

Introduction

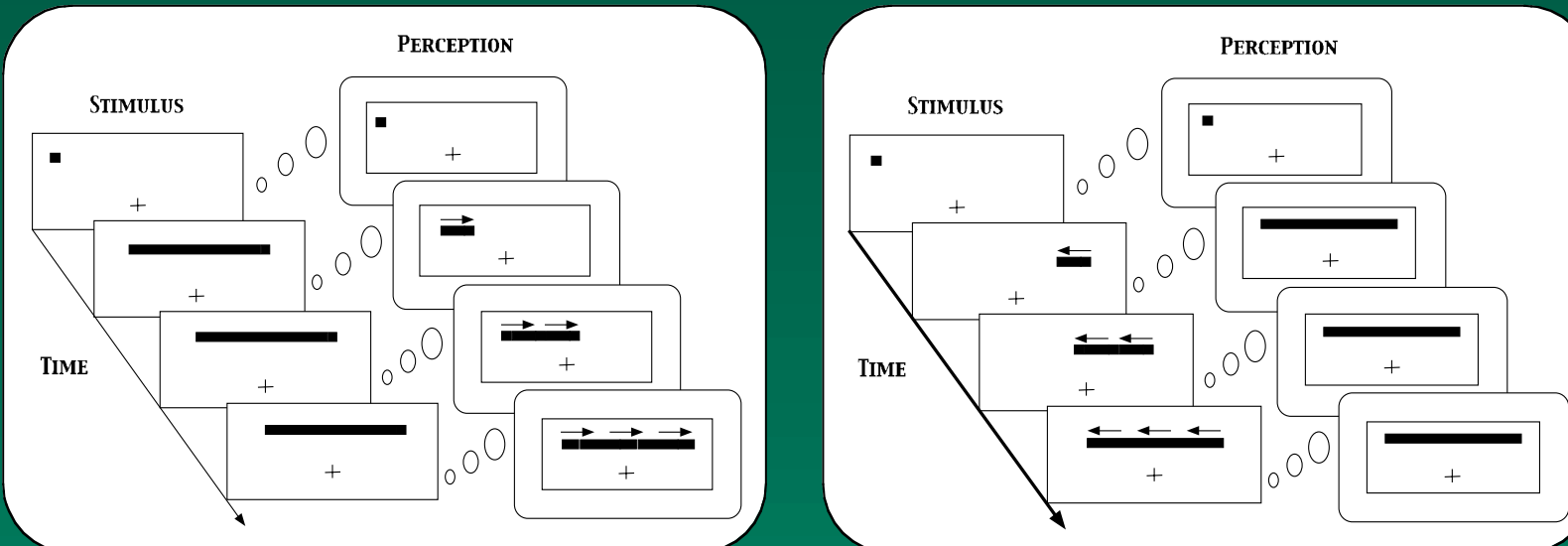
The purpose of this study is to determine the extent to which the hemodynamic response of human area MT+ is correlated with perceived but illusory motion as opposed to actual, but not perceived, stimulus motion. We compared the response of MT+ when subjects viewed displays of motion induced by the line motion illusion to displays in which motion opponent to the illusion had been added to eliminate the perceived motion. We found that MT+ is more recruited by perceived but illusory motion than by unperceived stimulus motion.

