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TMS reveals flexible use of form and motion cues in biological motion perception

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ABSTRACT

The perception of human movement is a key component of daily social interactions. Although extrastriate area MT+/V5 is closely associated with motion processing, its role in the processing of sparse 'biological motion' displays is still unclear. We developed two closed matched psychophysical tasks to assess simple coherent motion perception and biological motion perception, and measured changes in performance caused by application of TMS over MT+/V5. Performance of the simple motion discrimination task was significantly depressed by TMS stimulation, and highly correlated within observers in TMS conditions, but there was no significant decrement in performance of the biological motion task, despite low intra-observer correlations across TMS conditions. We conclude that extrastriate area MT+/V5 is an obligatory waypoint in the neural processing of simple coherent motion, but is not obligatory for the processing of biological motion. Results are consistent with a dual neural processing route for biological motion processing.

1. Introduction

Our ability to perceive the movements of other people's bodies is a key component of daily social interactions. We are so adept at recognising human body movements that highly impoverished point-light (biological motion) displays are sufficient to support the construction of sophisticated perceptual representations such as identity, intention and mood (review in Johnson and Shiffrar, 2013). Thus biological motion displays are widely used in studies of social movement perception.

Early psychophysical research demonstrated that motion-processing neurons in the visual cortex are involved in the processing of biological motion displays (coding speed and direction of dots; Mather et al., 1992). However other results indicate that form-processing systems are involved in biological motion processing (coding figure pose; Beintema and Lappe, 2002). In the neuroscience literature human cortical area MT+/V5 is known to be a crucial stage of the cortical motion processing pathway (Campana et al., 2002; Stevens et al., 2009), but its importance for biological motion processing is still in considerable doubt. Early neuroimaging studies by Grossman et al. (2000) and Grèzes et al. (2001) found that MT+/V5 was activated by biological motion displays. However, more recent research has shown a conflicting pattern of results. Patients with focal damage to MT+/V5 do not show deficits in biological motion perception (Gilaie-Dotan et al., 2015), and TMS applied over MT+/V5 does not affect the discrimination of upright versus inverted figures (Grossman et al., 2005), nor their motion direction (Vangeneugden et al., 2014).

One interpretation of this complex pattern of results is that there is a dual neural processing route for biological motion, one route involving motion processing via MT+/V5 en route to STS and the other by-passing MT+/V5 via the form-processing route which also projects to STS (Morel and Bullier, 1990). However issues with previous studies leave the issue open so the role of motion systems in the processing of biological motion is still unclear (Mather et al., 1992; Thornton et al., 1998; Troje and Westhoff, 2006; Beintema and Lappe, 2002; Beintema et al., 2006). In particular, although Grossman et al. (2005) found no effect of TMS over MT+/V5 on biological motion processing they only tested left MT+/V5 using off-line stimulation, which is less effective than on-line stimulation (van Kemenade et al., 2012). Moreover Grossman et al. (2005) used only biological motion displays, so it was uncertain whether their stimulation was more effective in disrupting other aspects of motion processing. We therefore designed a TMS experiment to test the role of MT+/V5 in biological motion, in which stimulation was applied while participants performed two very closely matched tasks. Furthermore we tested both hemispheres using online stimulation.

The control motion task (*Drift*) involved discriminating the

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direction of 13 coherently moving but randomly located signal dots (leftward versus rightward) embedded in a background of randomly moving noise dots. The biological motion task (*Walker*) involved discriminating the facing direction of a point-light treadmill walker also composed of 13 signal dots and embedded in a background of randomly moving noise dots. Stimuli in the two tasks were matched in terms of size, luminance, duration and average velocity. We first established a baseline level of performance in each task by determining the number of noise dots required to attain a specified level of performance, and then measured changes in performance due to TMS stimulation during the task.

2. Methods

2.1. Subjects

Twelve participants who were unaware of the purpose of the study participated in the experiments. Two of these participants were discarded by initial screening because they exhibited no discernible neural effects of TMS due to over-reaction to TMS side effects (tingling sensations, twitches, noise).

