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Human MT+ mediates perceptual filling-in during apparent motion

Taosheng Liu,^{a,*} Scott D. Slotnick,^b and Steven Yantis^a

^aDepartment of Psychological and Brain Sciences, Johns Hopkins University, Baltimore, MD, 21218, USA ^bDepartment of Psychology, Harvard University, Cambridge, MA, 02138, USA

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During apparent motion, spatially distinct items presented in alternation cause the perception of a visual stimulus smoothly traversing the intervening space where no physical stimulus exists. We used fMRI to determine whether the perceptual 'filling-in' that underlies this phenomenon has an early or late cortical locus. Subjects viewed a display comprised of concentric rings that elicited apparent motion (two concentric rings presented in alternation), flicker (the same rings presented simultaneously), or real motion. We independently localized the cortical regions corresponding to the path of apparent motion in early visual areas (V1, V2, VP, V3, V4v, V3A), as well as the human motion processing complex (MT+). Cortical activity in the path of apparent motion in early visual areas was similar in amplitude during both apparent motion and flicker. In contrast, cortical activity in MT+ was higher in amplitude during apparent motion than during flicker, but was lower in amplitude than during real motion. In addition, we observed overlap in the cortical loci of MT+ and the lateral occipital complex (LOC), a region involved in shape and object processing. This overlap suggests that these regions could directly interact and thereby support perceived object continuity during apparent motion.

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Introduction

When two spatially distinct stimuli are flashed in alternation with the proper temporal offset, they cause the perception of smooth and continuous motion. This phenomenon, known as apparent motion, is the basis for the perception of motion in television and motion pictures. Apparent motion has been extensively studied behaviorally (e.g., Kolers, 1973), dating back to early Gestalt psychologists (Wertheimer, 1912). However, despite a wealth of psychophysical literature on this topic, the neural mechanisms of apparent motion remain elusive.

A striking feature of apparent motion perception is that observers perceive the stimulus traversing the vacant visual space between the two flashed stimuli. Subjectively, the path of apparent motion is filled-in; apparent motion therefore provides a fruitful domain in which to investigate neural filling-in more generally (Pessoa and De Weerd, 2003). Yantis and Nakama (1998) reported evidence for perceptual filling-in during apparent motion by asking observers to rapidly detect the appearance of a target on or off the path of apparent motion. They found that the time required to detect the target was significantly greater when it appeared on the path of apparent motion than when it appeared off the path.

There are at least two neural models that could account for perceptual filling-in during apparent motion, one that proposes an early cortical locus and the other that proposes a late cortical locus. According to the early model, neural activity is evoked in the path of apparent motion within early visual areas, not by feedforward connections from the retinogeniculate pathway, but rather via lateral interactions within lower areas or feedback from higher areas such as human motion processing complex MT+. An analogy can be drawn to other contextual effects in early visual area, including brightness induction (Rossi et al., 1996), illusory contours (von der Heydt et al., 1984), amodal completion (Sugita, 1999), and texture filling-in (De Weerd et al., 1995), where response in early retinotopic areas was observed although no physical stimulus occupied the corresponding retinal location.

According to the late model, there is no neural filling-in within early visual areas. Instead, perceptual filling-in is mediated by higher levels of the cortical processing stream, particularly in MT+. Grossberg and Rudd (1992) proposed a multilayer neural network model of apparent motion in which responses from lowlevel units (V1, V2) were pooled within high-level units (MT+) through spatiotemporal summation. Their simulation showed that if low-level units were stimulated with the proper timing and spatial separation, a 'traveling wave' of activation would be formed in the high-level units, similar to the activation caused by smooth, real motion. This account does not include filling-in at early levels.

Both the early and late models of perceptual filling-in during apparent motion are physiologically possible, as neurophysiological studies of visual motion processing in monkeys have established that both V1 and MT contain direction-selective neurons, although a higher concentration of such neurons are found in MT (Lennie, 1998). A previous study reported that neurons in MT, but not V1, were responsive to long-range (>1° across the visual field) apparent motion (Mikami et al., 1986), thus lending some support to the late model; however, extrastriate apparent motion effects were not assessed in this study, leaving open the question of whether filling-in occurred within these regions.

