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Psychophysical and rTMS evidence for the presence of motion opponency in human V5

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Abstract

Background—Motion sensitive cells within macaque V5, but not V1, exhibit motion opponency whereby their firing is suppressed by motion in their anti-preferred direction. fMRI studies indicate the presence of motion opponent mechanisms in human V5.

Objective/hypothesis—We tested two hypotheses. 1) Performance of a motion discrimination task would be poorer when stimuli were constructed from pairs of dots that moved in counter-phase vs. in-phase, because counter-phase dots would activate motion opponent mechanisms in V5. 2) Offline 1Hz rTMS of V5 would impair discrimination performance for in-phase stimuli but not counter-phase stimuli, and the opposite effect would be found for rTMS of V1.

Methods—Stimuli were constructed from 100 dot pairs. Paired dots moved along a fixed motion axis either in counter-phase (motion opponent stimulus) or in-phase (non-opponent motion stimulus). Motion axis orientation discrimination thresholds were measured for each stimulus. Blocks of 300 trials were then presented at 85% correct threshold and discrimination accuracy was measured before and after 1Hz offline rTMS of either V1 or V5. Subjects were 8 healthy adults.

Results—Discrimination thresholds were significantly larger (worse) for counter-phase than in-phase stimuli ($p = 0.02$). V5 rTMS mildly impaired discrimination accuracy for the in-phase dot stimuli ($p = 0.02$) but not the counter-phase dot stimuli. The opposite effect occurred for V1 rTMS ($p = 0.05$).

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Conclusions—Opponent motion mechanisms are present within human V5 and activation of these mechanisms impairs motion discrimination. In addition, perception of the motion axis within opponent motion stimuli involves processing within V1.

Keywords

Visual cortex; repetitive transcranial magnetic stimulation; motion perception; primary visual cortex; MT; middle temporal area

Introduction

The detection and interpretation of motion is a fundamental property of vision. Cells that respond to motion can be found throughout the visual pathway [1]; however area V5/MT within the dorsal extrastriate visual cortex appears to be particularly specialized for motion processing [2]. Approximately 30% of cells in primate V1 are responsive to specific directions of motion whereas >90% of cells in MT are tuned for motion direction [3–6]. Many cells within primate MT also exhibit motion opponency, whereby cells are actively suppressed by motion in their anti-preferred direction [7, 8]. For example, Qian and Andersen [7] found that, as a population, cells within MT, but not V1, were suppressed by a counter-phase paired-dot stimulus which contained locally balanced motion direction signals. Furthermore, the responses of cells within MT to the paired dot stimulus were not reliably different from their responses to a non-directional flicker-noise stimulus [7]. These results were important because motion opponent mechanisms provide a potential mechanism for noise reduction in MT.

Evidence for motion opponency within the human MT+ complex (henceforth referred to as V5) has been provided by fMRI studies using grating stimuli [9, 10] and paired vs. unpaired dots [9]. The human MT+ complex encompasses multiple motion sensitive sub-regions including the homologues of MT and MST [11–14]. Psychophysical evidence also supports the presence of motion opponency in human V5 [15]. For example, motion opponent stimuli have been used to suppress the response of human V5 in order to investigate the mechanisms underlying perceptual learning of motion direction discrimination [16–18]. In one such study, Lu et al. [16] modified Qian and Andersen's paired dot stimulus to allow for a motion axis discrimination task to be performed by constraining the pairs of dots within the stimulus to move along a common axis. In addition, Lu at al. generated a non-opponent motion stimulus for use as a control by simply changing the phase of motion within each dot pair from counter-phase to in-phase. Specifically, within the counter-phase motion stimulus, paired dots moved towards and away from one another in order to activate motion opponent mechanisms. Conversely, within the in-phase stimulus, the dot pairs moved back and forth in unison with no opponency (Figure 1). Lu et al. found that, although behavioral performance was above chance, participants could not learn fine motion axis discriminations for the counter-phase stimulus. However, learning was possible for coarse motion axis discriminations. This result was replicated by Thompson and Liu [17] who found that the effect could not be explained by differences in task difficulty.

