). There was a significant difference between striate and extrastriate stimulation immediately after rTMS ($t(10) = 4.80$, $P = 0.00072$), but not at either of the other two time points ($P > 0.017$). Finally, post-hoc one-way t-tests were conducted to assess whether the post-rTMS measurements obtained immediately after rTMS differed reliably from baseline for either stimulation site. A significant deviation from baseline was found for both striate ($t(10) = 3.32$, $P = 0.0079$)) and extrastriate cortex ($t(10) = -2.55$, $P = 0.029$).

Our fMRI localization protocol provided strong functional activation in extrastriate visual cortex in all six participants tested. Table I shows the Talariach coordinates for the center of gravity of the activated extrastriate region in the left hemisphere and the coordinates for the center of the coil during rTMS stimulation (reconstructed from scalp measurements). Functional data and the corresponding rTMS extrastriate stimulation sites for the six participants are shown in Figure 3. The centers of gravity of the motion-sensitive regions revealed with fMRI were consistent with V5 activation as shown by a previous report using the same fMRI localization technique [Dumoulin et al., 2000]. It is clear from Figure 3 that there was generally good correspondence between the perception of moving phosphenes and the motion-sensitive extrastriate visual areas localized using fMRI in five of six of the participants tested. The one participant who showed a mismatch between moving phosphene perception and the location of motion-sensitive cortical areas (Fig. 3, S6) was rescreened for moving phosphenes after the fMRI data was collected

TABLE 1. The locations of left V5 as localized by fMRI and the rTMS stimulation site for six participants

| | fMRI-defined V5 | | | | rTMS stimulation site | | |
	X	Y	Z	Voxels	X	Y	Z
S1	−43	−72	8	1,958	−54	−95	9
S2	−36	−80	15	1,627	−47	−98	13
S3	−42	−67	−1	1,420	−59	−83	−2
S4	−40	−70	−7	771	−59	−88	−7
S5	−45	−58	5	1,310	−64	−73	2
S6	−44	−60	−4	1,581	−54	−95	−8
Mean (SE)	−47.7 (3.3)	−67.8 (8.1)	2.7 (8.2)	1,444 (397)	−56.2 (5.9)	−88.7 (9.4)	−1.2 (8.5)

