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Psychophysical Evidence for Spatiotopic Processing in Area MT in a Short-Term Memory for Motion Task

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[1]*Department of Neurobiology and* [2]*Jules Stein Eye Institute, David Geffen School of Medicine at University of California–Los Angeles;* [3]*Interdepartmental PhD Program for Neuroscience and* [4]*Department of Psychology and the Brain Research Institute, University of California–Los Angeles, Los Angeles, California; and* [5]*Institute of Neuroscience, Chinese Academy of Sciences, Shanghai, China*

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Ong WS, Hooshvar N, Zhang M, Bisley JW. Psychophysical evidence for spatiotopic processing in area MT in a short-term memory for motion task. *J Neurophysiol* 102: 2435–2440, 2009. First published August 19, 2009; doi:10.1152/jn.00684.2009. The middle temporal (MT) area has long been established as a cortical area involved in the encoding of motion information and has been thought to do so in retinotopic coordinates. It was previously shown that memory for motion has a spatial component by demonstrating that subjects do significantly worse on a match-to-sample task when the stimuli to be compared were spatially separated. The distance at which performance deteriorated (the *critical spatial separation*) increased at increasing eccentricities, suggesting that area MT was involved in the process. In this study, we asked whether optimal performance occurred when the stimuli were in the same retinotopic or spatiotopic coordinates. We found that the performance was best when the stimuli appeared in the same location in space rather than the same retinal location, after an eye movement. We also found that the relationship between retinal eccentricity and the critical spatial separation approximated that of area MT, as found previously. We conclude that area MT plays an important role in the memory for motion process and that this is carried out in spatiotopic coordinates. This conclusion supports the hypothesis that MT processing may have a spatiotopic component.

INTRODUCTION

It is well established that information about visual motion is processed in the middle temporal/extrastriate visual cortical V5 (MT/V5) area in both monkeys (Britten et al. 1992; Dubner and Zeki 1971; Maunsell and Van Essen 1983; Salzman et al. 1992) and humans (Huk et al. 2002; Tootell et al. 1995; Watson et al. 1993). It has also been suggested that cortical areas that play a role in encoding the features about a particular stimulus could also be involved in the retention of that information (Fuster and Jervey 1981; Zhou and Fuster 1996). This would suggest that MT could play a role in a memory for motion task. Indeed, this idea is supported by lesion (Bisley and Pasternak 2000), microstimulation (Bisley et al. 2001), and psychophysical (Zaksas et al. 2001) data in nonhuman primates. In particular, Zaksas et al. (2001) showed performance in a memory for motion task degrades slightly if the two stimuli to be compared are spatially separated by a critical distance. This distance increased as the eccentricity of the stimuli increased in a way that matched the receptive field sizes of neurons in area MT.

Area MT has generally been thought to operate in a reference frame linked to the retina (retinotopic) (Albright and Desimone 1987; Gardner et al. 2008). Recently, however, d'Avossa et al. (2007) showed that the responses in human MT have a processing component that uses a reference frame linked to locations in space (spatiotopic). This is supported by psychophysical evidence from adaptation and integration studies (Melcher 2005; Melcher and Morrone 2003), although not from the motion aftereffect (Knapen et al. 2009). Because we rarely fixate on the same spot in the world for >0.5 s at a time, one might expect that the processing of short-term memory for motion would occur in a spatiotopic reference frame rather than a retinotopic one. To test this, we asked whether the processing of memory for motion is better when two motion stimuli to be compared are presented in the same retinal or spatial locations. We also asked whether people have a critical spatial separation that increases with eccentricity and whether this correlates best with the receptive field sizes of neurons in area MT or neurons in other related areas. We found that the process is optimal in spatiotopic coordinates and that critical spatial separation matched the receptive field size of MT neurons. This suggests that MT may process memory for motion information in a spatiotopic coordinate system.