^{*} Corresponding author. Department of Psychology, New York University, 6 Washington Place, 8th floor, New York, NY 10003. Fax: +1-212-995-4349.

E-mail address: taosheng.liu@nyu.edu (T. Liu).

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A previous fMRI study in humans found that apparent motion activated MT+, but not V1 (Goebel et al., 1998; Muckli et al., 2002), consistent with the results of Mikami et al. (1986). However, Goebel et al. (1998) measured overall activity within retinotopically defined visual areas, rather than restricting the measurement of activity to the path of apparent motion. Thus, if a small or moderate filling-in effect was present, it may have been diluted due to the nonspecific region-of-interest (ROI); the resulting reduction in power may have caused such an effect to be missed.

In the present study, we tested the early and late models by measuring activity limited to the nonstimulated path of apparent motion. Two concentric rings were flashed in sequential alternation (Fig. 1a), evoking the perception of apparent motion in which a single ring appeared to be growing and shrinking. Brain activity was assessed in MT+ and the cortical representation of the path of apparent motion in early visual areas for three stimulation conditions: apparent motion, flicker, and real motion. The critical comparison was between the apparent motion condition and the flicker condition, as both involved identical sensory input except for the timing of the two rings. While the early model predicted greater neural activity during apparent motion than during flicker in both early visual areas and in MT+, the late model predicted such an apparent motion effect only in MT+.

Materials and methods

Subjects

Four subjects (three females) with normal or corrected-tonormal vision participated in the experiment. All subjects gave written informed consent according to the study protocol that had been approved by the Institutional Review Board at the Johns Hopkins University.

Main experiment: visual stimulus and task

Stimuli were presented via a projector onto a rear-projection screen located at the superior end of the scanner bore. Subjects viewed the display in supine position through a tilted mirror mounted to the head coil.

Three types of visual display were used in the main experiment: apparent motion, flicker, and real motion. Stimuli were shown in green on a gray background. A white fixation cross (subtending 0.4° of visual angle) was shown in the center of the screen throughout the experiment, and subjects were instructed to maintain central fixation. For the apparent motion condition, one cycle of the display contained two display intervals and two interstimulus intervals (ISIs). Two concentric rings were shown, one in each display interval for 200 ms (Fig. 1a). The radii of the inner and outer ring centers were 1.2° and 6.0° : their thicknesses were 0.2° and 1.1°. The differential ring thickness was used to compensate for cortical magnification (Duncan and Boynton, 2003). To maximize the quality of perceived apparent motion, the duration of the ISI was determined separately for each subject before the scanning session using the identical display system. Subjects viewed the alternating rings (fixed at 200 ms duration each) and adjusted the duration of the ISI until they perceived the strongest apparent motion. The ISIs for the four subjects were approximately 83, 117, 133, and 133 ms, respectively. Once the ISI was determined for each subject, the

length of a stimulus cycle was calculated (i.e., 2*200 ms + 2*ISI). For the flicker condition, the same two rings were displayed simultaneously for 200 ms in a cycle (Fig. 1b). In the real motion condition, the inner ring expanded smoothly into the outer ring (increasing eccentricity and thickness at the same time) and then contracted back to the inner ring in one cycle (Fig. 1c).¹

A blocked design was employed. For each condition, one block consisted of about 18 cycles of stimulus display (approximately 12 s) followed by a blank interval (approximately 8 s); the precise duration and number of cycles depended on the subject's ISI value. Each run in the scanner contained four blocks for each of the three conditions (12 blocks total); the order of the blocks was randomized. A 10-s fixation interval was inserted at the beginning and the end of each run. Each subject completed six runs in the scanner yielding 24 blocks per condition.

During the experiment, a detection task was employed to motivate subjects to attend to the stimulus rings. At random intervals from 2 to 11 s, a thin concentric red circle appeared for 40 ms within either the inner or the outer ring. Subjects were instructed to press a button when they detected the red 'target'. They were instructed to perform this task without moving their eyes from the central fixation point.

