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MT+/V5 Activation without Conscious Motion Perception: A High-Field fMRI Study

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While activity of MT+/V5 neurons is believed to be necessary for the conscious perception of visual motion, whether neural activity in MT+/V5 is a sufficient condition for the conscious perception of motion in vision still remains unanswered. A high-field (3.0 Tesla) functional magnetic resonance imaging (fMRI) study was designed and performed to answer this specific question. Eleven healthy subjects viewed a checkerboard pattern stimulus reversed in contrast at 0.2, 12, 30, and 60 Hz while being probed for activation in MT+/V5. At 0.2 Hz, all viewers perceived pattern-reversal which was stationary in position. However, at 12, 30, and 60 Hz, many subjects perceived apparent motion (e.g., vertical and horizontal flows) in the square pattern. At 12 and 30 Hz reversals, MT+/V5 was activated in all subjects (11/11). Nevertheless, three out of eleven (3/11) subjects denied motion perception in these conditions. At 60 Hz reversal, as many as seven out of eleven (7/11) subjects failed to see motion but activation in MT+/V5 was found in the majority (5/7) of the subjects. The results demonstrated that significant MT+/V5 activation occurs without accompanying subjective awareness of seeing motion in an apparent-motion stimulus, indicating that neural activity in MT+/V5 does not represent a sufficient condition for conscious perception of motion in vision.

Keywords: *apparent motion, illusory motion, consciousness, checkerboard pattern reversal*

Introduction

Evidence thus far indicates that intact neural activity in the human motion-sensitive cortical area MT+/V5 is a necessary condition for conscious experience of visual motion. Bilateral lesions in MT+/V5 result in cortical motion blindness,¹ disturbance of neural activities in MT+/V5 by transcranial magnetic stimulation compromises visual motion perception,² and activation of MT+/V5 is detected when motion is perceived with or without actual visual input of motion.^{3–7} Quantitative analyses of behavior and neuroimaging data have, in addition, demonstrated positive correlation between the level of MT+/V5 activity and awareness of motion (e.g., 6, 7). Nevertheless, one essential question, namely, whether neural activity in MT+/V5 is a sufficient condition for conscious

perception of visual motion, still remains unanswered. To answer this question would contribute to a better understanding of the neural mechanisms for conscious perception of motion, because, unlike parametric correlation studies, it illuminates the causal relationship between neural activity and perception.⁸ MT+/V5 has been reported to be sensitive to stationary flickers and luminance changes hinting insufficiency,^{5,9} but the relationship between MT+/V5 activation and consciousness of motion perception remains obscure because subjective perceptions were not assessed in these experiments. To address this specific issue, this high-field (3.0T) functional magnetic resonance imaging (fMRI) study investigated whether MT+/V5 was significantly activated in the absence of conscious perception of motion in a natural viewing condition in healthy viewers. The possibility of experimentally demonstrating this dissociation was accomplished by assessing neural activity in MT+/V5 using fMRI while subjects viewed a subtle

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apparent-motion stimulus, in which motion could or could not be perceived consciously depending on the subject. If MT+/V5 were to be activated in individuals who did not report seeing motion, the result would support the proposition that neural activity in MT+/V5 does not represent a sufficient condition for conscious perception of motion in vision.

The conventional visual stimulus of checkerboard pattern-reversal was utilized in an original manner as an apparent-motion stimulus in this study. Subjective perception of this stimulus was studied in a pilot study conducted prior to the main experiment in 30 healthy subjects (20–30 years, 15 males). A black-and-white checkerboard pattern was reversed in contrast at various frequencies (0.2, 12, 30, 60, and 100 Hz) while subjects freely viewed the stimulus (Fig. 1a). Viewers always reported perceiving pattern-reversal at 0.2 Hz and a matrix of gray squares at 100 Hz, both stationary in position (Fig. 1b). The 0.2 Hz reversal was too slow for apparent-motion perception, whereas the 100 Hz reversal was too fast as it exceeded the critical flicker fusion frequency threshold. On the other hand, subjects reported various perceptions at the intermediate frequencies of 12, 30, and 60 Hz in their first viewing of the stimulus. Many, but not all of the subjects spontaneously noticed apparent motion in the square pattern, most typically vertical or horizontal flows (Fig. 1b): The squares appeared to slide vertically or horizontally in step with each contrast reversal.