METHODS

Subjects

Nine (four female) adult human subjects (including three of the authors) participated in the study. Subjects had either normal or corrected-to-normal vision. Psychophysical experiments were approved through the UCLA Institutional Review Board. Before collecting data, subjects performed a training session of roughly 100 trials to acclimatize them to the task and response buttons.

Behavioral task

All the experiments were run using the REX system (Hays et al. 1982). Stimuli were presented on a 22-in. Viewsonic C225f monitor running at 100 Hz with a resolution of 1,024 × 768, which was placed 57 cm from the subjects' eyes. The subjects' eye positions were monitored by a SensoMotoric Instruments eye tracker and recorded at 1 kHz in REX. All subjects performed a variation of a match-to-sample task (Fig. 1) in which they were shown two random dot patterns, the *sample* and *test*, separated temporally by a 1,350-ms delay. Their task was to indicate, by pressing one of two buttons, whether the directions of motion were the same or different. The subjects received feedback in the form of an audible beep after a correct response. On each trial the sample moved in one of eight possible directions: the four cardinal directions and the four directions that are 45° from cardinal. On different trials, the test direction could differ from the sample direction by either a clockwise or counter-

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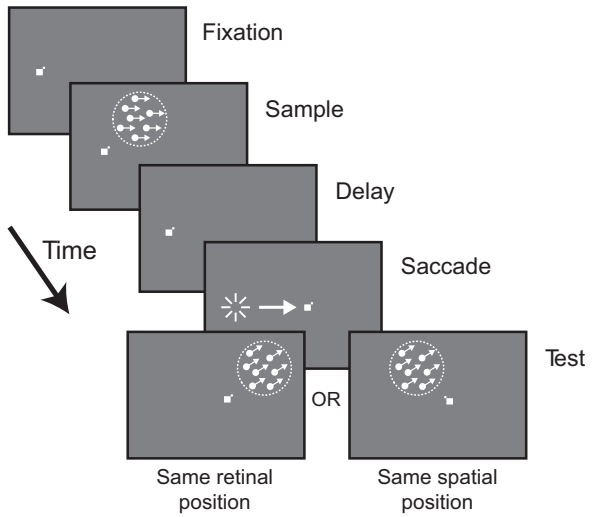

FIG. 1. The direction difference discrimination task. On each trial, the fixation spot could appear on either side of the screen and had a small mark that pointed toward the location where the stimulus would appear. The sample stimulus appeared for 500 ms and there was a 1,350-ms delay before the test stimulus appeared. During the delay, the fixation point jumped to the opposite side of the screen. The test stimulus appeared in either the same retinal or spatial location as the sample. Subjects indicated whether the dots in the sample and test stimuli were moving in the same direction by a button press.

clockwise rotation. The stimuli were created using VEX software (Laboratory of Sensorimotor Research, National Eye Institute) and consisted of moving dots within a stationary circular aperture. The dots all moved in the same direction (100% coherence). The lifetime of an individual dot was equal to the duration of the stimulus presentation (500 ms). The dot density was kept constant at 21%. The white dots were presented on a dark background in a dimly lit room to prevent the use of scotopic vision.

The first variation of the task was aimed at testing whether better performance would be seen when the two stimuli were in the same retinal or spatial locations (Fig. 1). In this task, the subject had to fixate a small square point 5° to the right or left of the center of the screen for 750–1,250 ms, after which the sample appeared at 7° eccentricity. The fixation point had a mark that pointed to the stimulus location, so there was no spatial uncertainty and the subjects could optimize their attentional strategy. This stimulus was followed by a delay that ranged from 450 to 900 ms, after which the fixation point jumped 10° to the other side of the screen. Subjects had 300 ms to execute a saccade to the new fixation point. The new fixation point had a mark that pointed to the test stimulus location and the test appeared at this location 1,350 ms after the sample stimulus disappeared. The test stayed on for 500 ms and was followed by a 250-ms delay, after which the fixation point dimmed, signaling to the subject that it was time to respond. The test was always placed at the same eccentricity as the sample, but could appear at two possible locations on the screen: the same spatial location as the sample or the same retinal location as the sample (Fig. 1). Direction differences were assigned using the method of constant stimuli; on each trial the direction difference was pseudorandomly chosen from a discrete set of eight direction differences and the subjects could not predict whether it would be a "same" trial, a difficult "different" trial, or an easy "different" trial. For data analysis, performance from all sessions was pooled (usually two to three sessions and an average of 475 trials per subject). Thresholds were defined as the smallest angle between sample and test directions that allowed for discrimination at the 75% correct level. These were calculated by fitting the data with a Weibull function, weighted by the number of trials at each point, using the maximum-likelihood method (Quick 1974; Zaksas et al. 2001).