Localizers and retinotopic mapping procedures

The early visual area localizer was designed to determine the cortical representations of the path of the apparent motion display in striate and extrastriate cortex. The inner and outer rings, as well as a middle ring (eccentricity: 2.5° , thickness: 0.6°) were presented consecutively in 11-s blocks. To maximize activation in early visual areas, the ring was filled with an 8-Hz flickering white–black checkerboard pattern (instead of the solid green color). There were 24 blocks in a single localizer run (8 blocks were presented in a fixed order of inner, middle, and outer conditions. Subjects were instructed to maintain central fixation throughout a run. As in the main experiment, subjects detected the presence of a red circle ('target'), which appeared at random intervals (2–11 s) in the ring that was displayed in the current block.

Retinotopic mapping was performed in the same scanning session as the main experiment, following well-established methods (DeYoe et al., 1996; Engel et al., 1997; Sereno et al., 1995; Slotnick and Moo, 2003; Tootell et al., 1997; Warnking et al., 2002). We used a rotating double-wedge checkerboard to map the polar angle component in early visual areas, where phase reversals demarcated the borders between early visual areas (Slotnick and Yantis, 2003). Each subject completed a single run, in which the two stimuli rotated for eight complete cycles at 42 s/cycle.

Scanning procedure

Magnetic resonance imaging was conducted on a 3 T Philips Intera MR scanner. T2*-weighted echo planar imaging was per-

¹ These parameters equated the distance traveled per unit time for apparent motion and real motion. But because the apparent motion stimulus only 'moved' during the ISIs, whereas the real motion stimulus moved continuously in a cycle, the perceived speed of the two types of motion may have been different, with apparent motion perceived as being faster. Importantly, a difference in perceived speed does not alter the interpretation of the results.



Fig. 1. A schematic showing the three display types used in the main experiment. The diagram depicts the structure of a single stimulation cycle for (a) apparent motion, (b) flicker, and (c) real motion. The dark rings in (c) represent the stimuli in intermediate locations moving smoothly and continuously from the innermost to the outermost positions, and back again in each cycle. The value of the ISI was determined separately for each subject so as to maximize the strength of apparent motion (see Materials and methods).

formed using a SENSE (SENSitivity Encoding) head coil (MRI Devices, Inc., Waukesha, WI) with a gradient-echo sequence (TR = 2 s, TE = 30 ms, flip angle = 90°). Twenty-six transverse slices were obtained in one volume to fully cover the occipital lobe (FOV = 240×240 mm, in-plane resolution = 3×3 mm, slice thickness = 3 mm, gap = 1 mm). A high-resolution anatomical image was also obtained for each subject using a T1-weighted multiplanar rapidly acquired gradient-echo (MPRAGE) sequence (TR = 8.1 ms, TE = 3.7 ms, flip angle = 8° , time between inversions = 3 s, inversion time = 748 ms, FOV = 256×256 mm, 1-mm isotropic voxels).

Data analysis

Individual subject-based data analyses were conducted using BrainVoyager (Brain Innovation, Maastricht, The Netherlands). The anatomic image was first transformed into Talairach space (Talairach and Tournoux, 1988), after which an automated cortical segmentation and reconstruction procedure was applied to obtain a surface reconstruction for the white–gray matter boundary. The surface was then inflated, cut along the base of the calcarine sulcus, flattened, and linear distortion corrected to less than 13%. All data analyses were conducted on this flattened representation of the cortical sheet (Dale et al., 1999; Fischl et al., 1999; Kriegeskorte and Goebel, 2001; Slotnick et al., 2003). Functional data were preprocessed, including slice time correction, motion correction, and linear trend removal (no spatial smoothing was performed). The functional images were then coregistered with the original high-resolution anatomical image. Finally, the 2D functional data were transformed into 3D Talairach space with 3-mm isotropic resolution.