Building on this previous work, a recent fMRI study found that counter-phase dots produced significantly less activity within V5 than in-phase dots and a trend in the opposite direction occurred within V1 [18]. In addition, after training, there was a correlation between increased learning and decreased V5 response for participants trained with counter-phase dot stimuli [18]. These results suggested that the performance of tasks involving counter-phase dots may rely on visual areas other than V5, such as V1, and that the counter-phase dot stimuli generated a noisy signal within V5 that was reduced during learning. The current study was designed to further investigate these possibilities. We first tested the hypothesis that motion axis discrimination thresholds would be higher for counter-phase dots than in-phase dots. The rational was that a nosier signal from V5 would elevate perceptual discrimination thresholds.

We then used offline 1 HZ repetitive transcranial magnetic stimulus (rTMS) to temporarily disrupt function within either V1 or V5 [19–21] and assessed the effect of this disruption on motion axis discrimination accuracy for both counter-phase and in-phase dot stimuli. Our hypothesis was that the effect of V5 rTMS on motion axis discrimination would be more pronounced for in-phase dots than counter-phase dots. This hypothesis was based on fMRI data, [18] which revealed an interaction between V5 and V1, whereby V5 showed a greater response to in-phase than counter-phase dots and V1 showed the opposite effect. This result suggested that processing of in-phase dot stimuli might rely primarily on V5 whereas processing of counter-phase dot stimuli might rely primarily on V1, presumably because V1 does not exhibit motion opponency.

Effects of V1 and V5 TMS on the performance of visual tasks have been reported using both online and offline stimulation protocols e.g. [21–28]. We chose to use offline rTMS because we wanted to match the testing conditions between the psychophysical and rTMS components of the study as closely as possible. This was important because the psychophysical task was attentionally demanding and we were concerned that the sensations and noise associated with online rTMS would distract participants.

Methods

Participants

Eight adult participants (mean age 28 years, 5 female) provided written informed consent and took part in the study. All participants had normal or corrected to normal vision, no previous history of neurological or psychiatric disorders, were not currently taking any medications and had no other contraindications to rTMS. Data from 6 patients were collected within the Department of Psychology and the Ahmanson Lovelace Brain Mapping Center at UCLA. Data from two additional participants were collected at the Neurorehabilitation Research Centre at McGill University. All study protocols were approved by the UCLA Medical Institutional Review Board and the McGill University Institutional Review Board.

Procedure

The experiment consisted of three sessions conducted on separate days; 1) motor and phosphene (moving and static) thresholding, 2) task practice and measurement of psychometric functions, and 3) measurements of task accuracy directly before and after rTMS of V5 and V1. A Magstim SuperRapid biphasic stimulator with a figure-8 coil was used for single pulse and repetitive TMS at both study sites.

Psychophysical stimuli and task

Psychophysical stimuli (Figure 1) were viewed binocularly from a distance of 120 cm (maintained by a chin rest) in a dark room. A viewing tube running from the chin rest to the monitor was used to exclude any extraneous orientation reference cues. Stimuli were presented with a vertical refresh rate of 60 Hz and a resolution of 800 × 600 pixels on a NEC MultiSync FE771SB monitor at UCLA and a 22-inch Sony Trinitron monitor at McGill. Stimuli were generated and presented using MatLab (MathWorks, Inc.) with the psychophysics toolbox [29, 30].

The psychophysical stimuli have been described previously [16–18] and were based on an original stimulus first described by Qian and Andersen [7]. Each stimulus consisted of a field of 200 dark dots (0.01 cd/m^2) presented on a light background (8.0 cd/m^2) within a circular aperture (7.8° diameter). Stimuli were presented for 200 ms followed by a one second response interval. The dots were presented in a “twin pair” configuration which removed any spatial cues for task performance requiring participants to rely on the motion signals present in the stimuli [16]. Each twin pair consisted of two identical pairs of dots positioned 0.06° to 0.15° apart from each other to form a parallelogram. The minimum distance between the two dots in each pair was 0.06° and the maximum was 0.30°. Dots moved at 2°/sec and each twin pair had a limited lifetime of 120 ms. Within the counter-phase stimuli the dots within each pair moved towards and away from each other (180° out of phase) along a common axis to activate motion opponent mechanisms in V5 [7]. Dot pairs within the in-phase motion stimuli (non-opponent) moved back and forth in unison (0° out of phase) along a common axis. Half of the twin pairs within the in-phase stimuli moved in one direction while the other half moved in the opposite direction. Therefore the global motion direction was balanced within both types of stimuli but only the counter-phase stimuli were also balanced for local motion. Within both types of stimuli 20% of the twin pairs were each allocated a random motion axis to encourage participants to attend to the whole display.