The second variation of the task was aimed at testing whether subjects had a critical spatial separation similar to that seen in the monkey. This task was similar to the task described earlier and differed only in the following ways. First, the fixation point was located at the center of the screen, so the subject was not required to make any saccades. Second, the stimuli could appear at 3, 7, or 14° eccentricity (although only one eccentricity was used in a block of trials). The aperture sizes and velocities were optimized for each condition (Table 1). Third, although the sample was always placed in the same location within a block, the test could appear in any of four locations: the same location as the sample or one of three different locations with various stimulus separations (Table 1). Within a block, both the sample and test were always placed in the same visual hemifield at the same eccentricity. Thus the sample and test appeared at locations around an imaginary circle, with separations measured directly between the center of the two stimuli. Fourth, the fixation point did not have a mark that pointed to the stimulus location, so there was some uncertainty in where the test could appear. Finally, within a session, only two direction differences were tested. These were chosen to be close to the subject's threshold. Data were analyzed if, within a session, there was a step function in performance in which the better performance was in the condition in which there was no spatial separation. Generally, a difference in performance can be seen only along the sloping portion of the psychometric function (see difference between functions in Fig. 2*A*). Because we sampled only two points on the function, we would sometimes get performance that was on the asymptotes. In these sessions we found no change in performance for any separation. Critical spatial separations were defined as the spatial separation of stimuli in the match-to-sample task that produced a decline in performance. These were calculated by fitting a sigmoid function to the performance data plotted as a function of the spatial separation and taking the midpoint of the function as the critical spatial separation.

RESULTS

Spatiotopic versus retinotopic

To ask whether optimal performance on a memory for motion task requires the sample and test to be in the same spatial or retinal locations, we recorded data from eight human subjects performing a direction-discrimination task. In the task, they compared the directions of motion of two coherently moving random-dot stimuli (*sample* and *test*), separated by a 1,350-ms delay during which a 10° saccadic eye movement was made to the right or left. In this paradigm the test could appear either in the same retinal or spatial location as the sample (Fig. 1).

Subjects' performance was better when the sample and test were placed in the same spatial location than when they were placed in the same retinal location. Figure 2*A* shows the data from a single subject. The performance of the subject is plotted against the angle of direction difference between the sample and test stimuli. To calculate the threshold, the data in each condition were fitted with a Weibull function and the threshold

TABLE 1. *Parameters of motion-stimuli presented at different eccentricities*

Eccentricity, deg	Stimulus Separations, deg	Diameter of Stimulus, deg	Speed of Dots, deg/s
3.5	0, 1.5, 2.5, 5.0	1.4	4
7.0	0, 3.0, 5.0, 10.0	3.0	8
14.0	0, 6.0, 10.0, 20.0	6.0	16