All participants had normal or corrected-to-normal visual acuity. All participants were screened with an interview for any condition that could increase the risks associated to the use of rTMS (Rossi et al., 2009). All participants understood the information given about TMS and gave written informed consent according to the Declaration of Helsinki. The study was approved by the Local Ethics Committee at University of Padova, where the data was collected.

2.2. Apparatus

Stimuli were generated using Matlab and Psychtoolbox (Brainard, 1997; Pelli, 1997) and displayed on a 19-in. ViewSonic G90fB monitor at a refresh rate of 75 Hz. The screen resolution was 1280×1024 pixels. Each pixel subtended $\sim 1.7'$ (0.028 deg). The background luminance was 35.7 cd/m^2, while luminance of dot stimuli was 89.7 cd/m^2, as measured using a Minolta LS-100 photometer. TMS was delivered via a Magstim Super-Rapid stimulator and a 70mm figure-of-eight coil.

Participants sat in a dark room and were immobilized with a chin rest placed at 57 cm from the screen. Viewing was binocular. They were instructed to fixate the centre of the screen and were given training to familiarize them with the stimuli and task.

2.3. Stimuli

2.3.1. Walker stimuli

Observers viewed a simulation of biological motion on a computer screen, developed using the algorithm described in Cutting (1978). The shifting pattern of dots generated by a step cycle of a walking figure (Walker) was sampled to create forty static views. A subset of fifteen consecutive views was presented for 26.66 ms each (400 ms in total). When this series of static frames was presented in rapid succession, observers reported a compelling impression a walking figure, as expected. Thirteen points were plotted in each frame to define the figure (signal); one for the head, two each (left and right) for the shoulders, elbows, wrists, hips, knees, and ankles. Dot size was 5 pixels ($\sim 0.14°$). They simulated the pattern generated by a sideways view of a person walking on a treadmill. In other words, the dot displacements contained no translatory component, only elliptical and oscillatory components. In half of the presentations (randomly selected) the figure faced to the right, and in the other half the figure faced to the left. The walker's torso was $\sim 2.3°$ and the entire figure was $\sim 6.5°$. The walking figure was embedded in a circular aperture (11.5°) of scrambled noise dots generated from the same motions as the walker but with each dot displaced to a new randomly selected starting location in the stimulus aperture. Previous research has shown that discrimination of walker direction becomes more difficult as the number of noise dots increases. However some walker dots (such as those located at the wrists and ankles) undergo much greater motion than others (such as those on the shoulders and hips), introducing marked variability in the effectiveness of individually added noise dots. In order to avoid this problem, we added noise dots in sets of thirteen corresponding to all the dots defining a walker. The facing direction of each set of noise dots was randomly set either to the left or the right. The number of sets of scrambled noise dots to present was determined separately for each participant before the main experiment (see baseline sessions).

In order to avoid observers performing the task by identifying consistent locations within the aperture at which specific walker dots were expected to occur, from trial to trial the screen x and y coordinates of the walker figure were randomly jittered by $\pm 1.2°$.

2.3.2. Drift stimuli

The observer viewed a cloud of dots presented within a circular aperture (11.5°) for a duration of 400 ms (15 frames). In order to ensure a close match with the Walker stimuli, 13 dots in random locations moved coherently leftwards or rightwards at the same velocity matched to the average velocity as the Walker dots, to define the signal. Noise dots were added in sets of 13 dots, randomly distributed in the stimulus aperture and each moving in a randomly selected direction (see Pilly and Seitz, 2009) at the same speed as the signal dots. Any dots which moved outside the border of the stimulus aperture re-appeared at the opposite side. Dot size was $\sim 0.14°$ and as for the *Walker* stimuli the number of sets of noise dots to present was determined individually for each participant (see Section 2.4.1).