A general linear model (GLM) approach was taken to localize cortical ROIs. Blocks of visual stimulation were modeled with delayed gamma functions, and contrasts between the fitted coefficients (beta weights) were evaluated using a weighted t test for statistical significance. For the early visual area localizer, activation associated with a particular stimulus ring was revealed by a linear contrast between a given ring size and the other two sizes (e.g., for the middle ring, the contrast was $2^{\text{middle}} - (\text{inner} + \text{outer}))$. To localize MT+, a GLM was constructed for the main experiment with three regressors, corresponding to the three stimulation conditions. A contrast was then made between the real motion and the flicker condition. The activated voxels near the ascending limb of the inferior temporal sulcus were defined as MT+ (Watson et al., 1993). The statistical threshold was set at P < 0.001 for the early visual area localizer and P < 0.01 for the contrast to localize MT+ (uncorrected for multiple comparisons). Note that the MT+ localizer does not provide a distinct ROI that is restricted to the path of apparent motion (see Discussion).

Retinotopic mapping methodology has been described in detail elsewhere (Slotnick and Yantis, 2003). Briefly, each voxel's signal time course was correlated with a series of phase shifted hemodynamic response functions, the maximum correlation of which indicated the phase of each voxel (with a minimum r = 0.20). Borders of early visual areas were drawn on the flattened cortical surface as indicated by phase reversals in the retinotopic map.

To conduct the ROI analysis, retinotopic borders were superimposed on the early visual area localizer results. The intersection of these two maps defined the cortical representation of each stimulus ring in each early visual area (including the intermediate ring that defined the filled-in region during apparent motion). For each ROI, defined as the intermediate ring's cortical representation in different retinotopic visual areas, the fMRI signal time course was extracted for the three experimental conditions: apparent motion, flicker, and real motion. The activity at time 0 (stimulus onset) was used as the baseline to calculate percent signal change. The mean activity within the 6-12 s window post-stimulus was used to index the magnitude of the response (as the BOLD signal was expected to reach its maximum value at about 6 s following stimulus onset, and begin to drop off following the end of each approximately 12 s block). Paired t tests were used to assess the significance of time course differences in magnitude.

Results

Results from the early visual area localizer revealed distinct bands of activation corresponding to the three stimulus rings. Representative data from one hemisphere are shown in Fig. 2. Superimposed on the localizer activity are the borders of visual areas obtained from retinotopic mapping. To determine the degree to which filling-in occurred within each visual area, fMRI signal was extracted from the cortical representation of the middle ring (medium-colored cyan in Fig. 2), which lay in the path of apparent motion.

The cortical representations of the middle ring were localized to ventral visual areas V1v, V2v, VP, and V4v and dorsal visual areas V1d, V2d, V3, and V3A for each hemisphere. Because there were no qualitative differences among the results from the four quadratic representations of the middle ring, the data were collapsed across quadrants. For each visual area, the time courses were then averaged across all subjects (Fig. 3a). There was no qualitative difference between the apparent motion and the flicker condition, although the real motion condition evoked a larger response, most notably in V1 and V2. A statistical test confirmed that there was no difference between the apparent motion and flicker condition (all P's > 0.05). However, a comparison between real motion and the weighted sum of apparent motion and flicker revealed significant effects in V1 and V2 [t(3) = 5.76, P < 0.05; t(3) = 3.23, P < 0.05;respectively], marginally significant effects in V3/VP (t(3) =2.60, P = 0.08), and a nonsignificant effect in V4v/V3a (P >0.1). This pattern of results were highly stable across subjects, especially in V1/V2. To illustrate, Fig. 3b shows individual subject time courses from area V1. Similar to the group average in V1, all subjects exhibited a greater response for real motion, with no appreciable difference between the apparent motion and flicker conditions. In fact, in some individual subjects, the



Fig. 2. Cortical representation of the localizer stimulus projected onto a representative flattened left hemisphere (subject HP). Different shades of colors denote the cortical activation associated with the three ring stimuli: blue for the inner ring, cyan for the middle ring, and green for the outer ring. Superimposed on the localizer activity are borders of early visual areas obtained from retinotopic mapping. Also shown in yellow is MT+, obtained from contrasting real motion and flicker.

activation time course for apparent motion and flicker does not resemble typical hemodynamic responses, probably reflecting noise-dominated activity.