Background

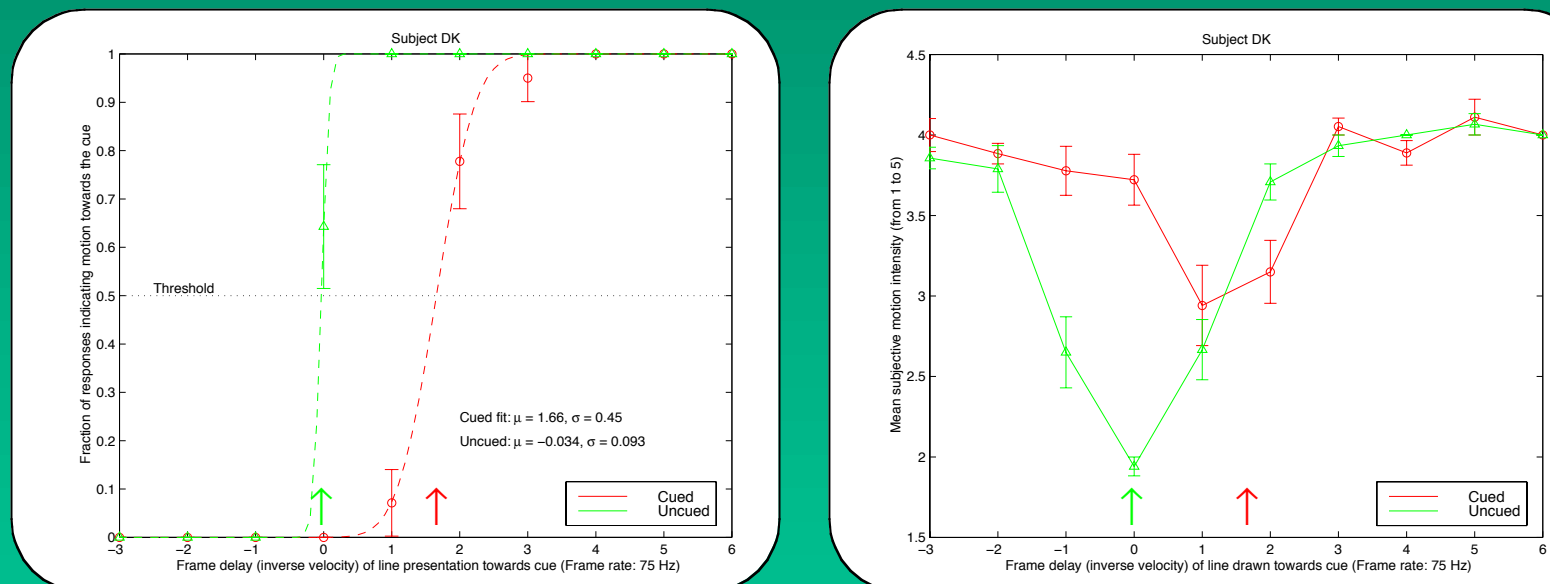
Human area MT+ is recruited by imagined motion (Goebel, et al., 1998) as well as by stationary stimuli producing illusory or implied motion (Tootell, et al., 1995; Zeki, et al., 1993; Kourtzi & Kanwisher, 2000). These studies show that MT+ is recruited when static stimuli are perceived as moving. Recently, Heeger, et al. (1999) showed that MT+ responds more strongly to gratings moving in a single direction than to opponent gratings for which no motion is perceived. This shows that MT+ is more strongly recruited by moving stimuli that are perceived as moving than by moving stimuli that are perceived as static. To further assess the perceptual dependence of MT+, we present a case that dissociates stimulus motion from motion perception. We use the line motion illusion (Hikosaka, et al., 1993) to produce illusory motion whose perception can be eliminated or diminished with the addition of physical motion in the opposite direction.

References
 Goebel, R., Khourram-Sefat, D., Muckli, L., Hacker, H. & Singer, W. The constructive nature of vision: direct evidence from functional magnetic resonance imaging studies of apparent motion and motion imagery. *European J Neurosci* 10:1563-1573.
 Heeger, D.J., Borsoi, G.M., Demb, J.B., Seidemann, E. & Newsome, W.T. 1999. Motion opponency in visual cortex. *J Neurosci* 19:7162-7174.
 Hikosaka, O., Miyachi, S. & Shimizu, S. 1993. Voluntary and stimulus-induced attention detected as motion sensation. *Perception* 22:517-526.
 Kourtzi, A. & Kanwisher, N. 2000. Activation in human MT/MST by static images with implied motion. *J Cog Neurosci* 12:48-55.
 Tootell, R.H., Reppas, J.B., Dale, A.M., Look, R.B., Sereno, M.I., Malach, R., Brady, T.J. & Rosen, B.R. 1995. Visual motion aftereffect in human cortical area MT revealed by functional magnetic resonance imaging. *Nature* 375:139-141.
 Zeki, S., Watson, J.D. & Frackowiak, R.S.J. 1993. Going beyond the information given: the relation of illusory visual motion to brain activity. *Proc R Soc Lond Ser B* 252:215-222.