2.4. Procedure

2.4.1. Baseline sessions

Separately for each stimulus type, participants performed a first block of 30 trials of direction discrimination (left vs. right) with a signal to noise ratio of 1:3 (for every signal dot there were three noise dots). Depending on their performance, the number of noise dots was decreased or increased in subsequent blocks until each participant reached a response accuracy of between 67% and 83% correct in two consecutive blocks with the same levels of noise. For one participant, who had a very rapid transition between accuracy below 67% and above 83% when increasing or decreasing the noise level by one unit, we used a noise level producing 90% of correct responses. This level of noise (one noise level for each stimulus type, *Walker* and *Drift*) was then used as the baseline in the TMS part of this study. Participants responded with a button press (non-speeded response). An ISI of 500 ms followed each button press. The order of presentation of the tasks was counterbalanced across participants.

2.4.2. Transcranial magnetic stimulation (TMS) sessions

Tasks were the same as those described in the behavioural sessions of the study. For each stimulus type, participants performed a direction discrimination task while rTMS was administered over either Cz, left MT+/V5 or right MT+/V5 in different blocks. Each block comprised 30 trials. In these blocks, the ISI was 3 s in order to minimize any potential risk due to temporal summation of neural excitation (Rossi et al., 2009). Fig. 1 illustrates the timeline of the Baseline and TMS sessions. The order presentation

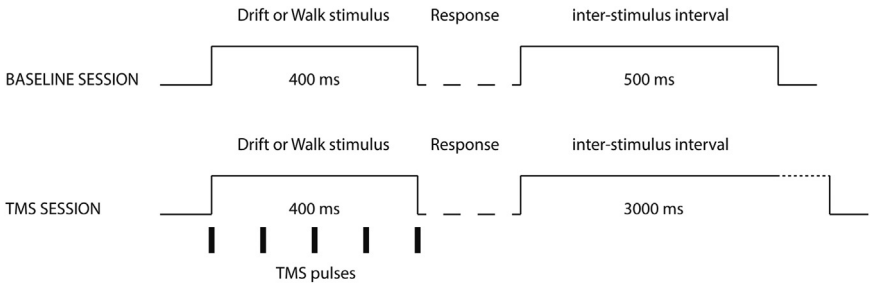

Fig. 1. Timeline of a single trial in the Baseline and TMS sessions. Stimulus duration was 400 ms, with TMS pulses delivered at 100 ms intervals during presentation in the stimulus.

of the tasks and the area stimulated was counterbalanced across participants.

For phosphene detection, the stimulation intensity was set at a value for which each subject perceived clear phosphenes with the eyes closed (65–80% of the maximum stimulator output-MSO). For the experiment the intensity was then set at 65% of MSO. A total of five pulses were delivered over a period of 500 ms (10 Hz). In particular, TMS pulses were delivered at the onset of the stimulus. For stimulation over MT+/V5 the coil was held tangential to the skull with the handle pointing upwards. Localization of stimulation sites aimed at targeting areas MT+/V5 was determined as follows (see Campana et al., 2002). Two stimulation sites were first roughly localized in all subjects by using predetermined coordinates: 3 cm dorsal to inion and 5 cm leftward or rightwards from there. For all subjects TMS pulses were delivered at these sites and then at sites from 0.5 to 1.0 cm away until the subjects reported the most vivid phosphenes in the contralateral hemifield and approximately at the centre of the visual field along the vertical axis. Subjects were asked about the size and position of the perceived phosphenes and whether they were moving or stationary. All participants perceived larger phosphenes (often referred as "elongated") when stimulated over the left or right MT+/V5 sites. Eight out of ten participants perceived moving phosphenes. At the TMS intensity we used it is common that not all subjects report moving phosphenes with stimulation of MT+/V5 (e.g., Campana et al., 2011; Silvanto and Cattaneo, 2010). In any case, for all subjects the characteristics of the phosphenes (Silvanto et al., 2007), together with the distance of the stimulated position from the inion strongly suggest that the sites correspond to area MT+/V5. Indeed, this technique provides a localization consistent with fMRI localisers (Thompson et al., 2009). None of the participants reported seeing phosphenes during the experiment, when the stimulator output was reduced to 65%.