The leftmost columns show Talairach coordinates for the center of gravity of left V5 as defined using fMRI and the corresponding volume of the activated region in units of 1 mm^3 voxels. The rightmost columns show the Talariach coordinates for the center of the TMS coil during rTMS stimulation of motion-sensitive extrastriate areas reconstructed from scalp measurements.
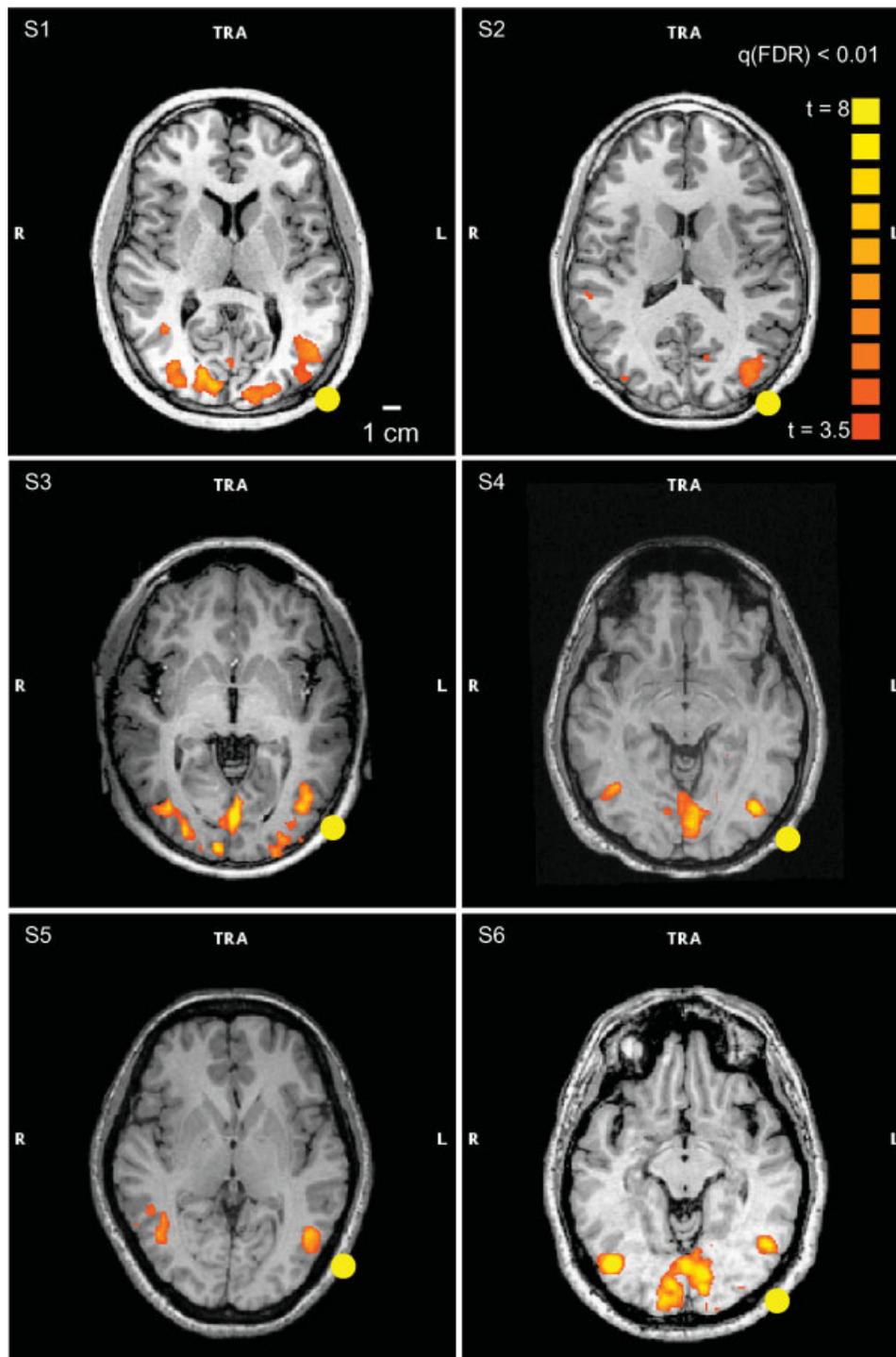
Figure 3.

fMRI localization of left motion-sensitive extrastriate visual areas (predominantly V5) and associated sites used during extrastriate rTMS (green circles). An axial slice through the Talairach registered brain that intersected both V5 and the TMS stimulation site is shown for each participant. fMRI activation is represented as a statistical t map thresholded for multiple comparisons at q (FDR) < 0.01. A good correspondence was found between the stimulation site chosen using moving phosphenes and the fMRI localization of motion-sensitive extrastriate areas in five of six participants.

to test whether the moving phosphene site was reliable. The participant reported reliable moving phosphenes in the same stimulation site used in the rTMS experiment even though it did not directly correspond to the fMRI-defined motion-sensitive areas. We were unable to deliver TMS pulses of sufficient intensity to elicit phosphenes over the fMRI-defined site due to strong facial twitches elicited in this participant if the coil was moved more than 1 cm anterior to the original stimulation site. It would not therefore have been possible to administer rTMS any closer to the fMRI-defined motion-sensitive cortical areas. Figure 3 also shows that the optimal phosphene induction sites are generally slightly posterior to area V5 suggesting that the stimulation may have targeted V5 and/or posterior extrastriate visual areas such as V3/V3a [Sunaert et al., 1999; Tootell et al., 1997], which contain pattern motion responsive neurons [Gegenfurtner et al., 1997].

