Recovery of fMRI Activation in Motion Area MT Following Storage of the Motion Aftereffect

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We used functional magnetic resonance imaging (fMRI) during storage of the motion aftereffect (MAE) to examine the relationship between motion perception and neural activity in the human cortical motion complex MT+ (including area MT and adjacent motion-selective cortex). MT+ responds not only to physical motion but also to illusory motion, as in the MAE when subjects have adapted to continuous motion report that a subsequent stationary test stimulus appears to move in the opposite direction. In the phenomenon of storage, the total decay time of the MAE is extended by inserting a dark period between adaptation and test phases. That is, when the static test pattern is presented after a storage period equal in duration to the normal MAE, the illusory motion reappears for almost as long as the original effect despite the delay. We examined fMRI activation in MT+ during and after storage. Seven subjects viewed continuous motion, followed either by an undelayed stationary test (immediate MAE) or by a completely dark storage interval preceding the test (stored MAE). Like the perceptual effect, activity in MT+ dropped during the storage interval then rebounded to reach a level much higher than after the same delay without storage. Although MT+ activity was slightly enhanced during the storage period following adaptation to continuous motion (compared with a control sequence in which the adaptation grating oscillated and no MAE was perceived), this enhancement was much less than that observed during the perceptual phenomenon. These results indicate that following adaptation, activity in MT+ is pronounced only with the presentation of an appropriate visual stimulus, during which the MAE is perceived.

**INTRODUCTION**

After viewing continuous motion in one direction, observers report that a stationary stimulus appears to move in the opposite direction, a phenomenon known as motion aftereffect (MAE) (Mather et al. 1998; Wohlgemuth 1911). Typically, this aftereffect lasts tens of seconds, but remarkably, it can be "stored" when the test pattern does not immediately follow the adaptation pattern (Spigel 1960; Wohlgemuth 1911). That is, if the observer closes his eyes for the normal duration of the MAE and then reopen them, the illusionary motion appears for an additional period only slightly shorter than the original duration, suggesting that the decay of the MAE does not necessarily proceed automatically with the passage of time.

Here we use functional magnetic resonance imaging (fMRI) to examine activity in the human extrastriate motion complex MT+ during and after storage of the MAE. Neuroimaging has shown that MT+ is activated by both physical motion (Tootell et al. 1995b; Watson et al. 1993; Zeki et al. 1991) and illusory motion (Zeki et al. 1993), including the MAE as shown by Tootell et al. (1995a). Furthermore, the decay of MT+ activity during the MAE correlates well with the decay of the perceptual illusion (Tootell et al. 1995a). We reasoned that if MT+ activation following adaptation is related only to observers' perception of motion, MT+ activity should be absent during a completely dark storage interval following adaptation when no motion is perceived, but should return when the static test is presented. However, if processing in MT+ is also related to nonperceptual factors, enhanced activation may also be observed during the storage interval following adaptation even though no motion is perceived.

**METHODS**

**Procedure**

fMRI was used to measure the blood oxygenation level dependent (BOLD) signal in seven normal, healthy subjects. First, we examined the "immediate MAE" by presenting a moving pattern followed by a stationary test with no delay. Subjects viewed a continuously contracting and rotating stimulus (36 s; Fig. 1, A and B). Subjects pressed a button when the MAE ended. Activation during this "MAE sequence" was compared with a "control sequence" in which the grating oscillated and no subsequent MAE was observed. Two scans were collected, each with two MAE sequences and two control sequences, providing four measures of immediate MAE.

Next, we examined the "stored MAE." Between motion adaptation and the stationary test, a storage interval was inserted in which subjects kept their eyes open in complete darkness while light from the video projector was occluded by a computer-triggered shutter such that the room became pitch black. The storage duration was determined for each subject based on the perceptual duration of the immediate MAE. Four scans were acquired, each with two...
MAE and two control sequences in counterbalanced order, giving eight stored MAE measures.

