

Differential brain activity states during the perception and nonperception of illusory motion as revealed by magnetoencephalography

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We studied visual perception using an annular random-dot motion stimulus called the racetrack. We recorded neural activity using magnetoencephalography while subjects viewed variants of this stimulus that contained no inherent motion or various degrees of embedded motion. Subjects reported seeing rotary motion during viewing of all stimuli. We found that, in the absence of any motion signals, patterns of brain activity differed between states of motion perception and nonperception. Furthermore, when subjects perceived motion, activity states within the brain did not differ across stimuli of different amounts of embedded motion. In contrast, we found that during periods of nonperception brain-activity states varied with the amount of motion signal embedded in the stimulus. Taken together, these results suggest that during perception the brain may lock into a stable state in which lower-level signals are suppressed.

racetrack illusion | visual motion perception

Visual motion has been studied using random-dot stimuli for many years (1, 2). In these stimuli, a random distribution of dots is displayed every few milliseconds. In each successive display or frame, most of the dots are displayed in new, randomly generated, positions. However, some percentage of the dots is displaced by a fixed distance in a particular direction. These coherently moving dots produce a motion signal in the direction of the displacement that can be perceived by subjects, as long as the percentage of coherently moving dots is above some threshold value. Typically, if none of the dots move in a coherent direction—that is, all dots move randomly from frame to frame—then no motion is perceived. More recently, a stimulus has been described in which motion is often perceived in the absence of any coherence between dots (3). This stimulus, referred to as the “racetrack,” consists of successive displays of random dots confined to an annulus. When no coherent motion exists, subjects often perceive rotary motion, which spontaneously flips in direction. Interestingly, the direction of perceived motion does not depend on the specific dot patterns shown. For example, on separate viewings of the same stimulus, a subject's time courses of the direction of perceived motion (which flip between clockwise and counter clockwise) are uncorrelated (4). In other words, a sequence of frames showing random dots may elicit clockwise perception in one viewing, but counter clockwise in another viewing.

In the study reported here, we used magnetoencephalography (MEG) to measure the brain activity of subjects as they viewed the racetrack stimulus. Because perception of rotary motion is uncorrelated with the particular features of any particular racetrack stimulus, we were able to analyze brain activity under conditions of perceptual awareness of motion and of non-awareness of motion independently of the stimulus that subjects viewed. We show here that brain activity in the posterior left hemisphere varied with perceptual awareness, when no coherent motion signal was available in the stimulus. Furthermore, we found that although brain activity differentiated states of per-

ception equally during stimuli with any of the motion coherences we studied (5–30%), perception did not increase until 10% dot coherence. We also show that the brain carries information about the amount of coherence in the stimulus, but only in the case that visual motion was not perceived. These results suggest that during perception, the brain may lock into a state with a reproducible activity pattern (5) in which lower-level features of the stimulus may be ignored or explained away (6, 7).

Results

Motion Perception. Subjects viewed the racetrack stimulus, an annulus of randomly placed dots whose positions varied over time (Fig. 1A). In some trials, the locations of all dots from frame to frame in the display were uncorrelated from their previous positions. In other trials, some percentage of the dots (5–30%) moved coherently: that is, through some fixed angle (Fig. 1B). All subjects reported seeing rotary motion under dot-coherence percentages ranging from 0 to 30%. In nearly all trials, periods of clockwise rotation and counter-clockwise rotation perception were intermixed with periods of no stable motion perception (the exceptions being that two subjects always perceived motion of one direction or the other at all times during the 30% motion-coherence trials). An example of the response of one subject to the 0% coherent dot stimulus is shown in Fig. 2A. Table 1 shows the mean length of time subjects indicated perception of motion or no motion for each of the dot coherences. In general, the mean length of perception of motion in any one direction was relatively stable across dot coherences until coherence reached 30%, in which case the mean length of time increased appreciably. Mean durations of periods where no motion was perceived went down as motion coherence went up. Interestingly, although there was no global motion signal in the 0% coherence stimulus, subjects reported a perception of rotational motion of the dots. As expected, the percentage of time that motion was perceived increased as dot coherence increased (Fig. 3, solid line).