Participants were asked to fixate on a point in the center of the display and judge whether the motion axis was clockwise or counter-clockwise from vertical on each trial. The fixation point disappeared when the moving dots were presented. The color of the fixation point directly before a trial indicated whether the subsequent stimulus would contain counter-phase or in-phase motion. Dot phase was kept constant for 10 trials and then changed for the subsequent 10 trials.

In the practice session participants completed 4 blocks of 80 trials with a motion axis rotated ±30° from vertical (i.e., a motion axis that was easily discriminated from vertical). Dot speed

was increased from 0.5°/sec to 2°/sec over the 4 blocks and stimulus duration was decreased from 800 ms to 200 ms. If a participant scored < 90% correct on a block, the block was repeated until 90% performance was achieved. Trial-wise auditory feedback was provided and percent correct scores were presented on the display screen after each block.

Once practice was complete, a psychometric function was measured using the method of constant stimuli. Task performance was assessed at five difficulty levels; ±20, 16, 12, 8, 4° from vertical with 160 trials presented per difficulty level. Stimuli were presented at a fixed difficulty in blocks of 80 trials (dot phase was reversed every 10 trials as described above). The first five blocks were presented in descending order of difficulty (from ±4 to 20°) and the second five blocks in ascending order of difficulty (from ±20 to 4°). Participants were provided with a break after the first five blocks. When the measurement was complete a Weibul function was fitted to the data and 85% correct thresholds were calculated for the counter-phase and in-phase stimuli. The psychometric function measurement was repeated at least twice and data were combined across repeats.

During the rTMS session, 300 trials of counter-phase and in-phase stimuli were presented at each participant's 85% correct threshold directly before and after each period of rTMS stimulation.

Motor and phosphene thresholding

Motor and phosphene thresholds were measured after participants had worn lightproof goggles for 15 minutes in order to dark-adapt [31]. Resting motor thresholds measured using standard techniques [31]. The center of a figure-of-eight coil (14 cm width) was positioned tangentially to the skull with the handle oriented backwards, 45 degrees from the midline. Single pulse TMS was delivered over the left motor cortex and surface EMG electrodes were used to record motor evoked potentials (MEPs) from the relaxed right first dorsal interosseous muscle. Peak to peak EMG amplitudes were used to assess MEP size. The coil was moved systematically over a 1×1 cm^2 interval grid covering the estimated region of the left motor cortex that was drawn on a tight fitting lycra cap. Pulses were first delivered at each grid point and then in between grid points. The site that elicited the largest magnitude MEP was designated as the motor hot spot. Once the hot spot had been identified, starting at a clearly suprathreshold intensity, the intensity of TMS delivered to the hotspot was lowered systematically in steps of 1% maximum stimulator output. The motor threshold stimulation intensity was reached when only 5 out of 10 pulses evoked MEP amplitudes greater than 50 microvolts. An active motor threshold was then measured by asking the participants to squeeze the thumb and forefinger together with a steady, light pinch grip that induced approximately 100 microvolts of EMG activity. TMS was delivered to the same hotspot and intensity was reduced in steps of 1% maximum stimulator output. Active motor threshold was defined as the stimulation intensity at which 5/10 pulses induced an MEP with an amplitude greater than 200 microvolts.