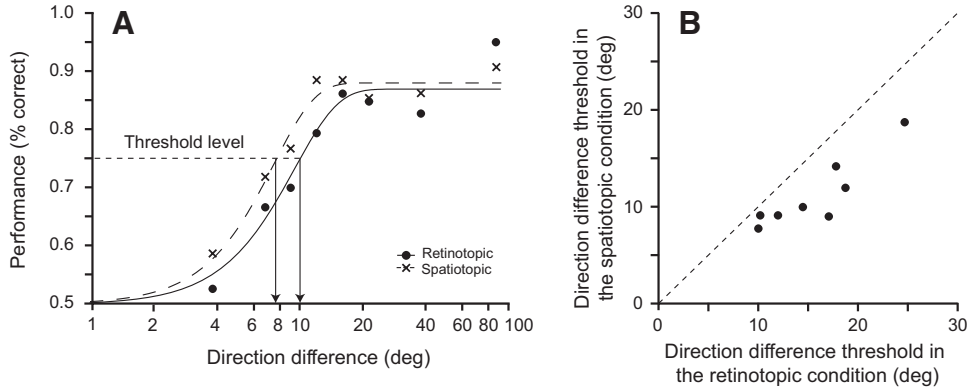

FIG. 2. Effect of test stimulus location on performance. *A*: the performance of a single subject is plotted against the angle of direction difference between the sample and test stimuli. Black circles show the data obtained in the retinotopic condition. Solid line shows the best fitted Weibull function ($R^2 = 0.919$; threshold: 10.03°); crosses show the data obtained in the spatiotopic condition; fit shown with a dotted line ($R^2 = 0.950$; threshold: 7.73°). *B*: the thresholds of 8 subjects in the spatiotopic condition plotted as a function of the thresholds in the retinotopic condition. Each point represents the data from a single subject. Across the population, the thresholds in the spatiotopic condition were significantly better than those in the retinotopic condition (paired *t*-test, $P = 0.0001$).

was defined as the direction difference at which the subject could perform the discrimination at 75% correct. The data obtained in the retinotopic condition is shown by the black circles (fit shown by solid line, $R^2 = 0.919$), whereas the data from the spatiotopic condition is denoted by crosses (fit shown by dashed line, $R^2 = 0.950$). The data demonstrate that the subject was able to discriminate smaller direction differences in the spatiotopic condition (threshold: 7.73°) than in the retinotopic condition (threshold: 10.03°). Indeed, at direction differences near to the threshold, the subject consistently performed better when the stimuli were in the same spatial positions.

All eight subjects showed better performance when the sample and test were in the same spatial location than when they were in the same retinal location (Fig. 2*B*). Here we compare the thresholds from each individual under the two conditions. All of the points fall below the dashed unity line, showing that all subjects were able to distinguish smaller angle differences in the spatiotopic condition compared with the retinotopic condition. Thus across the population, there was a significantly lower threshold in the spatiotopic condition compared with the retinotopic condition (paired *t*-test, $P = 0.001$). Independent of performance, saccade metrics were the same under both conditions for all subjects.

Performance at an unrelated location was not significantly better than performance at the retinotopic location. To test whether the better performance at the spatiotopic location was due to a local deficit at the retinotopic location rather than an enhancement at the spatiotopic location, we tested the five subjects who participated in all experiments in a control task. In this task, the test could appear at the same retinal location or at a different control location. The control location was at equal eccentricity to the sample, was not in the spatiotopic location, and was counterbalanced so that no retinal location was tested more often than any other location in either condition. As in the main task, a small point on the fixation spot indicated the location of the test stimulus. We found that performance was similar in the retinotopic and control conditions ($P > 0.95$, paired *t*-test), with thresholds (means ± SE) of 11.67 ± 1.32 and 11.64 ± 0.67° for the retinal and different conditions, respectively. In addition, the mean performance in the control condition was significantly worse than that in the spatiotopic condition when data from the same five subjects were compared ($P = 0.013$, two-tailed *t*-test assuming unequal variance). These data show that the difference between thresholds at the spatiotopic and retinotopic conditions was due to enhanced performance at the spatiotopic location.