Additionally, subjects were more accurate in correctly identifying the direction of motion at higher dot coherences. We cross-correlated each subject's response with the actual direction of the correlated dots, denoting χ as the maximum value of the cross-correlation function. (At 0% dot coherence, subject responses were cross-correlated with a simulated sequence of directions randomly generated in the same manner as the actual sequences.) The dashed line in Fig. 3 shows the relationship between χ and dot coherence.

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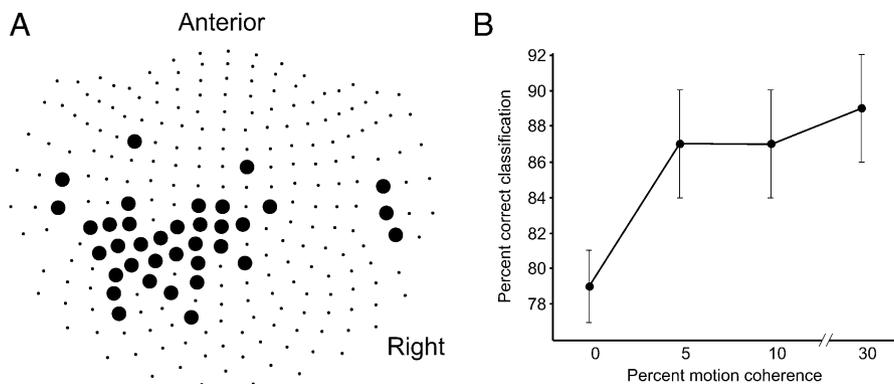


Fig. 4. Brain activity differences between perceptual states. (A) Location of sensors whose activity showed a significant difference between epochs of motion perception and epochs of no motion perception. Large circles in the sensor map indicate sensors with activity significantly different between perception and no perception portions of the trial. (B) Circles show how well patterns of brain activation could be used to classify whether or not the data were taken from a period of motion or no motion perception, using stepwise linear discriminant analysis. Error bars indicate \pm SEM.

90% in the case of 30% coherence. Table 2 shows classification results from individual subjects.

Neural Activity Related to Dot Coherence During Periods of Motion Perception and No Motion Perception. We tested whether neural activity recorded at each sensor varied, as a function of the dot coherence, under the conditions that motion was perceived or was not perceived. We found that in the cases that motion was perceived, only 3 of 248 sensors (1%) showed activity that varied with dot coherence. In the cases that motion was not perceived, however, 48 sensors (19%) recorded activity that differed between dot coherences. The locations of sensors with activity significant for dot coherence during perception and nonperception are shown in Fig. 5A (white triangles and black circles, respectively). The fact that sensors did not show significant changes in activity related to dot coherence in the perception condition could be attributed to their mean activity not varying with coherence, high within group variance, or some combination of both of these factors. We tested these possibilities by calculating the mean and SD of MEG signal for each sensor, across trials, for each coherence and perceptual condition. We

found that during nonperception, those sensors showing significant effects of coherence (black circles in Fig. 5A) had an average range of 41.1 fT across coherences. Those same sensors showed an average range of only 9.8 fT across coherences during motion perception. These values were highly significantly different (t test, $P < 0.00001$, $n = 48$ sensors). In contrast, within-group SD did not vary appreciably across perceptual conditions. During nonperception, the mean within-group SD of the 48 significant sensors was 56.5, 51.4, 54.9, and 59.3 fT for dot coherences of 0, 5, 10, and 30%, respectively. In the same sensors during motion perception, those values were 53.5, 53.8, 49.5, and 59.3 fT (values at 0, 5, and 30% coherence were not significant in t tests, $P > 0.3$; values at 10% coherence were significantly different at $P < 0.05$). These results indicate a similarity of activity across coherence conditions during motion perception.