DISCUSSION

rTMS can be used to bias the perception of plaid patterns constructed from two component sinusoidal gratings with unequal spatial frequencies toward either pattern or component motion. Delivery of offline 1 Hz rTMS over striate cortex favors the perception of pattern motion whereas 1 Hz rTMS over extrastriate visual areas favors the perception of component motion. This finding is direct evidence for the roles of human striate and extrastriate cortex in component and pattern motion perception, respectively, supporting previous correlational evidence from neuroimaging techniques [Huk and Heeger, 2002; Villeneuve et al., 2005; Wenderoth et al., 1999] and reports of perceptual deficits in patients with occipital lesions [Clifford and Vaina, 1999; Victor and Conte, 1994].

With regard to the way in which the visual system processes plaid stimuli to provide either a component or transparent percept, we have demonstrated that the percept can be manipulated by altering the relative activity of striate and motion-sensitive extrastriate areas of visual cortex. This finding is consistent with the idea that the two potential percepts compete for perceptual dominance. Our extrastriate result is consistent with a hierarchical processing approach within which component motion signals from V1 are fed into V5/MT where they may be combined by pattern motion selective neurons [Movshon et al., 1985; Perrone, 2004; Rust et al., 2006; Simoncelli and Heeger, 1998; Wilson et al., 1992]. It follows therefore that disrupting the function of V5 (and possibly V3/V3a) reduces the strength of pattern motion computations and biases perception in favor of component motion signals. The striate cortex result is more difficult to interpret in terms of some current models of plaid perception. If striate cortex is considered to be the primary gateway to extrastriate cortex [Felleman and Van Essen, 1991] it is not immediately clear why disruption of striate cortex would favor one perceptual state over another, because extrastriate processing

would also presumably be affected. It is possible that compromising the function of striate neurones would result in increased pattern selectivity further along the processing hierarchy in extrastriate cortex; however, the exact mechanism for this effect is not clear and a current model of plaid perception [Rust et al., 2006] may predict the opposite.

An alternative explanation would be that a weakening of the input to extrastriate cortex from striate cortex results in alternative inputs to extrastriate cortex having a larger role in determining the final percept. Bear in mind that with rTMS we are disrupting function rather than removing a region from processing entirely and that a small change in the relative weight of inputs to extrastriate cortex may be sufficient to bias the resulting percept. In this context it is a possibility that the effects of striate cortex stimulation may place a greater emphasis on the connections between extrastriate cortex and other thalamic visual areas [Sherman and Guillery, 1998, 2002] such as the LGN [Sincich et al., 2004] or the pulvinar [Casanova et al., 2001; Merabet et al., 1998]. The pulvinar is of particular interest as it has been shown to respond preferentially to pattern motion in humans [Villeneuve et al., 2005]. This interpretation of the data is, however, complicated by the fact that in the anesthetized cat, rTMS over V1 affects the visual response of dorsal LGN neurons [de Labra et al., 2007]. In addition, rTMS delivered over the posterior parietal cortex of the anesthetized cat has been shown to influence function in thalamic structures including the pulvinar [Valero-Cabre et al., 2007]. These effects appear to be mediated by a reduction in the cortical feedback to thalamic structures. It is currently unclear how a reduction in cortical feedback to the thalamus may influence plaid perception, although it has been demonstrated that feedback from higher cortical regions cannot completely account for pattern motion responses in the cat pulvinar [Merabet et al., 1998].

Finally it has been shown that striate cortex does contain a subpopulation of pattern motion responsive neurons that are only measurable in the absence of anaesthetic, suggesting a role of feedback from extrastriate cortical areas to striate cortex in the perception of plaid stimuli [Guo et al., 2004]. It is conceivable that a disruption of this feedback system either by weakening the feedback to striate cortex from extrastriate cortex or the ability of striate cortex to respond to the feedback could result in a perceptual bias toward either transparent or coherent motion.

It is clear from Figure 2 that rTMS over striate cortex had a greater perceptual effect than rTMS over extrastriate cortex. This may be due to the fact that the rTMS over striate cortex in one hemisphere may spread to the contralateral striate cortex due to their close proximity. For extrastriate cortex, however, stimulation was contained in one hemisphere and therefore the perceptual effects may have been reduced. It is possible to present stimuli in the peripheral visual field, and therefore to only one hemisphere, to optimize the effects of unilateral rTMS; however, we chose not to do this as it has been shown that

perception of plaids is altered in the periphery [Yo and Wilson, 1992]. In addition, the regions of striate cortex representing the periphery are deeper within the calcarine sulcus [DeYoe et al., 1996] and therefore less susceptible to rTMS. Figure 2 also shows the characteristic recovery from the effects of rTMS over time, confirming that our rest interval between stimulation sessions was sufficiently long.