Subjects who failed to see the apparent motion in their initial viewing readily and unanimously became aware of it after the experimenter informed them about the possibility of motion perception, ascertaining that the subjects understood what the apparent-motion looked like and that it had indeed escaped conscious perception when the viewers reported no motion regarding their first viewing of the stimulus. In other words, motion in this stimulus paradigm was like the Dalmatian drawn on a black-and-white, spotted background as shown in various textbooks on vision (e.g., 10): The dog is completely absent when viewed without knowledge of its presence, but is unquestionably there once the viewer is informed of the dog's presence. This feature of the current stimulus was especially suitable for the present experimental design. As opposed to more standard apparent-motion stimuli in which motion is highly salient^{11–14} or those in which motion and non-motion perceptions alternate between each condition while viewing,¹⁵ some naive viewers were unaware of even a possibility of perceiving motion in the present stimulus, providing

investigators with the unique opportunity to study MT+/V5 activity in the complete absence of consciousness of motion perception. The novelty of the checkerboard pattern-reversal stimulus as a motion stimulus presumably helped the participants not to expect any motion perception *a priori*.

An fMRI experiment was performed in follow up of the pilot study to probe MT+/V5 activation under the above conditions (12, 30, and 60 Hz) in which motion was not noticed consciously in some naive subjects. The 0.2 Hz stimulus was also included to serve as the baseline condition of no conscious motion perception for evaluating activation at 12, 30, and 60 Hz in each subject. (No subject perceived motion at 0.2 Hz reversal during the fMRI experiment also). This was an appropriate control because the spatial frequency of the stimulus, which might affect MT+/V5 activity,¹⁶ remained constant; in addition, occasional contrast reversals prevented retinal afterimages that could arise after prolonged exposures to a static high-contrast stimulus in a dark scanner room.

Materials and Methods

Subjects and stimuli

Eleven healthy subjects (19–27 years old, five males) with normal or corrected-to-normal vision participated. None of them had prior knowledge about the possibility of apparent-motion percept in the stimulus, and the fMRI data were obtained during their first exposure to the stimulus. During fMRI scans, the subjects viewed a 100% contrast checkerboard pattern stimulus, comprising 7 rows $\times$ 8 columns of squares ($1^\circ \times 1^\circ$ each), reversed in contrast (100%) at 0.2, 12, 30, or 60 Hz. The stimulation sequence was (0.2 Hz)-(0.2 Hz)-A-B-C-(0.2 Hz)-A-B-C-(0.2 Hz), where A, B, and C represented 20-s-long epochs of 12, 30, and 60 Hz reversals in orders that were randomized across subjects. The participants freely observed, via a mirror above the head coil, the stimulus projected onto a screen by an LCD projector (60 Hz refresh rate) in a dark scanner room. Stimulus presentation was controlled on a frame-by-frame basis using software specially designed for psychophysical and electrophysiological vision experiments (Little Stimulus Maker, <http://staff.washington.edu/jokelly/>). The 100 Hz reversal condition was excluded in the fMRI experiment due to hardware limitation of the LCD projector. Nonetheless, it was not critical to the current experimental design. A CRT monitor (100 Hz refresh rate) controlled by a VSG system (Cambridge Research Systems Ltd., UK) was utilized in the pilot study.

Fig. 1. Apparent-motion stimulus. A checkerboard pattern was reversed in contrast at various frequencies, namely 0.2, 12, 30, 60 and 100 Hz (**a**), which produced qualitatively distinct perceptions depending on the subject and reversal frequency conditions. Whereas the perceived images were always stationary at 0.2 Hz (pattern reversal) and 100 Hz (gray squares), some but not all viewers noted seeing apparent motions of the square pattern, e.g., vertical or horizontal flows (**b**), at 12, 30, and 60 Hz reversals in their first viewing of the stimulus.