Static and moving phosphene thresholds were then measured in order to localize V1 and V5 for rTMS stimulation. Following previous work [31], participants wore light-proof goggles during phosphene thresholding and were asked to keep their eyes open and look forwards. For V1 phosphenes, single pulses of TMS were delivered at 100% maximum stimulator

output (MSO, maximum field strength = 2 Tesla) over a 1 × 1 cm^2 interval grid covering the left occipital region with the rightmost grid boundary centered on a midline point 2 cm above the inion. The grid was marked on a tight fitting lycra swimming cap. The coil was held with the handle pointing upwards, parallel to the participant's spine. The grid position eliciting the most reliable phosphene approximately within the central 8° of the visual field was identified and stimulus intensity was gradually reduced until 5/10 pulses evoked a phosphene. This was the phosphene threshold intensity [see 31 for further details].

V5 phosphenes were induced by single pulses of TMS delivered at 100% MSO over a 1 × 1 cm^2 interval grid centered on a point 3 cm above the inion and 5 cm to the left until participants reported a moving phosphene [see 21 for a detailed description of this approach]. Once the optimal coil position for inducing a moving phosphene had been located, stimulus intensity was reduced to find the moving phosphene threshold (a moving phosphene reported on 5/10 pulses).

Repetitive transcranial magnetic stimulation

Nine hundred pulses of 1Hz TMS were delivered with an intensity corresponding to the active motor threshold. The use of active motor thresholds to calibrate stimulation intensity increased the tolerability of the rTMS paradigm because active motor thresholds are typically lower than phosphene thresholds. However, the use of active motor thresholds meant that stimulation was not specifically calibrated for visual areas.

The V1 and V5 stimulation sites corresponded to the optimal positions for inducing static (V1) and moving (V5) phosphenes within the left hemisphere as identified during the phosphene thresholding session. It is possible that other visual regions close to V1 and V5 were also affected by the rTMS and moving phosphenes can be elicited by stimuli of visual areas other than V5 [32]. However, the specific moving phosphene-based V5 localization approach that we used has acceptable agreement with fMRI localization of V5 [21]. We also note that we targeted the whole of V5 with rTMS and we were not able to specifically target sub-regions such as MT or MST with our phosphene-based localization technique. The order of V1 and V5 stimulation was randomized across participants and the two stimulation sessions were separated by at least 30 minutes to allow for stimulation effects to dissipate [21, 33]. Participants sat quietly with their eyes closed during the stimulation.

Results

Psychometric functions

Each participant's psychometric functions for in-phase and counter-phase dots are shown in Figure 2. Six of eight participants exhibited greater 85% correct thresholds for counter-phase than in-phase dots and two had similar thresholds for both stimuli. Overall, group mean motion axis discrimination thresholds were significantly higher for counter-phase (mean = 16.2°, SD = 8.2°) than in-phase dots (mean = 9.8°, SD = 2.0°), $t_7 = 3.0$, $p = 0.02$. Individual thresholds and psychometric function fits to the group data are shown in Figure 3. Individual thresholds for two participants were extrapolated from the psychometric function fits (the open symbols in Figure 3).

rTMS

The mean active motor threshold was 61% MSO (SD 12%). When stimuli were presented at threshold directly prior to rTMS, mean accuracy was 85% correct (SD 0.6) for counter-phase dots and 86% correct (SD 0.6) for in-phase dots. These means did not differ significantly ($t_7 < 1$). To assess the effect of rTMS on task performance, the post-rTMS accuracy for each condition was expressed as a percent change from pre-rTMS accuracy. As shown in Figure 4, although the effects of rTMS were small, rTMS of V1 reduced accuracy for counter-phase dots whereas rTMS of V5 reduced accuracy for in-phase dots. As the four conditions had unequal variances (Levine's test for equality of variances $p < 0.05$, compare the error bars and spread of raw data in Figure 4), non-parametric one sample Wilcoxen tests were used to assess whether these reductions were statistically significant from zero. Significant reductions in accuracy were found for counter-phase dots after V1 stimulation ($W_8 = 2.0$, $p = 0.05$) and in-phase dots after V5 stimulation ($W_8 = 2.4$, $p = 0.02$). No significant rTMS effects were found for counter-phase dots after V5 stimulation ($W_8 = 0.3$, $p = 0.8$), or in-phase dots after V1 stimulation ($W_8 = 0.6$, $p = 0.6$). There were no significant correlations between the motion axis orientation discrimination thresholds and any of the changes in task performance induced by rTMS (all p values > 0.1).

