

Close correlation between activity in brain area MT/V5 and the perception of a visual motion aftereffect

Sheng He*, Eric R. Cohen^{†‡} and Xiaoping Hu[†]

Studies in primate physiology and human functional neuroimaging have convincingly shown that the area of the brain termed MT/V5⁺ – which includes the middle temporal visual area MT/V5 along with adjacent motion-sensitive areas such as MST – is involved in the processing of motion information [1,2]. Tootell *et al.* [3] showed that the blood oxygenation level dependent (BOLD) signal measured by functional magnetic resonance imaging (fMRI) in the human MT/V5⁺ seemingly correlates with the strength of perceived motion aftereffect (MAE), the illusory motion of a stationary pattern that one sees after adapting to a moving pattern [4]. The signal in MT/V5⁺ decayed slowly during the period when the MAE was seen. It is possible that this slow decrease in MT/V5⁺ activity was unrelated to the perceptual experience of motion. After replicating Tootell *et al.*'s experiment, a modified version of the experiment was conducted in which a blank period was inserted between the adapting motion stimulus and the stationary testing pattern. The results demonstrated that MT/V5⁺ activity indeed decayed more slowly after an effective unidirectional motion adaptation than after bidirectional adaptation, without corresponding perception of MAE. Nevertheless, in a more conclusive experiment, we adapted observers to a unidirectional motion for a very long period and showed that the activity in MT/V5⁺ changed in synchrony with the presence and absence of perceived MAE, simply as a result of presenting a stationary visual stimulus in and out of the adapted retinal region.

Addresses: *Department of Psychology and [†]Center for Magnetic Resonance Research, University of Minnesota, Minneapolis, Minnesota 55455, USA. [‡]Program in Neuroscience, SUNY Health Science Center at Syracuse, Syracuse, New York 13202, USA.

Correspondence: Sheng He
E-mail: sheng@tc.umn.edu

Received: 22 July 1998
Revised: 7 September 1998
Accepted: 25 September 1998

Published: 26 October 1998

Current Biology 1998, 8:1215–1218
<http://biomednet.com/elecref/0960982200801215>

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Results and discussion

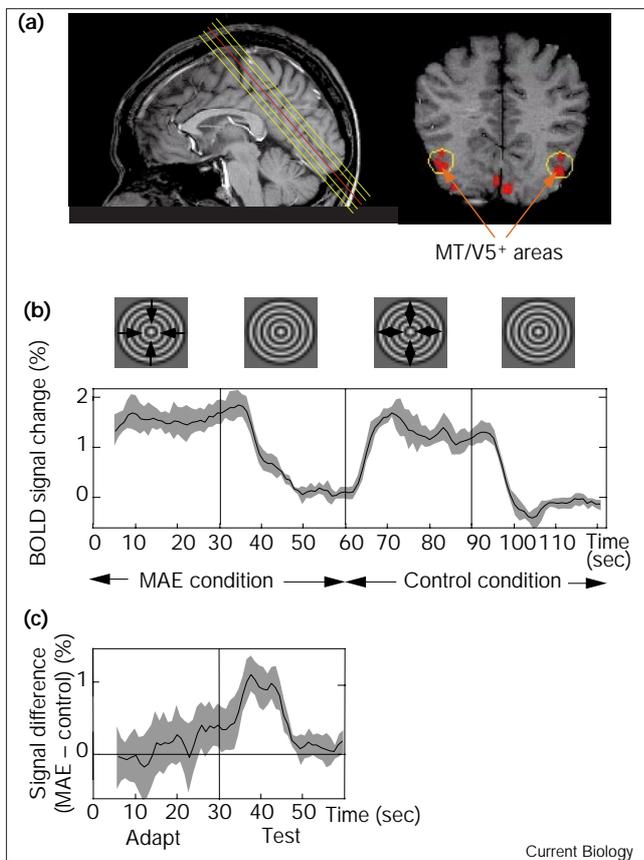
With a paradigm similar to that used by Tootell *et al.* [3], we measured MT/V5⁺ activity during motion adaptation and during a stationary pattern test. Each test cycle consisted of

two conditions: MAE and control. In the MAE condition, concentric rings contracted for 30 seconds, followed by the same pattern but stationary for 30 seconds. An MAE was observed in this condition. In the control condition, the rings alternated between expansion and contraction every 2 seconds for 30 seconds, followed by the same stationary rings for 30 seconds (Figure 1b). A very weak MAE or no MAE was seen in the control condition. This cycle of MAE condition followed by control condition (i.e. an epoch) was repeated four times in each fMRI run, which lasted 8 minutes. Five observers were studied.