We next turn to the responses in MT+. Fig. 4 shows the time courses from MT+ for the group average (top) and for each individual subject (bottom), which were averaged across MT+ in the left and right hemispheres. Real motion again evoked the largest response in the group average, followed by apparent motion with a medium level response, with flicker resulting in the lowest response amplitude. Real motion and apparent motion evoked a significantly higher response than the flicker condition [t(3) = 5.29, P < 0.05, for real motion vs. flicker; t(3) = 4.01, P < 0.05, for apparent motion vs. flicker], while the difference between real motion and apparent motion was only marginally significant [t(3) = 2.54, P = 0.08]. The individual subject responses in Fig. 4 also show that this pattern of results is consistent across subjects, with



Fig. 3. Averages of fMRI signal for the three conditions in the main experiment, obtained from the cortical representation of the middle ring. (a) Time course in each visual area averaged across subjects and quadrants. The error bar is the mean standard error of all the time points on a curve. The standard error was calculated based on four observations (four subjects). (b) Time course from the V1 representation of the middle ring (combined across the two representations in the left and right hemispheres) for each subject. The error bar is the mean standard error of all the time points on a curve. The standard error was calculated based on 24 observations (24 trials per condition per subject). The horizontal bar in the top-left panel denotes the approximate duration of the visual stimulus in a trial.



Fig. 4. Averages of fMRI signal for the three conditions in the main experiment, obtained from MT+. The top panel shows the average time course across subjects, and the bottom panels show the same data for each individual subject. The error bar is the mean standard error of all the time points on a curve. The standard error was calculated based on 4 observations (four subjects) for the top panel and 24 observations for the bottom panels (24 blocks per condition per subject). The horizontal bar in the top-left panel denotes the approximate duration of the visual stimulus in a trial.

the exception of subject HP, who had similar levels of response for the real motion and apparent motion. Critically, however, all subjects exhibited a higher level of activity for the apparent motion than the flicker condition.

Discussion

In this study, we conducted the definitive test of the filling-in hypothesis in lower retinotopic areas V1-V4. We found no evidence for such filling-in effects—apparent motion evoked the same level of activation as the flicker condition (Fig. 3). This result corroborates the predictions of the Grossberg and Rudd (1992) neural network model of apparent motion.

Our paradigm was sufficiently sensitive to detect filling-in within early visual areas if it had occurred, because (a) real motion elicited greater activity than both the apparent motion and flicker condition in nearly all early visual areas (showing that the experimental protocol could detect differential activity in those areas), and (b) apparent motion evoked significantly greater activity than flicker in area MT+ (showing that the apparent motion stimulus could produce a robust signal in an area that is known to be responsive to motion).

The difference between real motion and the other two conditions tended to decrease in progressively higher-level early visual areas. While activity associated with real motion was similar in amplitude across the early visual areas (approximately 1.5% signal change), activity evoked by apparent motion and flicker became systematically larger in higher visual areas (approximately 0.5% in V1 and V2 and approximately 1.0% in V3/VP and V3A/V4). This pattern of activity may be due to the larger receptive field sizes in higher visual areas (V1: <2°, V2: $2-4^{\circ}$, V4: $4-6^{\circ}$, estimated for an eccentricity of 5.5°; Kastner et al., 2001), which would have been more responsive to 'leakage' from stimulation of adjacent spatial locations. Among neurons with receptive fields covering the middle-ring location, many more in V4, as compared to V1, would be expected to receive sensory stimulation from both the inner and outer rings (which were separated by approximately 5°). The

crucial finding, however, is that the response to apparent motion and to flicker did not differ in these areas.

In contrast to the early retinotopic areas, MT+ showed a gradient of activity for the three stimulus displays (Fig. 4). Most importantly, apparent motion evoked a larger response than did flicker, a robust effect exhibited by all subjects. Such results reaffirm the role of MT+ in apparent motion perception, replicating previous findings (Goebel et al., 1998; Muckli et al., 2002). Furthermore, the present results demonstrate for the first time that filling-in of the path of apparent motion does not occur within lower retinotopic areas. This pattern of results supports the late model of filling-in during apparent motion.