Line motion illusion



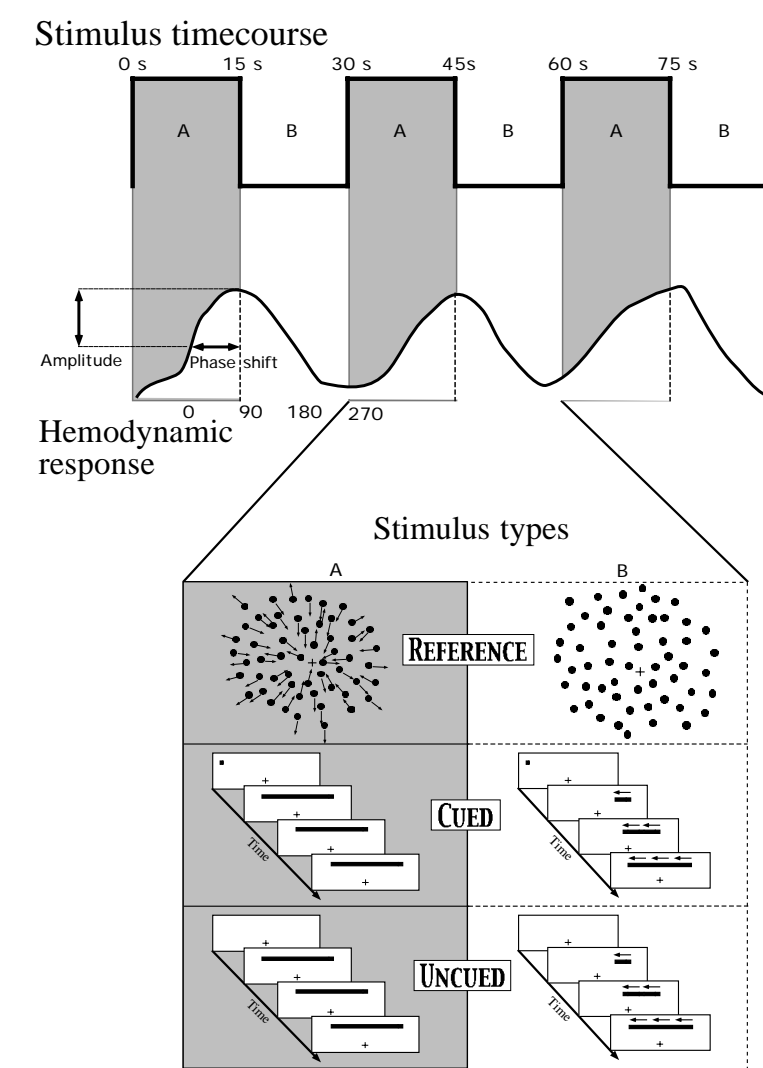
When the presentation of a line is preceded by a nearby spatial cue, the line appears to emanate from the cue and move away from it. This is the line motion illusion or motion induction effect. The strength of the effect may be determined by actually drawing the line with some velocity towards the cue to cancel the perceived illusory motion. These effects are illustrated above and quantified below.



Subjects viewed lines drawn at one of a number of randomly interleaved velocities, with or without preceding cues, and their 2AFC task was to determine the direction in which they perceived the stronger motion. The abscissa represents the frame delay or inverse of the line velocity. For example, at a frame delay of 2, the line was drawn in three sequential video frames towards the cue (if present). The basic effect of the illusion is evident for static lines (frame delay = 0): this subject responded randomly in the uncued case but always indicated that the line moved away from the cue in the cued case. The velocity cancellation threshold is the velocity that must be added opponent to the illusory motion such that the subject is equally likely to indicate either of the two directions of perceived motion.

In this task, the subject was instructed to rate the perceived strength of motion on a scale of 1 (static) to 5 (definite motion). The subject's impression of motion intensity reached a minimum near the cancellation thresholds for the cued and uncued stimuli.