Fig. 2. fMRI results. Activation maps in a representative subject indicated that significant neural activity in MT+/V5 (arrow) occurred at all stimulation frequencies, although this subject consciously perceived motion only at 12 Hz (**a**). Summary of results of all subjects ($N = 11$) shows that MT+/V5 activation without awareness of motion occurred in multiple cases for each stimulation condition (**b**, red digits). Conscious perception of motion did not occur without MT+/V5 activation (blue digits), by contrast. Single asterisk (*) indicates that the number includes one case of right, unilateral MT+/V5 activation, and double asterisks (**) indicate that one case of right and one case of left, unilateral MT+/V5 activation are included; activation was bilateral in all other cases. fMRI signal responses (parameter estimates in general linear model) in each subject's right and left MT+/V5 were plotted for all stimulation conditions (**c**), along with reported perceptions (filled circle, conscious motion perception; open circle, no conscious motion perception). Each line represents data from a single subject. Although there was no consistent relationship between perception and fMRI signal response, a subtle finding was that, at 60 Hz, the parameter estimates in right MT+/V5 (**c**, arrow) were greater in subjects who perceived motion consciously than in those who did not.

Immediately after imaging, participants were interviewed about their perceptions during the experiment, separately for each reversal frequency condition. The stimulus was played back at each frequency so that the different conditions were not confused. Subjects were first asked to report freely anything that they noticed about the stimulus condition. Those who did not spontaneously describe motion perception were then asked explicitly whether or not they noticed any motion. Subjects who responded negatively to the last question were regarded as being not conscious of the apparent motion during fMRI data acquisition.

The study was carried out in accordance with the human research guidelines of the Internal Review Board of the University of Niigata. Informed consent was obtained from all participants.

fMRI

A Signa LX 3.0T (GE Medical System, Waukesha, WI) system was used for imaging. Gradient echo echo-planar axial images were obtained using the following parameter settings: FOV, 200×200 mm; matrix, 64×64 ; slice thickness 5 mm; interslice gap, 2.5 mm; TR, 1000 ms; TE, 30 ms; flip angle, 70° . In-plane spatial resolution was approximately 3×3 mm. Each slab was restricted to 30 mm to ensure high field homogeneity, and motions were not corrected in post-processing as sessions in which brain motion exceeded 20% of the in-plane voxel size were redone.¹⁷

After spatial smoothing by a 5-mm full-width-at-half-maximum Gaussian kernel, the images were analyzed by Statistical Parametric Mapping software (SPM99, Wellcome Department of Cognitive Neurology, London, UK) using a delayed boxcar model function (convolved by haemodynamic response function) in the context of a general linear model for temporally correlated time series. Temporal filter settings were: high-pass, 160 s cutoff period; low-pass, haemodynamic response function. SPM $\{t\}$ was obtained for each stimulation condition of 12, 30, and 60 Hz, while the 0.2 Hz condition served as the control or “rest.” None perceived motion at 0.2 Hz reversal during the fMRI experiment as confirmed by the interview. The statistical threshold was set at $p = 0.001$ (uncorrected), $k = 0$. Data were analyzed individually for each subject. MT+/V5 was identified as a region in the inferior temporal sulcus (including its posterior continuation) or its ascending limb that exhibited a clear peak in SPM $\{t\}$ at 12 Hz reversal.⁹ The peaks were evident in SPM $\{t\}$ even in cases in which the activation did not reach statistical significance. Mean ($\pm$ SD, in mm) coordinates of the MT+/V5 in this study were (48 ± 4 , -68 ± 7 , -3 ± 5) in the

right hemisphere and (-46 ± 7 , -69 ± 7 , -1 ± 7) in the left hemisphere in the standard space of the Montreal Neurological Institute (MNI) template, which were similar to those reported previously.^{5,9,18}

