Brain Stimulation 9 (2016) 876–881

Contents lists available at ScienceDirect

Brain Stimulation

journal homepage: www.brainstimjrnl.com

Psychophysical and rTMS Evidence for the Presence of Motion Opponency in Human V5

Benjamin Thompson [a,b,*], Choi Deblieck [c], Allan Wu [d,e], Marco Iacoboni [d,f,g], Zili Liu [h]

[a] School of Optometry and Vision Science, University of Waterloo, Canada
[b] School of Optometry and Vision Science, University of Auckland, New Zealand
[c] AcCENT (Academic Center for ECT and Neuromodulation), University Psychiatric Center – KU Leuven (University of Leuven) – Campus Kortenberg, Kortenberg, Belgium
[d] Ahmanson-Lovelace Brain Mapping Center, UCLA, Los Angeles, CA, USA
[e] Department of Neurology, David Geffen School of Medicine at UCLA, Los Angeles, CA, USA
[f] Department of Psychiatry and Biobehavioral Sciences, David Geffen School of Medicine at UCLA, Los Angeles, CA, USA
[g] Brain Research Institute, David Geffen School of Medicine at UCLA, Los Angeles, CA, USA
[h] Department of Psychology, UCLA, Los Angeles, CA, USA

ARTICLE INFO

Article history:
Received 24 November 2015
Received in revised form 22 April 2016
Accepted 30 May 2016
Available online 11 June 2016

Keywords:
Visual cortex
Repetitive transcranial magnetic stimulation
Motion perception
Primary visual cortex
MT
Middle temporal area

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 1 Hz 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 1 Hz 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 ($p = 0.05$).
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.

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

* Corresponding author. Tel.: +1 519 888 4567 x 39398; fax: +1 519 725 0784.
E-mail address: ben.thompson@uwaterloo.ca (B. Thompson).

1935-861X/
http://dx.doi.org/10.1016/j.brs.2016.05.012

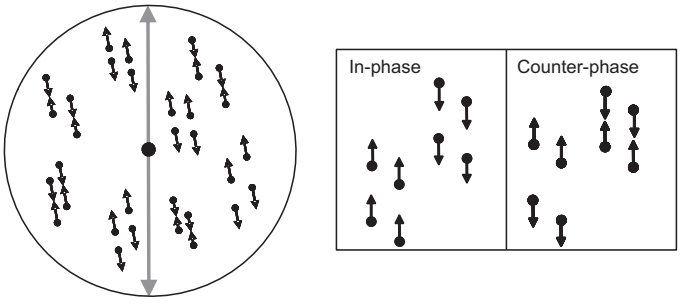

Figure 1. Schematic representations of the psychophysical stimuli. Left: Counter-phase dot twin pairs with a motion axis orientation counter-clockwise from vertical. The gray arrow represents a vertical motion axis orientation and the black arrows indicate the motion direction of each dot. Right: Schematic examples of in-phase and counter-phase twin pairs (two twin pairs per panel). Black arrows indicate the motion direction of each dot.

human MT+ complex encompasses multiple motion sensitive sub-regions including the homologs 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 et 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 toward 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 (Fig. 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 rationale was that a noisier signal from V5 would elevate perceptual discrimination thresholds.

We then used offline 1 Hz repetitive transcranial magnetic stimulation (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. Refs. [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 (Fig. 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