A post-hoc fMRI localization of extrastriate stimulation sites was conducted to identify the cortical areas underlying the optimal phosphene induction sites. This confirmed that the perception of moving phosphenes was a largely reliable technique for functionally locating motion-sensitive areas in human extrastriate cortex including area V5 and probably including V3/V3a in some participants. The technique is not accurate in all participants, however, which may have contributed to the smaller average effects of rTMS on extrastriate regions as compared with striate regions. In the one participant who showed a mismatch between the optimal phosphene induction site and motion-sensitive cortical areas localized using fMRI (S6), it is possible that at the high threshold of 85% MSO required to elicit moving phosphenes, some stimulation of motion-sensitive areas may have occurred, particularly during rTMS.

Our results differ from those reported by Saint-Amour et al. [2005] who found that while striate cortex rTMS disrupted the dichoptic combination of plaid components (components presented separately to each eye), binocular perception (both components presented to both eyes) was not altered. These discrepancies can be accounted for by differences in viewing conditions, the tasks used and rTMS procedures. Based on the direct link reported by Saint-Amour et al. [2005] between the effects of rTMS and viewing conditions, we used monocular viewing to increase the potential of rTMS over striate cortex to influence perception. In addition, the task employed by Saint-Amour et al. [2005] was optimized for assessing the efficacy of dichoptic combination of components and therefore always required perceptual reports based on a pattern motion percept. In that task, participants were required to classify a plaid as moving upward oblique, horizontal or downward oblique based on whether the motion direction was judged to be more or less than 22.5° from horizontal. In the present study, we used a task optimized for measuring the presence or absence of pattern motion measured both by a subjective report and an objective measurement of the precise direction perceived by the participant when pattern motion was reported. Given the modest effects of rTMS, it appears that task optimization is essential to accurately measure specific effects. Finally, while Saint-Amour et al. [2005] used a fixed coordinate as their stimulation site in all participants, we selected a stimulation site individually for each participant based on optimal phosphene induction. This may have allowed us to induce a stronger effect with the same stimulation parameters employed by Saint-Amour et al. [2005].

Our results demonstrate that the way in which plaid patterns are consciously perceived can be directly manipu-lated with rTMS. In addition, the effects of rTMS over striate and extrastriate cortex are consistent with previous observations in neurological patients with lesions affecting these areas. The double dissociation between striate and extrastriate cortex in plaid perception demonstrated here has implications both for our understanding of motion perception and by extension the way in which the human cortex may handle complex processes with multiple competing outcomes.

REFERENCES

Adelson EH, Movshon JA (1982): Phenomenal coherence of moving visual patterns. Nature 300:523–525.

Beckers G, Homberg V (1992): Cerebral visual motion blindness: Transitory akinetopsia induced by transcranial magnetic stimulation of human area V5. Proc Biol Sci 249:173–178.

Beckers G, Zeki S (1995): The consequences of inactivating areas V1 and V5 on visual motion perception. Brain 118:49–60.

Benjamini Y, Hochberg Y (1995): Controlling the false discovery rate—A practical and powerful approach to multiple testing. J R Stat Soc B Methodol 57:289–300.

Born RT, Bradley DC (2005): Structure and function of visual area MT. Annu Rev Neurosci 28:157–189.

Braddick O (1993): Segmentation versus integration in visual-motion processing. Trends Neurosci 16:263–268.

Brainard DH (1997): The psychophysics toolbox. Spat Vis 10:433–436.

Brighina F, Piazza A, Daniele O, Fierro B (2002): Modulation of visual cortical excitability in migraine with aura: Effects of 1 Hz repetitive transcranial magnetic stimulation. Exp Brain Res 145:177–181.

Campana G, Cowey A, Walsh V (2002): Priming of motion direction and area V5/MT: A test of perceptual memory. Cereb Cortex 12:663–669.

