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Original Articles

The Role of Human Brain Area hMT+ in the Perception of Global Motion Investigated With Repetitive Transcranial Magnetic Stimulation (rTMS)

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ABSTRACT

Background: Psychophysical evidence suggests that the perception of the motion and color of moving stimuli are determined separately in the human brain. Here we aim to determine the role of visual cortical areas hMT+ and V1/V2 in each task by measuring the effect of rTMS of each area using an off-line continuous theta-burst stimulation (cTBS) protocol.

Methods: In the motion task, the direction of moving dots was identified using a global motion stimulus that avoids tracking, and in the detection task for the same stimulus, the presence of the dots was detected regardless of motion. Performance was measured using forced-choice methods in 8 subjects, both before and at 4 time-intervals in the 1-hour after brain stimulation. All experiments were done using achromatic and isoluminant, red-green chromatic stimuli.

Results: Performance on global motion for both achromatic and chromatic stimuli was significantly impaired following cTBS of visual area hMT+, with a maximum effect occurring 11 min after stimulation. In comparison, there was no effect of cTBS on the motion task for areas V1/V2 or the vertex (control). cTBS did not affect the detection task in either area.

Conclusions: Our experiments validate the use of cTBS as an advantageous off-line rTMS protocol for studying visual areas. The results indicate a causal link between neural activity in area hMT+ and perception of motion of isoluminant chromatic stimuli. We conclude that area hMT+ is part of a common pathway processing the global motion of chromatic and achromatic stimuli, but is not involved in their detection.

Introduction

Psychophysical evidence accumulated over several decades has shown that human color vision is poor in the perception of motion. This is thought to arise from the distinct specializations of the dorsal and ventral streams in primate vision for the attributes motion and color, respectively, with good processing of motion but poor sensitivity to color in the dorsal pathway and good processing of color but little sensitivity to motion in the ventral pathway. An overlap of function between the two streams appears to remain, however, allowing color vision to perform on motion tasks under a range of conditions. Such tasks include direction discrimination of isoluminant chromatic gratings at contrasts above threshold [1,2], motion discrimination on global motion tasks at isoluminance [3], tasks using higher order motion stimuli [4–6] and the perception of motion after-effects generated by isoluminant chromatic stimuli [7,8]. In color vision, a clear dissociation has been found between two different types of visual threshold: stimulus detection (color/form threshold) and the discrimination of its direction of motion (motion threshold) [3,9]. This is based on the surprising observation that luminance noise masks the motion of chromatic stimuli but not their detection: as luminance noise contrast increases, chromatic stimuli show no change in detection threshold (visibility) but loose their perceived motion, eventually appearing static. This supports the idea that motion and detection thresholds are independently determined, with different physiological origins.

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Here we aim to determine the physiological origins of chromatic global motion perception versus color detection. We aim to test two linked hypotheses, that hMT+ is involved in chromatic global motion thresholds but not chromatic detection thresholds, by selectively and temporarily impairing processing in two different areas of the human visual cortex using repetitive Transcranial Magnetic Stimulation (rTMS). We predict that stimulation of area hMT+ will selectively impair performance on discriminating the direction of motion of chromatic stimuli but will not affect performance on the detection of the stimulus. In addition, we measure the effect of rTMS applied to areas V1/V2 on motion and detection thresholds, with the aim of determining their comparative roles in these two tasks. As V1/V2 are not selective areas for global stimulus attributes, such as motion, we do not expect pronounced effects on motion discrimination, but might expect an effect on color detection [10].

On-line [11–16], and off-line [17] TMS have previously been shown to be effective at reducing, or improving [18] motion sensitivity using a range of different stimuli and tasks, stimulation protocols, and brain areas targeted. Here we use a continuous theta-burst stimulation protocol (cTBS) [19], an off-line rTMS protocol, which is relatively novel to vision testing. As part of the study, we aimed to identify the time course for the effects of cTBS, which has not been well established yet for vision. We use global motion stimuli, as these are well suited to reveal the motion selective functions of area hMT+, and can also be used for color detection tasks. We also run all experiments on achromatic stimuli as a control and to verify the effectiveness of cTBS. This is the first attempt to determine the relative selectivity of dorsal area hMT+ (in relation to V1/V2) for color and global motion by direct stimulation of the human brain.