Stimulus



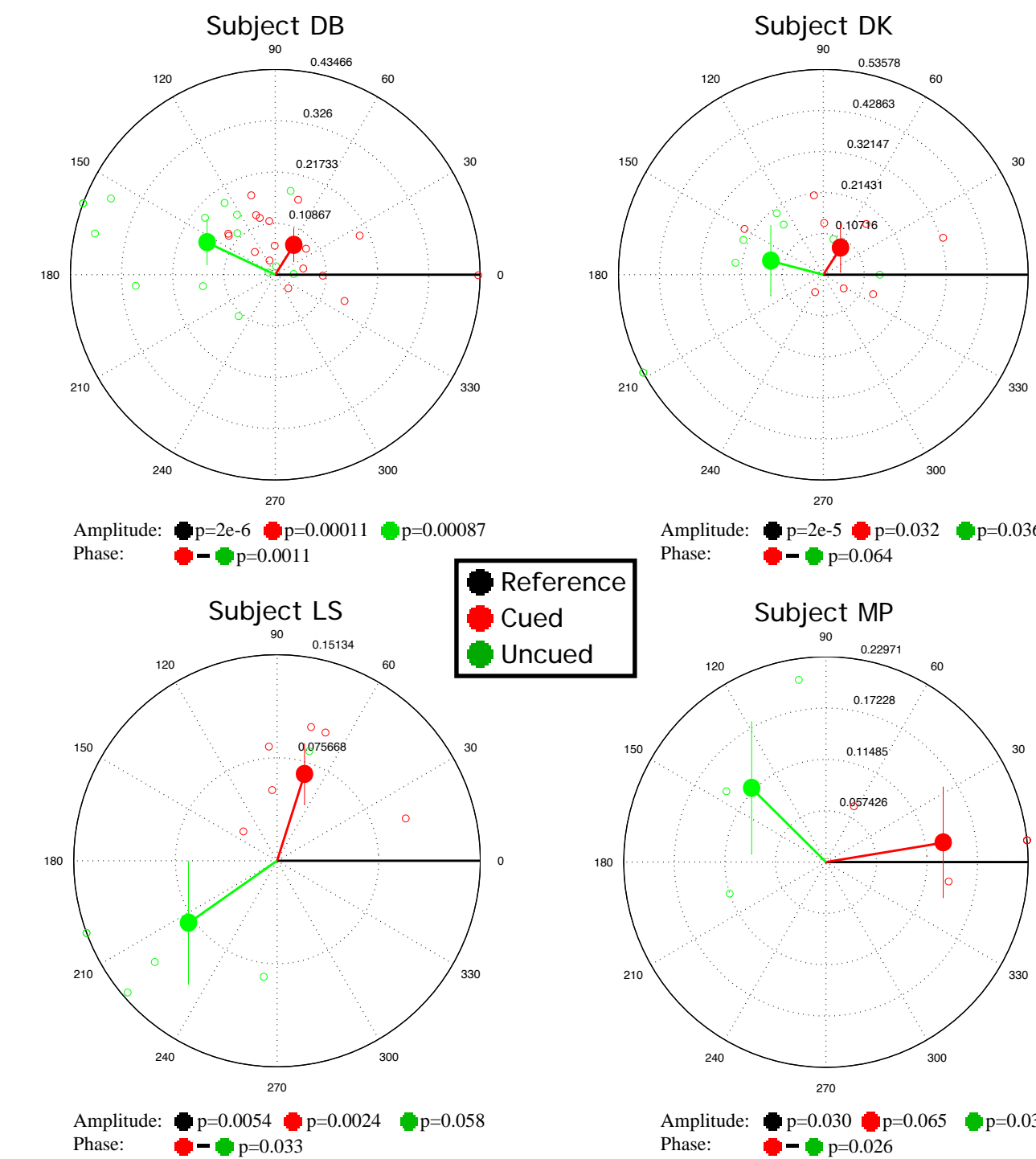
Hypothesis

MT+ is more correlated with perceived motion than with stimulus motion. The chart below demonstrates the stimuli and their hypothesized MT+ responses. Note that if the perception of motion is reversed with the addition of the cue, the idealized responses in the cued and uncued conditions should be 180° out of phase. The two types of stimuli are otherwise identical except for the presence or absence of the cue.