Casanova C, Merabet L, Desautels A, Minville K (2001): Higher-order motion processing in the pulvinar. Prog Brain Res 134:71–82.

Castelo-Branco M, Formisano E, Backes W, Zanella F, Neuenschwander S, Singer W, Goebel R (2002): Activity patterns in human motion-sensitive areas depend on the interpretation of global motion. Proc Natl Acad Sci USA 99:13914–13919.

Clifford CW, Vaina LM (1999): Anomalous perception of coherence and transparency in moving plaid patterns. Brain Res Cogn Brain Res 8:345–353.

de Labra C, Rivadulla C, Grieve K, Marino J, Espinosa N, Cudeiro J (2007): Changes in visual responses in the feline dLGN: Selective thalamic suppression induced by transcranial magnetic stimulation of V1. Cereb Cortex 17:1376–1385.

Deblieck C, Thompson B, Iacoboni M, Wu AD (2008): Correlation between motor and phosphene thresholds: A transcranial magnetic stimulation study. Hum Brain Mapp 29:662–670.

Delicato LS, Derrington AM (2005): Coherent motion perception fails at low contrast. Vision Res 45:2310–2320.

DeYoe EA, Carman GJ, Bandettini P, Glickman S, Wieser J, Cox R, Miller D, Neitz J (1996): Mapping striate and extrastriate visual areas in human cerebral cortex. Proc Natl Acad Sci USA 93:2382–2386.

Dumoulin SO, Bittar RG, Kabani NJ, Baker CL Jr, Le Goualher G, Bruce Pike G, Evans AC (2000): A new anatomical landmark for reliable identification of human area V5/MT: A quantitative analysis of sulcal patterning. Cereb Cortex 10:454–463.

Felleman DJ, Van Essen DC (1991): Distributed hierarchical processing in the primate cerebral cortex. Cereb Cortex 1:1–47.

Fierro B, Brighina F, Vitello G, Piazza A, Scalia S, Giglia G, Daniele O, Pascual-Leone A (2005): Modulatory effects of low- and high-frequency repetitive transcranial magnetic stimulation on visual cortex of healthy subjects undergoing light deprivation. J Physiol 565:659–665.

Fitzgerald PB, Fountain S, Daskalakis ZJ (2006): A comprehensive review of the effects of rTMS on motor cortical excitability and inhibition. Clin Neurophysiol 117:2584–2596.

Gegenfurtner KR, Kiper DC, Levitt JB (1997): Functional properties of neurons in macaque area V3. J Neurophysiol 77:1906–1923.

Grossman ED, Battelli L, Pascual-Leone A (2005): Repetitive TMS over posterior STS disrupts perception of biological motion. Vision Res 45:2847–2853.

Guo K, Benson PJ, Blakemore C (2004): Pattern motion is present in V1 of awake but not anaesthetized monkeys. Eur J Neurosci 19:1055–1066.

Hotson J, Braun D, Herzberg W, Boman D (1994): Transcranial magnetic stimulation of extrastriate cortex degrades human motion direction discrimination. Vision Res 34:2115–2123.

Hotson JR, Anand S (1999): The selectivity and timing of motion processing in human temporo-parieto-occipital and occipital cortex: A transcranial magnetic stimulation study. Neuropsychologia 37:169–179.

Huk AC, Heeger DJ (2002): Pattern-motion responses in human visual cortex. Nat Neurosci 5:72–75.

Hupe JM, Rubin N (2003): The dynamics of bi-stable alternation in ambiguous motion displays: A fresh look at plaids. Vision Res 43:531–548.

Hupe JM, Rubin N (2004): The oblique plaid effect. Vision Res 44:489–500.

Kammer T, Puls K, Erb M, Grodd W (2005): Transcranial magnetic stimulation in the visual system. II. Characterization of induced phosphenes and scotomas. Exp Brain Res 160:129–140.

Kim J, Wilson HR (1993): Dependence of plaid motion coherence on component grating directions. Vision Res 33:2479–2489.