Results

Results of the fMRI experiment clearly indicated dissociation of MT+/V5 activation from conscious perception of motion. Activation maps in a representative subject, who perceived apparent motion at 12 Hz but denied seeing it at 30 and 60 Hz conditions, are shown in Fig. 2a. Regardless of perception, this subject exhibited significant MT+/V5 activation at all frequencies. Figure 2b summarizes the results of all subjects. At 12 and 30 Hz contrast reversals, MT+/V5 was activated in all eleven subjects, including three viewers who did not report seeing any motion. At 60 Hz reversal, seven subjects failed to see motion but MT+/V5 was activated in the majority (5/7) of these viewers. Subjects who did not perceive motion reported that they saw pattern-reversals or stationary flickers. In no case did conscious perception of motion occur without MT+/V5 activation (blue digits, Fig. 2b).

Discussion

The above results unambiguously demonstrated that significant neural activity in MT+/V5 as detected by fMRI did not represent a sufficient condition for the conscious perception of motion in vision. Conscious perception of motion did not occur without MT+/V5 activation, consistent with the established notion that intact neural activity in MT+/V5 is a necessary condition for the conscious perception of visual motion, whether veridical or illusory.¹⁻⁸ Also demonstrated in this study by fMRI for the first time were significant MT+/V5 responses to a checkerboard pattern reversing in contrast at a frequency as high as 60 Hz.¹⁶

This experiment did not address the question what neuronal substrates underlay awareness or conscious perception of motion in the visual modality. However, more detailed examination of the current data may suggest some clues. fMRI signal responses (SPM parameter estimates) in each subject's right and left MT+/V5 were plotted concurrently with reported perceptions (Fig. 2c). Although no clear cut relationship between fMRI signal response and consciousness of motion perception was evident, a subtle finding indicated a statistically significant effect of greater fMRI responses for conscious than for unconscious pro-

cessing of motion in right MT+/V5 at 60 Hz reversal (Fig. 2c, arrow), Mann-Whitney's $U = 3$, $p < .05$ (uncorrected for multiple comparisons), whereas the same test yielded negative results in the other five conditions. They are potentially interesting results for the purpose of identifying neural correlates of conscious motion perception, but further experiments are necessary to confirm these findings. In addition, it is extremely difficult, if not impossible, to definitively ascribe quantitative differences in fMRI signal responses to any of the possible changes in the underlying neural activities as increased firing rate in each neuron, greater number of firing neurons, more synchronization, etc. Hence, a valid conclusion of this experiment was that significant neural activity occurred in MT+/V5 without accompanying consciousness of motion perception.

How should we interpret our results in light of the current state of knowledge regarding the role of MT+/V5 in motion processing? MT+/V5 neurons in human,^{5,9} as well as MT neurons in monkeys,¹⁹ are sensitive to flickers and luminance changes even if the stimuli are stationary in space. Temporal changes in luminance at a certain location in the visual field may be indicative of displacement of an object into or out of that specific location. Therefore, neurons in MT+/V5 (and MT) may simply respond to all visual inputs that are potentially associated with motion. It would then follow that its activation represents a necessary but not sufficient condition for conscious perception of motion. In fact, following visual input a broad range of computationally possible percepts becomes represented in the brain without reaching consciousness.^{20–23} It thus appears highly plausible that, as presented herein, MT+/V5 neurons are recruited to processing “motion” visual information that can potentially be perceived consciously as motion. Flicker perceptions were often reported when the motion was not perceived consciously in this experiment, hinting the existence of some understated relationship between flicker perception and motion perception, both of which involved MT+/V5 activity. Future research on how conscious vision is affected by neural activity in MT+/V5 is warranted.

Conclusion

Significant MT+/V5 activation was observed without accompanying subjective awareness of seeing motion in an apparent-motion stimulus. The finding indicates that neural activity in MT+/V5 does not represent a sufficient condition for con-

scious perception of motion in vision.

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