Discussion

Our first hypothesis was that motion axis discrimination thresholds would be poorer for counter-phase dot stimuli than in-phase dot stimuli. The rational for this hypothesis was that counter-phase dots would activate motion opponent mechanisms within V5 whereas in-phase dots would not [7, 16]. Therefore, we expected the counter-phase stimulus to generate a noisy response from V5 and impair processing of motion axis information. Psychometric measurements of motion axis discrimination thresholds for each type of stimulus were consistent with this idea. Specifically, mean motion axis discrimination thresholds for counter-phase dot stimuli were almost a factor of 2 higher than those for in-phase dot stimuli. This result is in agreement with data from an earlier fMRI study of perceptual learning [18]. In that study it was found that perceptual learning improved motion axis discrimination for counter-phase dot stimuli and that greater improvements were associated with greater reductions in BOLD response within V5. Thompson et al. (2013) proposed the following explanation for these results. Since the response of V5 to opponent motion is comparable to its response to flicker noise [7], neural signals at V5 may be indistinguishable from noise when counter-phase dots are viewed. A noisy response at V5 limits motion axis orientation discrimination. Therefore a potential mechanism for the improvements in motion axis discrimination that resulted from perceptual learning was noise reduction at V5. The reduced BOLD signal at V5 that accompanied the behavioral improvement of motion axis discrimination, as found by Thompson et al. (2013), was consistent with the hypothesis that noise was reduced at V5.

Although motion direction discrimination was poorer for counter-phase dots than in-phase dots, participants were still able to perform the task. Furthermore, perceptual learning can induce large improvements in coarse motion direction discrimination for counter-phase dot stimuli [16–18]. Therefore it is clear that coarse motion axis information can be extracted

from counter-phase dot stimuli by at least one motion sensitive cortical area. V1 is highly likely to be involved in this process. A sizable proportion of cells within V1 are sensitive to local motion directions [3–6] and the majority of motion opponency studies have reported an absence of motion opponency within V1 [7, 9, 10, 18], but see [33]. However, local motion processing within V1 would not discriminate between the signal and the noise twin-pairs present within our stimulus leading to a reduction in sensitivity to small changes in motion axis orientation. In contrast, V5 is more suited to the extraction of fine motion axis information from in-phase dot stimuli than V1 due to its ability to integrate motion information over larger areas of the visual field and a high tolerance to external noise [2].

We used inhibitory offline rTMS to test our second hypothesis that the processing of motion axis orientation 1) relies on V1 to a greater extent than V5 for counter-phase dot stimuli and 2) relies on V5 to a greater extent that V1 for in-phase dot stimuli. Importantly, task difficulty was matched precisely for the counter-phase and in-phase dot stimuli at 85% correct discrimination accuracy. The results of the rTMS experiment broadly supported our hypothesis. rTMS of V5 significantly impaired discrimination performance for the counter-phase but not the in-phase dot stimuli. The opposite was true for rTMS of V1. However, the magnitude of the rTMS effects was small. This may have been due to the use of an offline rTMS protocol rather than an online protocol, the use of phosphenes to localize stimulation sites rather than functional MRI localization data [34], the use of unilateral rTMS and bilateral stimulus presentation, our relatively small sample size or a combination of these factors.

An unexpected effect was that the variance was much higher for the conditions that did not show a significant effect of rTMS (counter-phase dots combined with V5 stimulation and in-phase dots combined with V1 stimulation) than those that did. This violation of the equal variance assumption prevented us from demonstrating a significant interaction between stimulation site (V1 vs. V5) and stimulus (counter-phase vs. in-phase) that would have provided stronger evidence for a dissociable effect of V1 vs. V5 rTMS. Nevertheless, our rTMS results are consistent with fMRI measurements demonstrating a significantly stronger response in V5 relative to V1 for in-phase stimuli and a marginally stronger response to counter-phase stimuli in V1 relative to V5 [18].