MT/V5⁺ activation was roughly equal during the motion-adaptation phase of both the MAE and control conditions, but the decay of the activity was slower in the MAE condition relative to the control condition (Figure 1b). The difference can be clearly seen by subtracting the time course of the control condition from that of the MAE condition (Figure 1c). The difference in the BOLD signal starts to increase at the onset of the stationary pattern. This result is very similar to that obtained by Tootell *et al.* [3]. This result suggests that, when we see motion (real or illusory), MT/V5⁺ areas are active. Participation of MT/V5⁺ may be a necessary condition for motion perception. But is the activity in areas MT/V5⁺ a sufficient condition for observers to perceive motion? In the next experiment, we explored the possibility that MT/V5⁺ activity observed during the period when MAE was perceived might not be linked directly to the perception of MAE, but rather might be due to differential adaptation status.

When a blank screen instead of a spatial pattern is presented for a short period of time after motion adaptation, an MAE is not perceived, but will appear if a stationary testing pattern is subsequently presented. This phenomenon is known as storage of the MAE [5]. Presumably, MT/V5⁺ neurons are still in the adapted state during the blank storage period. Logically, if MT/V5⁺ activity is sufficient for the perception of motion, there should be no activity in MT/V5⁺ when an observer does not see motion. Measuring MT/V5⁺ activity during the blank period (when no motion is seen) provides an opportunity for determining whether MT/V5⁺ activity is always correlated with motion perception. The design of the MAE storage experiment is very similar to that of the simple MAE experiment described above. During each epoch, instead of presenting the stationary pattern immediately after the motion-adaptation period, we left the screen blank for 10 seconds at the background luminance level (dark gray). A stationary test pattern was subsequently presented for

Figure 1



(a) Slice position and representative MT/V5⁺ areas. Left, five functional slices were aligned on an anatomical sagittal image of the brain, parallel to the calcarine sulcus, with two slices above and three below. Right, significant activation comparing moving rings with stationary rings in the middle slice (red line in the left image), shown in pseudocolor overlaid on a T1-weighted anatomical image. Circles indicate the areas we determined to be the presumptive MT/V5⁺ areas for the functional analysis as defined by both anatomical position and functional motion selectivity. (b) Averaged MT/V5⁺ BOLD signal time-course. Data from experiment 1 (five observers) have been collapsed into one epoch containing two conditions: MAE and control. For the MAE condition, the direction of adapting motion is constant during the 30 sec period; for the control condition, the direction of adapting motion alternated in reverse directions every 2 sec (contracting – expanding – contracting ...). As a result, an illusory motion could be seen in the MAE condition, but not in the control condition. The time-course data show that after adaptation the signal in the MAE condition decayed more slowly than in the control condition. In this and the following figures, grey shadows on either side of the line are ± 1 SEM at every time point. (c) Signal difference obtained from subtracting the control condition from the MAE condition. MT/V5⁺ activation was roughly equal during the adaptation period, but starting from the beginning of the stationary test, the signal is higher in the MAE condition than in the control condition. This pattern is similar to that reported by Tootell *et al.* [3].