Relationship between retinal eccentricity and critical spatial separation

Having previously shown that the critical spatial separation correlated with the receptive field size of MT neurons in the monkey (Zaksas et al. 2001), and then finding that the optimal reference frame was in spatiotopic coordinates in humans, we asked what the relationship was between retinal eccentricity and critical spatial separation in the human. Given that area MT is traditionally thought to operate in retinotopic coordinates, we proposed two plausible reasons that could explain the difference between our result and the previous animal result. First, humans may not use MT, in which case the critical spatial separation, representing the receptive field size, may be different in the two species. Second, the assumption that MT operates in only a retinotopic coordinate frame may be incorrect (d'Avossa et al. 2007); thus our results may still implicate area MT in this task. To test these two possibilities, eight subjects performed a direction-discrimination task in which the sample and test always appeared at the same eccentricity, but could be separated by varying degrees of visual angle. In any given block of trials, only one of three eccentricities (3.5, 7, and 14°) was tested and within the block the stimulus size, speed of the dots, and separation distances were kept constant (Table 1).

As eccentricity increased, the distance between stimuli required to induce a drop in performance increased. For each eccentricity from each subject, a sigmoidal function was fitted to the data points and the midpoint of the function was taken as a measure of the critical spatial separation. For example, Fig. 3 shows the performance from the same single subject as in Fig. 2*A* plotted against the separation distance between the sample and test stimuli. The red circles and fit demonstrate the subject's performance at 3.5° eccentricity, the blue at 7° eccentricity, and the black at 14° eccentricity.

The relationship between critical spatial separation and retinal eccentricity was consistent among all the subjects; there

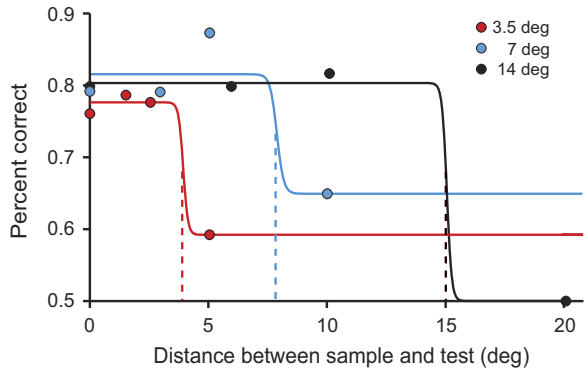

FIG. 3. Performance as a function of stimulus separation for 3 eccentricities. The performance of a single subject (same as in Fig. 2*A*) is plotted against the separation distance between the sample and test stimuli for 3 eccentricities (27 ± 1.9 trials per point). Red circles show data from 3.5° eccentricity (midpoint of fit: 3.94); blue circles from 7° eccentricity (midpoint: 7.90); black circles from 14° eccentricity (midpoint: 15.07).

was an increase in critical spatial separation as eccentricity increased. The average critical spatial separations for the eight subjects are plotted in Fig. 4 as a function of eccentricity (black circles). The critical separation for locations closer to the fovea was smaller and increased with distance, consistent with the relationship between eccentricities and receptive field sizes in various visual areas in the monkey (solid black lines). Importantly, the critical spatial separations in the human are similar to those found in the monkey (triangles; Zaksas et al. 2001) and most consistent with the receptive field sizes for MT neurons. When a linear fit was made through the raw critical spatial separations from our data, the confidence intervals for slope and offset included the slope and offset calculated from the MT data (Albright and Desimone 1987) but for none of the other cortical areas.

DISCUSSION

We have shown that thresholds for direction discrimination in a memory for motion task are better when the sample and test stimuli are placed in the same spatial locations compared with when they are placed in the same retinal location or in a control location following a saccade. This is perhaps unsurprising given our experience in everyday conditions—the motion information we use in short-term memory comes from motion in space rather than motion that is tied to the retina. More surprising was the finding that the critical spatial separation that induces the behavioral differences in performance best approximated the size of receptive fields in MT—an area generally thought to process information in an exclusively retinotopic coordinate frame.