Stimulus period	A	B
Line type	Static	Moving
Cued		
Physical motion	Little	Yes
Perceived motion	Yes (illusory)	Little (cancelled)
Hypothesized MT+ response		
Uncued		
Physical motion	No	Yes
Perceived motion	No	Yes
Hypothesized MT+ response		

Results

The graphs below show the data for four different subjects. The small open circles represent the phase angle (relative to the reference scan phase) and the amplitude (in percent modulation) of the mean response within the MT+ region of interest for a single experimental scan. Each scan type was measured several times within a scanning session and replicated across different scanning sessions. The large filled circles represent the vector mean phase and amplitude of all the individual scans in each condition. As predicted, the responses to the cued and uncued conditions were essentially opposite in phase, indicating that the cue caused an inversion of motion perception that was independent of the stimulus motion. Our analysis has revealed some evidence of a phase drift during the cued scans that may explain their apparent phase lag, but further investigation is required to confirm this. Other data indicate that early visual areas, unlike MT+, do not exhibit this phase reversal effect.



Conclusion

When the motion content of perception differs from the motion content of the stimulus, human MT+ activity is more correlated with the motion of perception than with the motion of the stimulus.

Methods

Scanning parameters
 •GE 1.5 T Scanner with a custom multiphase surface coil
 •Bite bar for head restraint
 •GE EPI Sequence, TR=3.0 sec, TE=40 ms, FA=90
 •6 oblique slices, 5 cm thick separated by a 0.5 mm gap
 •3.125 x 3.125 x 5 mm voxel volume
 •4:12 min scan: 12 sec blank period then eight 30-sec stimulus cycles

Data analysis
 •Subtract linear trend from each voxel time series and divide by its mean intensity
 •Select ROI as the subset of voxels at the anatomical location of MT+ whose responses to a radial dot motion reference scan are highly correlated ($r > 0.5$) with the stimulus frequency
 •Fit sinusoid of stimulus frequency to the time series of each voxel and calculate the vector average phase and amplitude of the voxels within the ROI for each experimental condition
 •Compute vector average phase and amplitude response for the individual experiments in each condition (reference, cued or uncued) from all scanning sessions.

Statistics for each subject
 •Amplitude: Test whether the response amplitude for each experimental condition is greater than zero with a one-tailed t-test on the amplitude components of each measurement projected in the direction of the mean response for that condition.
 •Phase: Test whether the phases of the cued and uncued conditions differ using a two-tailed t-test on their amplitude components projected in the mean reference scan direction.

Details

Display: Stimuli were presented on an LCD display calibrated to deliver gray scale luminositites ranging from approximately 1.6 to 139.2 cd/m² viewed through 10x binoculars at a total path distance of approximately 4.57 m. The entire display subtended approximately 35 x 26° of visual angle.

Reference Scan: Subjects fixated while viewing a field of high contrast (97.8%) small (0.18°) dots with a density of about 1.5 dots/cm² confined to an annulus between 1.05 and 10.5° from the fixation point. During the first 15 sec of each cycle (A), the dot field radially expanded and contracted at 7.3°/sec. During the second 15 sec of each cycle (B), the dots were static.

Line motion stimuli: Two sets of 13 parallel lines in both the upper and lower hemifields were used to try to maximally activate MT+. See the diagram to the right for dimensions. This same stimulus was also used for the psychophysical tests described above. The presentation velocity resolution was limited by the frame rate of the display, and it was therefore not always possible to present a velocity precisely at the measured velocity cancellation threshold. However, since the threshold is strongly dependent on the contrast of the lines for contrasts below 10%, the threshold could be tuned with an adaptive procedure to an integral number of frames by varying the luminosity of the lines and background while the subjects were in the MRI scanner. This ensured that the stimulus velocity would be as close as possible to the cancellation threshold for each subject. The contrast of the lines varied from approximately 3.6 to 97.8%. The cues were presented at the maximum intensity, and their contrast ranged from 63.9 to 97.8%. No cues were presented during the uncued experiments, but the stimuli were otherwise identical.

Timecourse: For the first 15 sec of each cycle (A), the lines appeared in a single video frame. During the second 15 sec of each cycle (B), the lines appeared in several sequential video frames starting at the end farthest from the cue (if present) and moving towards the line by the cue. When present, the cue preceded the line by 150 ms and remained illuminated for 150 ms. Each line remained illuminated for 400 ms. New stimuli appeared after a random interval of 1 to 1.5 sec. Subjects were instructed to fixate the fixation point and to decide in which direction each line appeared to move. No responses were made during the scans.

Stimulus Dimensions