20 seconds. Thirteen observers were tested on this condition, and data from three of them were excluded from further analysis because of excessive head motion. If MT/V5⁺ activity strictly correlates with the perceived MAE, we would expect no difference between the control

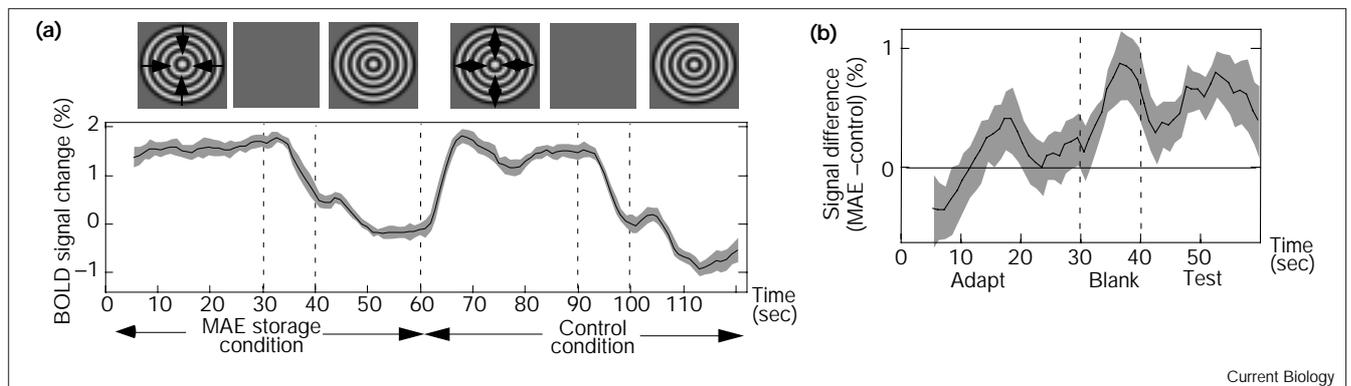
and MAE conditions during the 10 second storage period. What we found, however, was that MT/V5⁺ activity decreased more slowly in the MAE storage condition than in the control condition (Figure 2a), even though an MAE was not seen in either condition during the blank period. As expected, an MAE was seen during the testing period of the storage condition. Subtracting the control condition from the MAE storage condition reveals two peaks (Figure 2b) — one during the storage period and one corresponding to the testing period.

The fact that the MT/V5⁺ activity remained elevated during the blank storage period called into question the interpretation of Tootell *et al.*'s experiment [3] and our first experiment that the MT/V5⁺ activity observed after adaptation was related to the perceived MAE. To further test if an MAE can indeed activate MT/V5⁺, a long-duration motion-adaptation condition was adopted. It has been shown that the MAE can be experienced after very long delays following long-duration adaptation, but only when the testing pattern is presented at the same retinal location as the adapting pattern [6]. Such long-term storage of the MAE, in conjunction with its retinotopic specificity, allows for a more direct test of whether or not the presence and absence of a perceived MAE alone can modulate activity in MT/V5⁺.

Volunteers were first adapted to a contracting motion for 15 minutes, fixating either at the top or the bottom of the pattern (each observer only fixated at one point, counterbalanced across observers). The fMRI scan took place immediately after the adaptation (Figure 3a). Observers were instructed to shift their fixation position every 30 seconds following voice cues. Alternating fixation between the adapted point and an unadapted point generated an alternating experience of seeing and not seeing an MAE. Seven observers participated in this experiment, and data from two were excluded because of questionable identification of MT/V5⁺ areas. The long adaptation followed by alternating fixation point produced an alternating experience of seeing a strong MAE and not seeing an MAE. The results show that activity in MT/V5⁺ was clearly modulated in synchrony with the perception of MAE (Figure 3b). The experiments reported here demonstrate again that both real motion and illusory motion (MAE) can activate MT/V5⁺.

Although in most cases motion perception is coupled with the activity in MT/V5⁺, our MAE storage experiment demonstrates that activity in MT/V5⁺ does not necessarily initiate conscious motion perception. In other words, activation of MT/V5⁺ is not a sufficient condition for perceiving motion. This is the first time that a dissociation between MT/V5⁺ activity and the perception of motion has been observed in the normal population. Zeki and Ffytche [7] found that a slow-moving stimulus presented in the blind field of a patient, G.Y., who had a damaged V1

Figure 2



(a) Schematic stimulus pattern and averaged BOLD signal time course. Between 30 and 40 sec and between 90 and 100 sec, the field was blank. MT/V5⁺ activity dropped more slowly in the MAE storage condition (unidirectional adaptation) compared with the control condition (reverse-direction (bidirectional) adaptation). (b) The signal difference obtained by subtracting the control condition from the MAE

storage condition. Two peaks were evident: one corresponds to the slower decrease during the blank period of MT/V5⁺ activity following a unidirectional adaptation; the second peak reflects the elevated activity during the perception of an MAE in the MAE storage condition compared with the control condition.