Our rTMS results also demonstrate that offline rTMS protocols can be used to temporarily alter neural processing in both V1 and MT. This is in agreement with previous studies that have employed either standard rTMS protocols [19–21, 35] or theta-burst stimulation [23, 36] in offline visual cortex rTMS protocols. In particular, our results show that 1 Hz rTMS can temporarily affect processing in V1 and V5 as evidenced by small, but significant reductions in psychophysical discrimination performance.

Together, the results from the two experiments reported here further support the idea that motion opponent mechanisms are present within human V5. Furthermore, by exploiting motion opponency, we found that a very simple stimulus manipulation (simply reversing the relative phase of dot pairs) could alter the relative importance of V1 and V5 for performance of a motion axis discrimination task.

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Highlights

- rTMS of V1 impairs perception of motion opponent stimuli
- rTMS of V5 impairs perception of non-motion opponent stimuli
- Motion discrimination is poorer for motion opponent than non-motion opponent stimuli

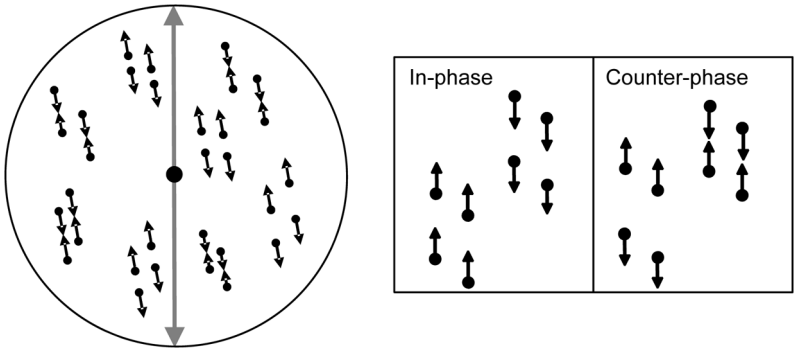

Figure 1.

Schematic representations of the psychophysical stimuli. Left: Counter-phase dot twin pairs with a motion axis orientation counter-clockwise from vertical. The grey arrow represents a vertical motion axis orientation and the black arrows indicate the motion direction of each dot. Right: Schematic examples of in-phase and counter-phase twin pairs (two twin pairs per panel). Black arrows indicate the motion direction of each dot.