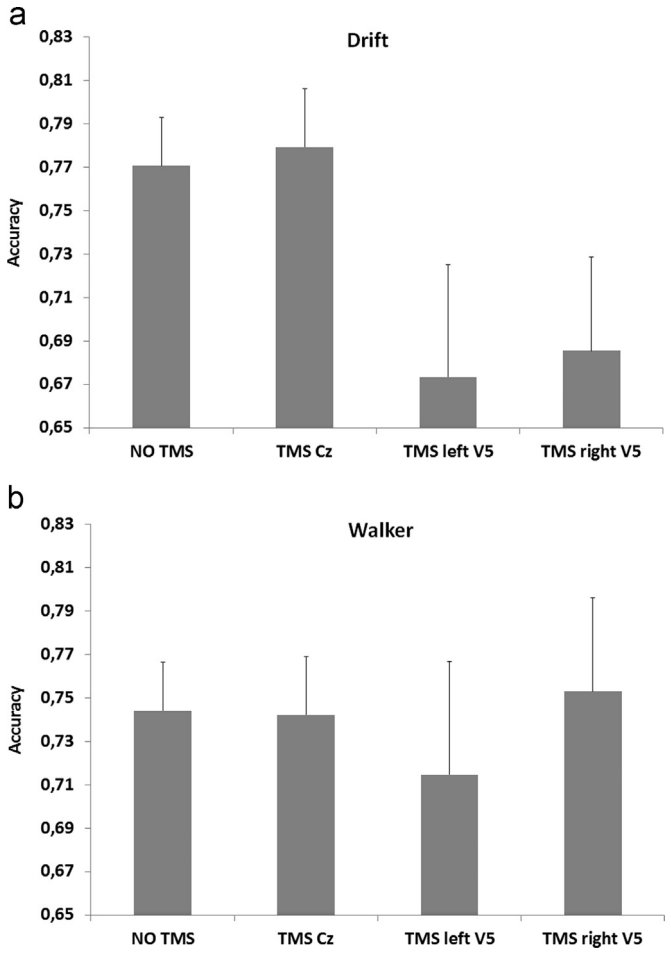

Fig. 2. Direction discrimination performance as a function of stimulation condition. (a) Mean percentage correct discrimination of direction for the *Drift* stimulus (±1 SEM). TMS over MT+/V5 significantly depressed performance relative to TMS over Cz. (b) Mean percentage correct discrimination of direction for the *Walker* stimulus (±1 SEM). There was no significant difference in performance between the TMS conditions.

3. Results

Fig. 2a plots mean direction discrimination accuracy for the *Drift* stimuli for each TMS condition. Performance was much lower when TMS was applied to MT+/V5 than with no TMS or when it was applied to Cz. Fig. 2b plots corresponding data for the *Walker* stimuli. There is relatively little difference in performance level between the conditions.

We ran a Shapiro-Wilk test in order to evaluate the normality of our data distributions. In no condition were data distributions significantly different from a normal distribution ($SW_{10} < 0.88$, $p > 0.05$ for all conditions). The sphericity assumption was assessed with Mauchly's test, but was never found to be significant ($W_2 > 0.06$, $p > 0.05$).

A *t*-test between the *Drift* and the *Walker* conditions when TMS was not applied (No TMS condition; left-most columns in Fig. 2a and b) yielded no significant difference between these two data sets ($t_9 = 1.09$, $p = 0.304$), indicating that the level of difficulty of the two tasks was equivalent.

Since the No TMS condition is not strictly comparable to the active stimulation conditions due to the absence of specific interference such as audible noise, tingling skin sensations or even twitches that TMS might cause, we did not include this condition in subsequent analyses. TMS over Cz was taken as the baseline condition, where no neural interference on visual motion perception is expected but all other interfering effects of TMS are present.