visual area could sometimes activate MT/V5⁺, but not enough to initiate his conscious motion perception, even though he did have the ability to see motion in his blind field. V1 damage in G.Y. deprived him of form vision in the blind field [7]. In our storage MAE condition, the blank field provided a medium of light without form. The MT/V5⁺ activity observed may be similar to the formless activation in G.Y.'s MT/V5⁺, especially because the adaptation motion speed we used was relatively slow (1 degree per second). However, other more sensitive measures may reveal certain behavioral consequences of the elevated MT/V5⁺ activity level. In a similar experiment, Culham *et al.* [8] found substantially smaller (though statistically significant) activation in MT/V5⁺ during the MAE storage period. The key difference is that their storage period was black, whereas ours was dark gray. Some observers in our experiment did see dynamic noise in the blank field in the initial 1–2 seconds after motion adaptation. This may partly contribute to the slower decay of MT/V5⁺ activity observed in the MAE condition. Single-unit recording studies in primates will help to elucidate the details of neural activity during this period.

The result of our alternating fixation (and correspondingly alternating motion experience) experiment leaves little doubt that MT/V5⁺ activity was modulated in synchrony with purely subjective motion experience. The perception of an MAE arose from the presence of a stationary pattern in the adapted retinal region. The rise and fall of the MT/V5⁺ activity, even a few minutes after motion adaptation, can only be related to the subjective motion experience. This result also demonstrates that both the experience of an MAE and the neural activity associated

with it can be stored and revived over a relatively long duration. Our results together with previous findings from other groups [3,9] suggest that MT/V5⁺ activity is closely correlated with the perception of motion, although the activity in MT/V5⁺ alone is not sufficient to generate coherent motion perception.

Materials and methods

Subjects

All subjects were neurologically normal volunteers recruited from the University of Minnesota community. Approximately equal numbers of males and females were studied. The study was approved by the University of Minnesota's Human Subjects Committee.