An unresolved issue is how the observed activity in MT+ could mediate the perceptual phenomenon of filling-in during apparent motion. One possibility is that there is neural filling-in within retinotopic MT+ that corresponds to the path of apparent motion. Another possibility is that MT+ cells simply respond when an apparent motion stimulus matches their spatiotemporal receptive fields, without explicit spatiotopic filling-in; such activity would be interpreted by the visual system as representative of the stimulus traversing the motion path. Huk et al. (2002) have recently reported a retinotopic organization in human MT+ using fMRI, but the retinotopy they reported with respect to center versus periphery was relatively coarse (see also Tootell et al., 1995). Our MT+ localizer was not designed to locate a subregion of MT+ that responded only to the path of apparent motion, and our early visual area localizer did not activate a retinotopic subregion of MT+. Thus, localizing the subregion of MT+ that responds only to stimulation in the path of apparent motion may prove to be difficult. Given these considerations, the present data cannot distinguish between these alternatives, and further experiments with retinotopic mapping of MT+ will be needed to test these possibilities. Nevertheless, our results show that MT+ is the first area in the visual cortical hierarchy that responds to apparent motion, and hence is the earliest visual area in which neural filling-in for the path of apparent motion could occur.

As noted earlier, Yantis and Nakama (1998) reported behavioral evidence that the identification of a letter target is selectively impaired when it appears in the path of apparent motion compared to when it appears in an objectively matched location off the path. One possible neural mechanism for this effect, that early filling-in interferes with extrastriate cortical target processing in the motion path, has been disconfirmed by the present study. Another possible explanation for their results is that the motion and form processing pathways have overlapping cortical substrates, such that motion processing might interact with (e.g., interfere with) the processing of form.

To investigate this possibility, subjects in the present study also participated in a scanning session to localize the lateral occipital complex (LOC), a region specialized for object processing (Grill-Spector et al., 2001; Kourtzi and Kanwisher, 2000; Malach et al., 1995). The procedure and stimuli followed closely those of Kourtzi and Kanwisher (2000). Blocks of intact and scrambled novel shapes were alternated (separated by blank intervals), and subjects performed a one-back matching task to maintain vigilance. To identify the cortical locus of LOC, the regressors associated with intact and scrambled images were contrasted (P < 0.01, uncorrected for multiple comparisons). In Fig. 5, MT+ is shown in yellow and LOC in red. Data are displayed on individual hemispheres (LOC



Fig. 5. Cortical representation of MT+ and LOC, shown on flattened reconstruction of individual hemispheres for each subject (LH: left hemisphere, RH: right hemisphere). The dashed circle indicates the lateral occipital region where MT+ and LOC are located. MT+ is shown in yellow and LOC is shown in red. Green indicates regions of overlap. LOC could not be localized for subject KL's right hemisphere.

could not be localized in subject KL's right hemisphere). Note that MT+ and LOC had overlapping cortical regions (shown in green) in all hemispheres in which both areas could be localized.

These results support the idea that motion and form pathways interact, by showing that there is a cortical region of overlap in which such an interaction could occur (Ferber et al., 2003; Murray et al., 2003; Zhuo et al., 2003). Because LOC is likely to play a critical role in object recognition (Grill-Spector et al., 2001; Kourtzi and Kanwisher, 2000; Malach et al., 1995), the activation of MT+ by the apparent motion stimuli might disrupt the processing of other stimuli that are processed by LOC, leading to an impairment in identification performance (Yantis and Nakama, 1998).

A recent study also reported overlapping activation of MT+ and LOC, and found shape-selective response in subregions of MT+ (Kourtzi et al., 2002). In this study, MT+ was defined by contrasting moving and stationary dots, a commonly used procedure. Here we defined MT+ by contrasting continuously moving and flickering rings and obtained similar results. Our study thus provides additional evidence for the interaction between the motion and form processing streams in the LOC/MT+ region, a conclusion also supported by recent behavioral studies (Liu and Cooper, 2003; Stone, 1999).

Although our results rule out neural filling-in of the path of apparent motion within early visual areas, the phenomenology of a single, continuous, moving object still begs explanation. One possibility is that the subregion in LOC that is activated by motion supports object continuity by maintaining an object representation through spatiotemporal transformation (Kahneman et al., 1992), thus producing the perception of a single object traversing space. Further research is needed to investigate this possibility.

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