Our interpretation of these data rests on the assumption that the task will be performed optimally when the same processing unit is involved at critical junctures within the trial. By moving a stimulus to a new location, a new unit with the appropriate spatial receptive field will be recruited and the transfer of information from one unit to another will introduce noise. We observe this noise as a slight decrease in performance. Thus our interpretation of the data is that the areas involved in the storage and comparison of this information must have a spatiotopic reference frame because performance was reduced when the test stimulus was placed in the same retinal location or a control location following a saccade. The simplest explanation for our finding is that information is automatically transferred to the appropriate processing unit during a saccade. This could occur via a remapping mechanism similar to that seen in the lateral intraparietal area (Duhamel et al. 1992; Kusunoki and Goldberg 2003), the frontal eye fields (Umeno and Goldberg 1997), the superior colliculus (Walker et al. 1995), and a number of visual areas (Nakamura and Colby 2002). In this case, by placing the test in the same retinal location after a saccade, the decrease in performance results from shifting the information back to the original unit, which had just had the information shifted away by the remapping mechanism.

We think it unlikely that the dim lighting in the room biased performance toward a spatiotopic coordinate frame. Our reason for this is that in studying the motion aftereffect in a dimly lit room, Knapen et al. (2009) found the effect in the retinotopic location rather than a spatiotopic location, suggesting that the presence of light does not automatically set all motion processing to a spatiotopic reference frame. Conversely, using slightly different stimuli in a dark room, Ezzati et al. (2008) found a weak motion aftereffect in the spatiotopic location in addition to that in the retinotopic location. This suggests that light is not necessary for spatiotopic processing.

It is also possible that the better performance in the spatiotopic condition does not represent improved performance at the spatiotopic location, but rather that it is due to a local deficit in performance at the retinotopic location attributed to adaptation or some other low-level process. This is unlikely to be explained by adaptation, given that adaptation causes the repulsion of directions of motion near to the adapting stimulus, which would predict better performance at the retinotopic location than at the spatiotopic location (Wenderoth and Wiese

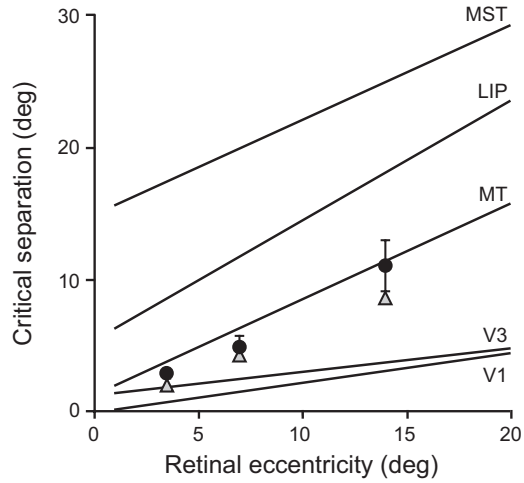

FIG. 4. Effect of eccentricity on critical spatial separation. Black circles show the mean critical spatial separations measured from 8 subjects as a function of eccentricity. The lines of best fit from data comparing receptive field sizes of neurons in cortical areas: primary visual cortex (V1), extrastriate visual cortical area (V3), middle temporal area (MT), lateral intraparietal area (LIP), and medial superior temporal area (MST) with eccentricity (Albright and Desimone 1987; Ben Hamed et al. 2001; Desimone and Ungerleider 1986; Dow et al. 1981; Felleman and Van Essen 1987) are plotted for comparison. Gray triangles show the critical spatial separations recorded from monkeys in a similar task (Zaksas et al. 2001). The variation of the critical spatial separation with eccentricity measured is similar to that of the monkey and most consistent with the receptive field sizes for MT neurons.

2008). Our sample stimulus was only 500 ms and the directions changed on each trial, so it is unlikely that adaptation played a major role in this task. In line with this, we found no difference in performance between the control condition and the retinotopic condition, but we did find a significant difference between the control condition and the spatiotopic condition. This suggests that the better performance at the spatiotopic location implies a benefit at this location, rather than a deficit at the retinotopic location.