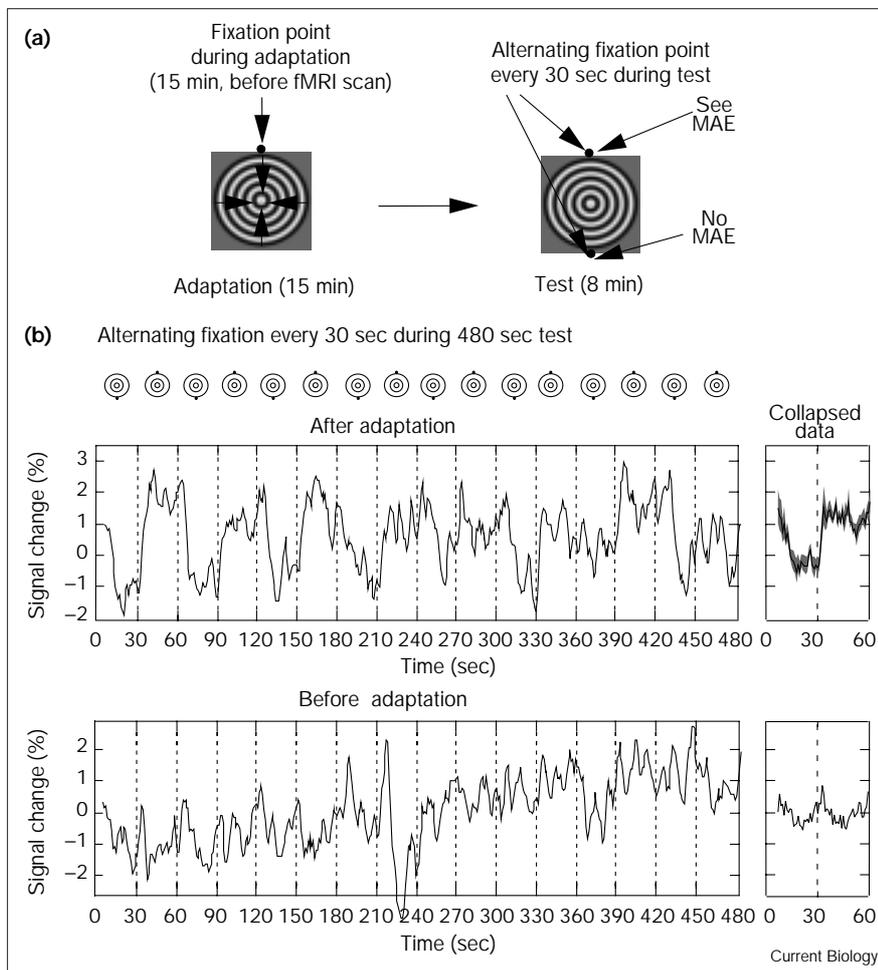
Stimuli

Stimuli were generated with a PowerPC Macintosh computer, and displayed with a video projector onto a translucent screen placed outside the scanner bore. Observers in the scanner viewed the stimuli through a mirror placed just above their eyes and tilted at approximately 45°. The stimulus pattern consisted of concentric rings of 2 cycles per degree at 30% contrast, with radial extent of 4°. During the experiment, the pattern could be either stationary, contracting or expanding at the speed of 1 degree per second (schematically depicted in Figures 1b, 2a).

fMRI scan and data processing

A 1.5 T Siemens Vision MR system was used. At the beginning of each study, sagittal scout images were acquired for the identification of the calcarine sulcus. Five slices (6 mm thick) were positioned parallel to the calcarine sulcus, two above and three below. During the MAE study, T2*-weighted images were acquired at these slice positions using a single-shot echo-planar imaging (EPI) sequence (TR/TE: 1 sec/55 msec, matrix: 64 × 64, FOV: 20 × 20 cm²). T1-weighted images of the same slices were acquired for anatomic overlay. The data were processed using the software package 'Stimulate' [10]. Significant ($p < 0.001$) activation was detected with cross-correlation analyses [11] using an 'ideal' time course as a template (e.g. high activation during motion, low activation during stationary period, with a proper hemodynamic delay). Motion selectivity in a MT/V5⁺ localization scan

Figure 3



(a) Observers adapted to a contracting pattern for 15 min before being scanned, while fixating either at the top or the bottom point of the pattern. During the 8 min scan that started immediately after adaptation, observers shifted their fixation every 30 sec between the top and bottom point of a stationary pattern. For some observers, an MAE could be seen even towards the end of the 8 min test when they looked at the adaptation point. **(b)** MT/V5⁺ BOLD signal time course when observers switched their fixation every 30 sec between the top and the bottom of the stationary pattern. The upper panel shows the averaged data from five observers after adapting to a contracting stimulus for 15 min. The observers' data were normalized so that all time courses began with the negative phase (the unadapted position) before averaging. The activity of area MT/V5⁺ is clearly in synchrony with the perceptual experience of motion. Shifting fixation on the same test pattern before motion adaptation resulted in no systematic modulation of the MT/V5⁺ activity (lower panel). The two small boxes on the right illustrate the collapsed data (8 min time course averaged into one 60 sec epoch), showing strong modulation in the post-adaptation condition but not in the pre-adaptation condition.

(the same as the control condition in the first experiment) together with anatomical knowledge were used to locate the MT/V5⁺ areas. Typically, MT/V5⁺ areas reside on the lateral cortical surface near the occipito-temporal-parietal junction. The MT/V5⁺ areas were found on the slices placed beneath the calcarine sulcus (Figure 1a). Activation time courses for each experimental condition were obtained for each observer's MT/V5⁺ region and then averaged across observers. Time course curves were smoothed with a three-point moving average operator. Standard error of the means (SEM) at each time point were calculated based on the mean of individual observers. The shadows around the time course curves represent ± 1 SEM.

Acknowledgements

We thank Patty Costello and Essa Yacoub for their help in running the fMRI experiments, Patrick Cavanagh for commenting on the manuscript, and our volunteers for their cooperation. Supported by University of Minnesota start-up fund, Grant-in-Aid to S.H. and NIH grant R01 MH55346 to X.H.

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