Stimulus

The stimulus consisted of a radial grating (rotating clockwise at 0.375 rev/s, 16 cycles, 6 Hz, 50% contrast) superimposed on a concentric grating (contracting at 1.57/s, 4 cycles/deg, 6 Hz, 50% contrast). Psychophysical pretesting indicated that the poststorage MAE was most robust for a combined grating (compared with either grating alone), for contraction during adaptation (compared with expansion) (Bakan and Mizusawa 1963), and for a small stimulus (2.5° visual angle, compared with a large one, 7.5°, \( P < 0.001 \)). A small red dot was placed in the center of the display to provide a fixation point. The small size and the concentric/radial configuration make the stimulus particularly ineffective for eliciting smooth pursuit or optokinetic nystagmus. Nevertheless, we used an infrared eye-tracker with two subjects outside the magnet to verify comparable fixation across all conditions.

Image analysis

Each session began with an independent scan to identify regions with a greater response to the stimulus in motion compared with stationary presentation. Moving and stationary states alternated every 18 s, and during motion states the grating reversed direction every 2 s. Based on activation in this independent scan, MT+ included all contiguous activated voxels (\( P < 0.01 \), in \( t \)-tests using Stimulate software) (Strupp 1996) near the ascending limb of the inferior temporal sulcus (ITS) (Watson et al. 1993). Functional signal time courses for MT+ were extracted from subsequent runs and averaged within subjects. We then performed group analyses of the extracted data using paired \( t \)-tests (2-tailed, unless otherwise specified). We conducted a separate analysis to identify regions activated during the immediate MAE (by comparing the signal for the immediate MAE vs. the control period over the time during which the subject reported perceiving the MAE). This analysis was used to select a second region at the junction of the intraparietal sulci (IPS) and transverse occipital sulci (TrOS; Fig. 1C), a region we have called TrIPS. Activation in this region was then examined during the stored MAE scans. Because both MT+ and TrIPS were predefined by independent criteria, no correction for multiple voxelwise comparisons was necessary. We also performed an exploratory voxel-by-voxel subtraction to find regions activated during the storage interval (compared with the dark control interval, \( P < 0.01 \)).
STORAGE OF THE MOTION AFTEREFFECT ASSESSED BY fMRI

MRI scans

Images were collected with a 4.0-Tesla Siemens-Varian MRI system using a surface coil placed at the occipital pole. Eight slices aligned parallel to the calcarine sulcus sampled occipital, occipitotemporal, and posterior parietal cortex with a slice thickness of 6 mm and an in-plane resolution of 3 mm. Each volume (8 slices) was sampled once every 1.2 s. Functional data were collected using T2*-weighted segmented gradient echo echoplanar imaging (time to echo (TE) was 20 ms, time to repeat (TR) was 70 ms, flip angle = 15°, 2 segments/plane, navigator-corrected) superimposed on high-resolution T1-weighted anatomic images. Subjects' heads were stabilized using a custom head restraint system. We excluded any (2) scans in which motion artifacts were observed in a cinematic loop. Time courses within each voxel were corrected for linear drift.

RESULTS

MT+ was activated during both the immediate and stored MAE. Consistent with Tootell et al. (1995a), the MT+ signal was higher during the immediate MAE than in the stationary control test (P < 0.001) in all subjects (Fig. 2A). Following a storage interval lasting the duration of each subject's immediate MAE (average 16 s, range 12–26.4 s), subjects experienced an aftereffect lasting a further 11.8 s on average, indicating that the MAE was well-stored (74% of the average MAE duration). For both the stored MAE and control sequences, the signal in MT+ dropped substantially during the dark period and then increased when the stationary test stimulus was presented (Fig. 2B). Moreover, during the stored MAE, the signal increased to a much higher level than in the control sequence (as described in Fig. 2C, P < 0.001). To compare the amplitude of the MAE with and without storage, we superimposed each subject's MAE-specific MR signal for the stored MAE onto the immediate MAE sequence, aligning them with respect to the time elapsed after adaptation (as described in Fig. 2D). MT+ activity was much higher during the stored MAE than for the immediate MAE, which had largely dissipated by that time (Fig. 2E, P < 0.05).