Having found that there is a spatial component involved in processing memory for motion in the monkey, Zaksas et al. (2001) showed that the critical spatial separation changed with eccentricity in a way that matched the receptive field sizes in area MT. In our study, we looked to see whether this would also be seen with humans. Our logic is that the critical spatial separation gives an indication of the region of space covered by the processing unit. Since the most basic processing unit in cortex is the neuron, we interpret this to mean the receptive field sizes of the neurons within the brain area involved in this process. The theory is that if the two stimuli are separated but still close enough that they would both fall within the neurons' receptive fields, then no decrement would be seen because the processing would remain within the set of neurons (i.e., the processing unit). Conversely, if the two stimuli are separated by more than a receptive field diameter, then information would have to be transferred from one set of neurons to another. In this case, noise would be introduced and performance would suffer. In Fig. 4, we superimposed the mean critical spatial separations of our data (circles) on the plotted receptive field sizes of neurons in cortical areas: primary visual cortex (V1), extrastriate visual cortical area (V3), middle temporal area (MT), lateral intraparietal area (LIP), and medial superior temporal area (MST), as taken from the literature (Albright and Desimone 1987; Ben Hamed et al. 2001; Desimone and Ungerleider 1986; Dow et al. 1981; Felleman and Van Essen 1987). On their own, the data from our study appear to best correspond to the receptive field to retinal eccentricity relationship of area MT; when taken together with the monkey data, the association only becomes stronger. It should be noted that the critical spatial separation measurements in this study should be viewed as rough approximations of the actual values. This task was imperfect in the sense that we neither collected full psychometric functions for each separation, nor did we test enough separations to get an accurate representation of when the performance begins to drop. However, the data are still clear enough to show that the performance drop occurred at greater distances at greater eccentricities and the estimates of the critical spatial separations are similar to the previous estimates in the monkey. We should also note that the only evidence linking the spatiotopic effects with MT is the relationship between the critical separation and eccentricity. Although psychophysics can never link, with 100% certainty, the role of a cortical area with the process being studied, ours does so as convincingly as possible. Given that MT is the only cortical area with a receptive field profile that matches our critical separation measures and is also involved in processing motion and memory for motion information, we can think of no other plausible explanation for our results.

Area MT has been well studied in the monkey and is traditionally thought of as a retinotopic area. Recently, it has been suggested that MT may be involved in spatiotopic processing. Evidence for this comes from a psychophysical study that showed that the integration of motion information over time can be performed in spatiotopic coordinates (Melcher and Morrone 2003) and from a functional magnetic resonance imaging study that showed spatiotopic blood oxygenation level–dependent (BOLD) information in MT (d'Avossa et al. 2007). However, a more recent study found no evidence for spatiotopic processing in the BOLD response (Gardner et al. 2008) and results from psychophysical studies on motion or direction aftereffects, both thought to involve MT, have predominantly found evidence for retinotopic processing with weak if any evidence for spatiotopic processing (Ezzati et al. 2008; Knapen et al. 2009; Wenderoth and Wiese 2008). Interestingly, apart from the presence of gain fields (Bremmer et al. 1997), there is no electrophysiological evidence to support the idea of MT as processing spatiotopic information, although one study, examining a codebook readout of a population of neurons, did not find evidence of pure spatiotopic processing (Krekelberg et al. 2003). Our data appear to strongly support the hypothesis that MT in the human can process visual motion information in a spatiotopic coordinate frame. Indeed, our data would suggest that it is a default mechanism, since there was a significant difference in performance under the two conditions and the subjects were always aware of where the stimuli would appear. Whether this is unique to the human or whether MT neurons in the monkey will be shown to have spatiotopic properties—such as perisaccadic remapping—is yet to be shown.

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