A two-way within-subjects ANOVA with motion type (Drift vs. Walker) and TMS site (Cz, left MT+/V5, right MT+/V5) as factors

showed a significant effect of TMS site ($F_{2,18}=4.11$, $p=0.034$, $\eta_p^2=0.31$) and of the interaction between motion type and TMS site ($F_{2,18}=3.84$, $p=0.041$, $\eta_p^2=0.30$), suggesting that TMS at certain sites affected performance on only one type of visual motion. In fact, Bonferroni-corrected post-hoc *t*-tests showed a significant decrement in task performance using TMS over left ($t_9=3.35$, $p=0.018$) or right MT+/V5 ($t_9=3.58$, $p=0.012$) relative to TMS over Cz, but only for the Drift motion type, not for the Walker motion type ($t_9=0.72$, $p=0.980$ and $t_9=-0.50$, $p=1$ respectively for TMS over the left and right MT+/V5, with respect to TMS over Cz). The Scaled JZS Bayes Factor (BF; Rouder et al., 2009; Morey and Rouder, 2011) calculated on these *t*-tests support this view: BFs of 7.07 and 9.67 provide substantial evidence in favour of the alternative hypothesis (Jeffreys, 1961) when comparing the accuracy obtained on the Drift stimulus with TMS over Cz with respect to TMS over the left or right MT+/V5 respectively, whereas BFs of 0.29 and 0.26 provide substantial evidence in favour of the null hypothesis when comparing the accuracy obtained on the Walker stimulus with TMS over Cz with respect to TMS over the left or right MT+/V5 respectively.

4. Discussion

Results indicate that TMS applied to MT+/V5 was very effective in interfering with the *Drift* task: Stimulation in either hemisphere was sufficient to cause a significant decrement in performance. On the other hand, TMS had no significant effect on performance in the *Walker* task. Given that the two tasks were closely matched in terms of both stimulus properties and baseline psychophysical performance, the obtained difference cannot be explained in terms of variations between the tasks. The decrement in performance due to TMS is quite severe (approximately 10%), in line with previous studies of direction discrimination under magnetic stimulation (Beckers and Homberg, 1992; Cowey et al., 2006; Sack et al., 2006; Stevens et al., 2009). Evidence also indicates that the effect of TMS is quite spatially specific to the area of the cortex stimulated so our effect is highly likely to be due to stimulation of MT+/V5 (Bona et al., 2015). The effects produced by online rTMS are likely due to an increase in neural noise that might reduce the signal-to-noise ratio (Miniussi et al., 2013). Online rTMS would mainly excite the less active neurons (state-dependent TMS effects theory: Silvanto and Muggleton, 2008; Silvanto et al., 2008), which in the case of our studies are those MT+/V5 neurons not tuned to the specific stimulus presented. This increase in neural activity would counteract the specific activation of neurons tuned to the stimulus, thus online rTMS is likely to interfere with performance more than the general and aspecific reduction in excitability produced by offline 1 Hz stimulation (Sandrini et al., 2011).

Data are consistent with the dual processing route hypothesis: MT+/V5 is not an obligatory waypoint in the neural processing of biological motion, though it *is* obligatory for discrimination of coherent drift motion. To further test the hypothesis, we examined the intra-subject correlations in task performance across TMS conditions. When the same processing route is used in different conditions, then correlations between performance in those conditions should be high. However if different processing resources are recruited in different conditions, then correlations between performance should be lower. For the Drift task there was a very high correlation between TMS over Cz and TMS over left ($r=0.86$, $p=0.001$) and right MT+/V5 ($r=0.82$, $p=0.004$) respectively. On the other hand for the Walker task there was no significant correlation between performance with TMS over Cz and TMS over left ($r=0.42$, $p=0.229$) and right MT+/V5 ($r=0.40$, $p=0.254$) respectively. Correlations between TMS conditions thus support the hypothesis of a dual processing route for processing biological motion.

Recent psychophysical and computational studies are consistent with flexible use of form and motion cues in biological motion (Thirkettle et al., 2009; Thurman et al., 2010; Singer and Sheinberg, 2010). Psychophysical and computational studies by Thurman et al. (2010) indicate that biological motion perception relies more on form-based processing strategies as motion information becomes less available. In their study motion information was manipulated by varying exposure time. In our study motion information was presumably corrupted by the application of TMS over MT+/V5, and we infer that the high level of task performance we observed in this condition was due to the use of a form-based processing strategy.

In summary, using closely matched tasks we found that TMS applied over cortical area MT+/V5 disrupted discrimination of coherent motion direction but did not disrupt discrimination of biological motion facing-direction. Results are consistent with flexible use of motion cues in biological motion perception, mediated by a dual neural processing route.

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