Lang N, Siebner HR, Ernst D, Nitsche MA, Paulus W, Lemon RN, Rothwell JC (2004): Preconditioning with transcranial direct current stimulation sensitizes the motor cortex to rapid-rate transcranial magnetic stimulation and controls the direction of after-effects. Biol Psychiatry 56:634–639.

Machii K, Cohen D, Ramos-Estebanez C, Pascual-Leone A (2006): Safety of rTMS to non-motor cortical areas in healthy participants and patients. Clin Neurophysiol 117:455–471.

Majaj NJ, Carandini M, Movshon JA (2007): Motion integration by neurons in macaque MT is local, not global. J Neurosci 27:366–370.

Marg E, Rudiak D (1994): Phosphenes induced by magnetic stimulation over the occipital brain—Description and probable site of stimulation. Optom Vis Sci 71:301–311.

Merabet L, Desautels A, Minville K, Casanova C (1998): Motion integration in a thalamic visual nucleus. Nature 396:265–268.

Movshon JA, Adelson EH, Gizzi MS, Newsome WT (1985): The analysis of moving visual patterns. In: Chagass C, Gattass R, Gross C, editors. Pattern Recognition Mechanisms. Rome: Vatican Press. pp 117–151.

Movshon JA, Newsome WT (1996): Visual response properties of striate cortical neurons projecting to area MT in macaque monkeys. J Neurosci 16:7733–7741.

Orban GA (2008): Higher order visual processing in macaque extrastriate cortex. Physiol Rev 88:59–89.

Pack CC, Livingstone MS, Duffy KR, Born RT (2003): End-stopping and the aperture problem: Two-dimensional motion signals in macaque V1. Neuron 39:671–680.

Pascual-Leone A, Bartres-Faz D, Keenan JP (1999): Transcranial magnetic stimulation: Studying the brain-behaviour relationship by induction of 'virtual lesions'. Philos Trans R Soc Lond B Biol Sci 354:1229–1238.

Pascual-Leone A, Walsh V (2001): Fast backprojections from the motion to the primary visual area necessary for visual awareness. Science 292:510–512.

Pelli DG (1997): The VideoToolbox software for visual psychophysics: Transforming numbers into movies. Spat Vis 10:437–442.

Perrone JA (2004): A visual motion sensor based on the properties of V1 and MT neurons. Vision Res 44:1733–1755.

Rafal R (2001): Virtual neurology. Nat Neurosci 4:862–864.

Rodman HR, Albright TD (1989): Single-unit analysis of pattern-motion selective properties in the middle temporal visual area (MT). Exp Brain Res 75:53–64.

Rust NC, Mante V, Simoncelli EP, Movshon JA (2006): How MT cells analyze the motion of visual patterns. Nat Neurosci 9:1421–1431.

Sack AT, Kohler A, Linden DE, Goebel R, Muckli L (2006): The temporal characteristics of motion processing in hMT/V5+: Combining fMRI and neuronavigated TMS. Neuroimage 29:1326–1335.

Saint-Amour D, Walsh V, Guillemot JP, Lassonde M, Lepore F (2005): Role of primary visual cortex in the binocular integration of plaid motion perception. Eur J Neurosci 21:1107–1115.

Sheppard BM, Pettigrew JD (2006): Plaid motion rivalry: Correlates with binocular rivalry and positive mood state. Perception 35:157–169.

Sherman SM, Guillery RW (1998): On the actions that one nerve cell can have on another: Distinguishing "drivers" from "modulators". Proc Natl Acad Sci USA 95:7121–7126.

Sherman SM, Guillery RW (2002): The role of the thalamus in the flow of information to the cortex. Philos Trans R Soc Lond B Biol Sci 357:1695–1708.

Siebner HR, Lang N, Rizzo V, Nitsche MA, Paulus W, Lemon RN, Rothwell JC (2004): Preconditioning of low-frequency repetitive transcranial magnetic stimulation with transcranial direct current stimulation: Evidence for homeostatic plasticity in the human motor cortex. J Neurosci 24:3379–3385.

Silvanto J, Cowey A, Lavie N, Walsh V (2005a): Striate cortex (V1) activity gates awareness of motion. Nat Neurosci 8:143–144.