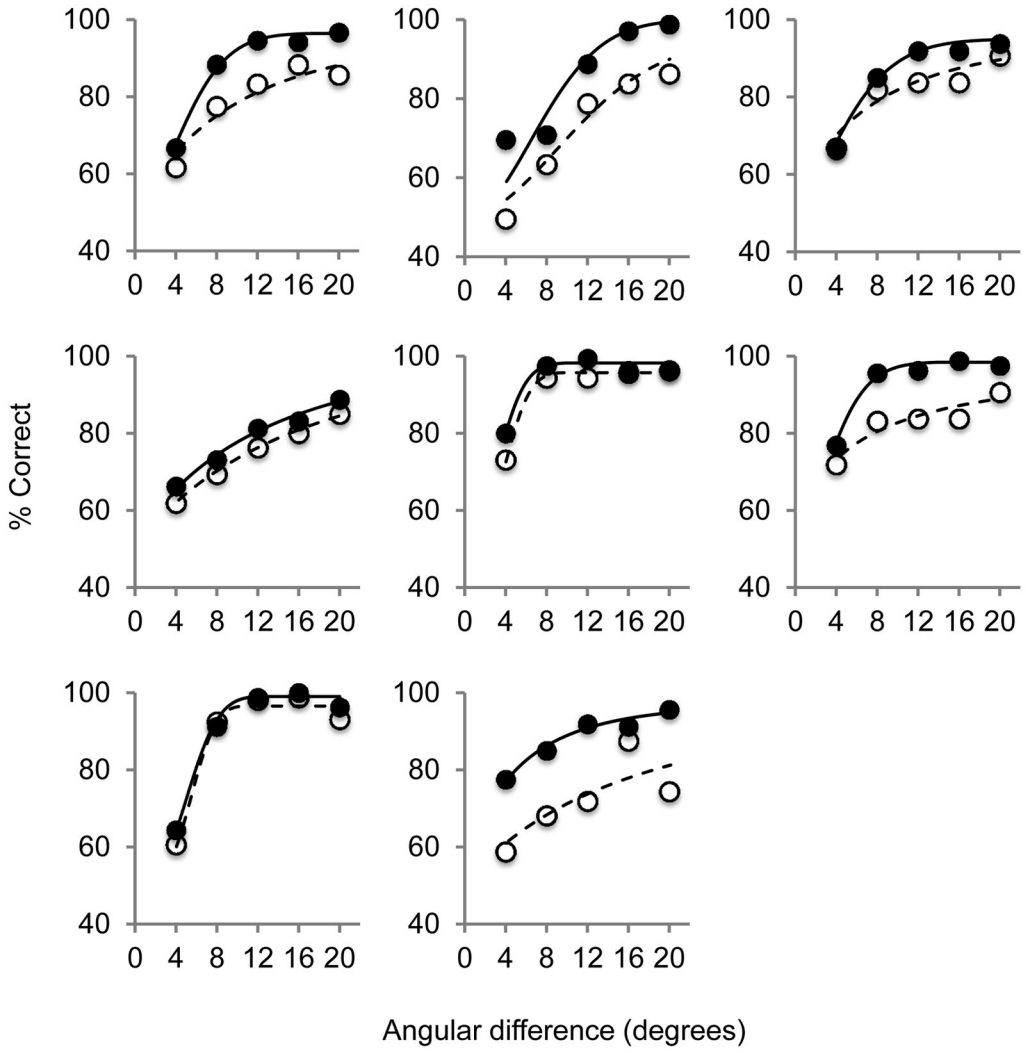

Figure 2.

Psychometric functions for each participant for both the in-phase (closed circles) and counter-phase (open circles) dot stimuli. The majority of participants exhibited greater accuracy for the in-phase stimuli.

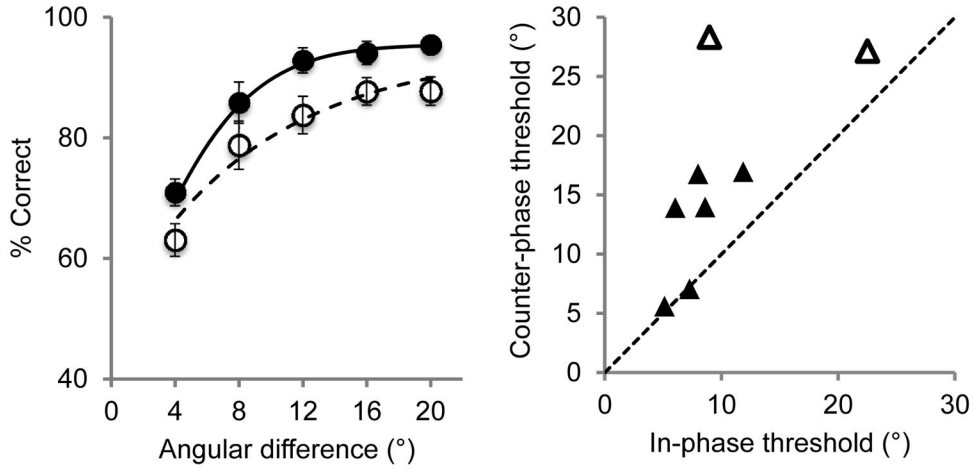

Figure 3.

Left panel: Average psychometric functions for in-phase dots (filled symbols) and counterphase dots (open symbols). Accuracy was poorer for counter-phase dots. Error bars show ± 1 SEM. Note that error bars represent between subjects error whereas statistical significance represents within-subjects differences. Right panel: Individual motion axis discrimination thresholds corresponding to 85% correct accuracy for in-phase and counter-phase dots. Data points above the dashed unity line indicate larger (worse) thresholds for counter-phase dots than in-phase dots. The open symbols indicate thresholds that were extrapolated from the psychometric function fit.