The MT+ signal was also marginally elevated during storage (0.3% higher signal in MAE vs. control sequence); however, this elevation was weaker (P < 0.01) than during the stored MAE (0.9%). Specifically, although the MT+ signal dropped during the storage interval in both conditions, the drop was less pronounced for the MAE sequence compared with the control sequence (Fig. 2B), a difference that was small but statistically significant in the group analysis (P < 0.05). The MT+ enhancement during storage may be more pronounced when the storage interval is not completely dark, as indicated by fMRI data from two other groups who presented a dark gray screen (on a black background) during MAE storage (He et al. 1998; R. Tootell, personal communication). However, storage during complete darkness, as used here, makes it unlikely that our enhanced activity arises from any perceived motion during storage or from peripheral contours that influence the MAE and its storage (Anstis and Reinhardt-Rutland 1976; Stelow and Day 1971).

MAE-specific activation was observed in an additional region, TriPS, near the junction of the IPS and TrOS (Figs. 1C and 3A). Like MT+, this region showed a rebound at the onset of the poststorage MAE (Fig. 3, B and D), with greater activity during the stored MAE than the control period (Fig. 3C, P < 0.05, 1-tailed) and a higher signal elevation during the stored MAE than the immediate MAE (for the same time period following adaptation, Fig. 3E, P < 0.05, 1-tailed). A very slight elevation during storage was not significant (P = 0.10, 1-tailed). TriPS may correspond to visual area V3A, which is motion selective (Tootell et al. 1997) and is activated by the MAE, but to a lesser degree than MT (Tootell et al. 1995a). A subtraction to identify regions that were active during storage of the MAE (compared with the dark period in the control sequence) revealed significant activity in the superior parieto-occipital fissure (area SPO) (Tootell et al. 1996) of
FIG. 3. Data for the TrIPS region at the junction of the TrOS and IPS. A: activation during immediate MAE and control sequences, as in Fig. 2A. B: average time course in stored MAE and control sequences, as in Fig. 2B. C: group data for the comparison between beginning of stored MAE (1st 8.4 s) and control period, as in Fig. 2C. D: comparison of MAE specific time courses (difference between MAE and control sequences) for immediate and stored MAE, as in Fig. 2D. E: group data for the comparison between stored MAE (1st 8.4 s) and equivalent postadaptation time period of the immediate MAE, as in Fig. 2E.

all subjects, warranting further study with more optimal coil placement.

DISCUSSION

After adaptation to continuous motion, activation in area MT+ showed a sharp drop during a dark storage interval, followed by a rebound when a stationary test was presented and illusory motion was perceived. Although the MT+ signal was slightly elevated during the dark storage interval following adaptation when no motion was perceived (relative to the control sequence), this elevation was much weaker than during the MAE percept. Taken together, our results suggest that activity in MT+ is closely correlated with the perception of motion [and other transient displays that contain motion energy, such as flicker (e.g., Tootell et al. 1995b)]. These results are in agreement with a recent neuroimaging study of a patient with Riddoch syndrome (arising from a lesion in area V1), who was sometimes, but not always, aware of visual motion (Zeki and Ffytche 1998). Activation in the patient’s MT+ (area V5) was higher, as in our case, when the subject was aware of motion and weaker than in cases in which he was unaware of the motion (although some activation was observed even without awareness). Our results also suggest that a second area, possibly V3A, is also strongly activated during the perception of motion.

This study provides the first physiological study of the well-established psychophysical effect of storage. Traditional MAE models rely on explanations based on “fatigue”
of the neurons tuned to the adapted direction (Barlow and Hill 1963; Sutherland 1961). Fatigue models predict that recovery from adaptation would proceed independent of the visual stimulus; clearly this is not the case, psychophysically or physiologically. Rather, storage is more easily incorporated by alternative models that interpret motion adaptation in terms of gain control or recalibration (Anstis et al. 1998; Barlow 1990) in which the presence of a static pattern is essential for renormalization. In these models, adaptation is accompanied by changes in neural connectivity [perhaps based on mutual inhibition between neurons tuned to different directions (Cornsweet 1970; Grunewald and Lankheet 1996)] that lead to an imbalance in the firing rates within direction-specific populations. Although adaptation-related changes in circuitry must be maintained during the storage interval, our results clearly show that they alone do not activate MT+ to a high degree. Rather, only when an appropriate visual stimulus is presented [or perhaps any visual stimulus (He et al. 1998)], are the effects of the imbalance expressed, producing enhanced activity in MT+, which is correlated with the perceived MAE.

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