Silvanto J, Lavie N, Walsh V (2005b): Double dissociation of V1 and V5/MT activity in visual awareness. Cereb Cortex 15:1736–1741.

Silvanto J, Muggleton NG, Cowey A, Walsh V (2007a): Neural activation state determines behavioral susceptibility to modified theta burst transcranial magnetic stimulation. Eur J Neurosci 26:523–528.

Silvanto J, Muggleton NG, Cowey A, Walsh V (2007b): Neural adaptation reveals state-dependent effects of transcranial magnetic stimulation. Eur J Neurosci 25:1874–1881.

Silvanto J, Pascual-Leone A (2008): State-dependency of transcranial magnetic stimulation. Brain Topogr 21:1–10.

Simoncelli EP, Heeger DJ (1998): A model of neuronal responses in visual area MT. Vision Res 38:743–761.

Sincich LC, Park KF, Wohlgemuth MJ, Horton JC (2004): Bypassing V1: A direct geniculate input to area MT. Nat Neurosci 7:1123–1128.

Smith AT (1992): Coherence of plaids comprising components of disparate spatial frequencies. Vision Res 32:393–397.

Stewart L, Battelli L, Walsh V, Cowey A (1999): Motion perception and perceptual learning studied by magnetic stimulation. Electroencephalogr Clin Neurophysiol Suppl 51:334–350.

Sunaert S, Van Hecke P, Marchal G, Orban GA (1999): Motion-responsive regions of the human brain. Exp Brain Res 127:355–370.

Talairach J, Tournoux P (1988): A Co-planar Stereotaxic Atlas of a Human Brain: 3-Dimensional Proportional System: An Approach to Cerebral Imaging. Stuttgart: Thieme Medical Publishers. Chapter viii, pp 122.

Thompson B, Aaen-Stockdale CR, Mansouri B, Hess RF (2008a): Plaid perception is only subtly impaired in strabismic amblyopia. Vision Res 48:1307–1314.

Thompson B, Mansouri B, Koski L, Hess RF (2008b): Brain plasticity in the adult: Modulation of function in amblyopia with rTMS. Curr Biol 18:1067–1071.

Tinsley CJ, Webb BS, Barraclough NE, Vincent CJ, Parker A, Derrington AM (2003): The nature of V1 neural responses to 2D moving patterns depends on receptive-field structure in the marmoset monkey. J Neurophysiol 90:930–937.

Tootell RB, Mendola JD, Hadjikhani NK, Ledden PJ, Liu AK, Reppas JB, Sereno MI, Dale AM (1997): Functional analysis of V3A and related areas in human visual cortex. J Neurosci 17:7060–7078.

Valero-Cabre A, Payne BR, Pascual-Leone A (2007): Opposite impact on C-14-2-deoxyglucose brain metabolism following patterns of high and low frequency repetitive transcranial magnetic stimulation in the posterior parietal cortex. Exp Brain Res 176:603–615.

Victor JD, Conte MM (1994): Investigation of a patient with severely impaired direction discrimination: Evidence against the intersection-of-constraints model. Vision Res 34:267–277.

Villeneuve MY, Kupers R, Gjedde A, Ptito M, Casanova C (2005): Pattern-motion selectivity in the human pulvinar. Neuroimage 28:474–480.

Walsh V, Pasual-Leone A (2003): Transcranial Magnetic Stimulation: A Neurochronometrics of Mind, MIT Press.

Wenderoth P, Watson JD, Egan GF, Tochon-Danguy HJ, O'Keefe G J (1999): Second order components of moving plaids activate extrastriate cortex: A positron emission tomography study. Neuroimage 9:227–234.

Wilson HR, Ferrera VP, Yo C (1992): A psychophysically motivated model for 2-dimensional motion perception. Vis Neurosci 9:79–97.

Yo C, Wilson HR (1992): Perceived direction of moving two-dimensional patterns depends on duration, contrast and eccentricity. Vision Res 32:135–147.

Zhao B, Chen H, Li B (2005): Pattern motion and component motion sensitivity in cat superior colliculus. Neuroreport 16: 721–726.