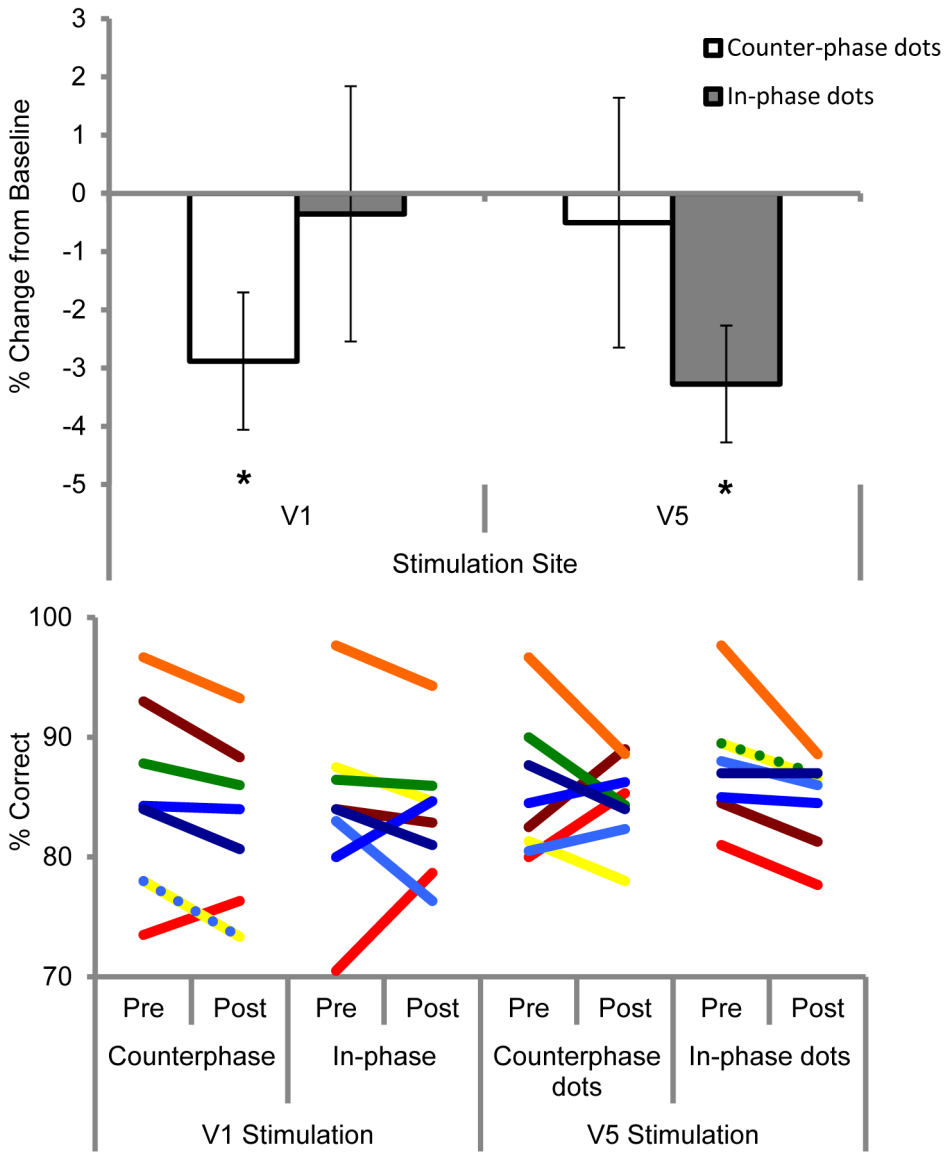

Figure 4.

The effect of rTMS over V1 and V5 on task performance. The top panel shows mean percent change from baseline for each condition. Open bars show data for the counter-phase dot stimulus and filled bars for the in-phase dot stimulus. Bars on the left are for V1 stimulation and bars on the right for V5 stimulation. Errors bars show ± 1 SEM and asterisks indicate a significant change from baseline. The lower panel shows raw percent correct scores of each participant for each condition. Each colour denotes a different participant. The dashed lines indicate overlapping data.