Materials and methods

Participants

Eleven healthy participants (5 female, 6 male) took part in the experiments and all had normal or corrected to normal vision, and normal color vision assessed by the Farnsworth–Munsell 100-hue color test (Munsell Color Company Inc, 1957). Written consent was obtained from all participants and none reported any contra-indications to rTMS. Experiments were approved locally by the Ethics Review Board of the Montreal Neurological Institute and were performed in accordance with the ethical standards of the Declaration of Helsinki (1964), and established TMS safety protocols [20].

Psychophysical apparatus

Stimuli were generated using Cambridge Research Systems ViSaGe video-graphics card with 14-bit contrast resolution, connected to a Sony Trinitron (GDM 500DIS) monitor (Sony Corporation, Tokyo, Japan) with a spatial resolution of 1024 × 768 pixels and 120 Hz frame rate. Calibration of this equipment has been described previously [3]. All stimuli were viewed binocularly in a dimly lit room at a viewing distance of 62 cm.

Visual stimuli

Stimuli (Fig. 1A) were limited lifetime random dot kinematograms (RDKs) with a diameter of 12°, a gray background (mean luminance of 51 cd/m^2). Motion sequences of 50 luminance or chromatic Gaussian blobs (sigma = 0.25° and FWHM of 0.58°) appeared and disappeared with a limited lifetime duration of 240 ms, and each blob moved at 5.4 deg/s. Stimulus presentation was ramped on and off in a Gaussian temporal envelope (sigma = 0.125 s). The centers of the stimuli were 6° away from the fixation mark in the right visual field.

Stimuli were designed to isolate the luminance (achromatic) or the L/M (red/green, RG) cone opponent mechanism and were represented within a three-dimensional cone contrast space [21,22]. The isoluminant point was determined for each participant using a minimum motion method as previously described [3].

Transcranial magnetic stimulation

Apparatus

TMS was delivered using a Magstim Super Rapid2 biphasic stimulator with an air-cooled figure eight 70 mm coil (Magstim, UK). Participants were blindfolded and seated in a chair with a chinrest in order to minimize movement throughout stimulation.

Localization of visual areas V1/V2 and hMT+

All participants received stimulation over the left hemisphere [23–25]. In preliminary experimental sessions, areas hMT+ and V1/V2 were localized using a functional phosphene method in order to designate the correct stimulation site in each individual [24,26]. In this procedure, single TMS pulses with 70–80% maximal stimulator output (MSO), were delivered over the striate cortex, targeting the primary visual cortex by placing the coil at 4 cm above the inion and 2 cm to the left [15,27–29]. The handle of the coil pointed upwards, parallel to the participant's spine, and was moved systematically over this area until the participant reported the perception of a clear stationary phosphene in his/her central visual field. Localization of area hMT+ was found by systematic stimulation of an area approximately 3 cm dorsal and 5 cm lateral from the inion with the TMS coil pointing down at 45° to the spine of the participant [24,28]. The point that elicited the strongest moving phosphene was designated as area hMT+. If a participant was unable to perceive a phosphene, double pulses of stimulation were applied (80% MSO, 50 ms inter-stimulus interval) [29,30]. All participants described moving phosphenes when area hMT+ was stimulated and stationary phosphenes during area V1/V2 stimulation. The coil-position within each target brain area that elicited the most vivid phosphene responses were marked using a stereotaxic image guiding system (Brainsight, Rogue Research Inc, Montreal, Canada), which was used to co-register each participant's head with an MRI scan and ensured the same site was stimulated across testing sessions. The vertex, located at the intersection of the inion, nasion and interaural lines, was used as a control site for stimulation in order to control for non-specific effects of TMS, such as auditory clicking sounds and sensory tapping sensation on the scalp, without targeting specific brain sites related to the tasks [26].

Continuous theta-burst stimulation protocol

cTBS was delivered at 45% MSO as bursts of three 50 Hz pulses every 200 ms (5 Hz) over a 41 s stimulation period, cumulating in a total of 600 pulses given in a continuous train [19,29,31].

Experiment 1: effect of contrast on coherence threshold (psychophysics)

Prior to the rTMS experiments, the effect of stimulus contrast on motion coherence thresholds (direction discrimination) was determined for both achromatic and isoluminant chromatic stimuli. Motion coherence thresholds were acquired using a method of constant stimuli (MCS) with a 1AFC protocol in which the subject indicated in which direction, left or right, the stimulus moved. Coherence threshold was 82% correct. Coherence thresholds were measured as a function of stimulus contrast, scaled in multiples of detection threshold, in three subjects. Contrast detection