Finally, we tested how patterns of neural activity varied with motion coherence. We again used a stepwise linear discrimination analysis to classify epochs of data as one of four motion coherences (0%, 5%, 10%, or 30%). If classification in this case was found to be high, this would be an indication that patterns of brain activity varied with, or carried information about, motion coherence. We found that for every subject who viewed motion coherences above 0%, classification of motion coherence was higher during epochs when motion was not perceived. Across subjects, the average correct classification of motion coherence was significantly greater than chance (59%; t test, $P < 0.05$; chance classification was 25%) during epochs when motion was not perceived (Fig. 5B). However, classification of coherence was much lower during periods of motion perception, not differing significantly from chance (34%; t test, $P = 0.09$). Classification was significantly higher during nonperception than periods of motion perception (t test, $P < 0.05$). In the classification analyses (Figs. 4B and 5B), sensors entered into the stepwise classifier were primarily a subset of those that showed significant activity in the ANCOVA (Figs. 4A and 5A), likely reflecting redundant information carried by neighboring sensors.

Discussion

A number of visual stimuli have been developed that attempt to dissociate the stimulus form from perceptual awareness (8). We show in this article the first neural signals recorded during the viewing of a novel stimulus, the racetrack, which at times elicits the perception of rotary motion (3). We recorded MEG signals during times of motion perception and nonperception under conditions of various, underlying, "true" motion strengths: from no motion signal to an underlying motion signal so strong that it elicited perception over 90% of the time. MEG signals represent

Table 2. Motion coherence classification results

Motion coherence (%)	Subject	Percent of correct classification
0	1	90
0	2	86
0	3	73
0	4	79
0	5	91
0	6	70
0	7	96
5	3	100
5	4	82
5	5	93
5	6	84
5	7	88
10	3	97
10	4	69
10	5	100
10	6	81
10	7	100
30	3	83
30	5	87
30	6	100

cols were approved by the Institutional Review Boards of the University of Minnesota and Minneapolis Veteran's Affairs Medical Center.

Stimulus. The racetrack stimulus consisted of a changing display of white dots (on a black background) whose positions were confined to an annulus (Fig. 1A). Every 35 ms, the dots were redrawn in new positions, with the condition that they were distributed evenly across the annulus. In different trials, different proportions of dots were redrawn in random locations and the rest moved coherently (i.e., through a constant angle) in either a clockwise or counter-clockwise direction (Fig. 1B). The percents of correlated dots (motion coherences) used were 0%, 5%, 10%, and 30%. During each trial of motion coherence greater than zero, motion direction (clockwise or counter-clockwise) was determined randomly every 3 s, with an equal probability of each direction at each 3-s interval.

We tailored various parameters of our stimuli to each subject, so that during a prerecording trial using fully randomized dots (0% coherence), each saw rotation approximately half of the time. The inner diameter of the annulus ranged from 14 to 19°, and the outer diameter ranged from 19 to 27°. The number of dots in each frame of the stimulus was constant for each subject, but varied from 56 to 100 across subjects. For all subjects, the stimulus was displayed at 85 Hz, and the dots were randomly changed every three frames (every 35 ms). Stimuli were projected onto a screen 60 cm above the subjects' eyes by a liquid crystal display projector located outside of the recording room.

Task. Subjects viewed the racetrack stimulus while fixating at a cross in the center of the display. On each trial, the stimulus was presented for 120 s during which time the subjects pressed one of two buttons on a mouse indicating what direction of motion they perceived, if any. Subjects pressed and held a button with the index or middle finger of their right hand if they perceived counter-clockwise or clockwise motion, respectively. During periods in which they perceived no rotary motion, subjects did not press either button. Subjects were instructed to fixate the cross located at the center of the annulus and to refrain from blinking for the duration of the stimulus. Two subjects viewed only the 0% coherence stimulus. The other five subjects each viewed the 0% the stimulus for two trials and viewed one trial each of stimuli with 5, 10, and 30% motion coherence.

MEG Recording. Subjects viewed the racetrack stimulus as the MEG data were acquired from a 248-channel axial gradiometer MEG system (Magnes 3600 WH; 4D-Neuroimaging), which was located within an electromagnetically shielded room to reduce environmental noise. MEG data were acquired at 1,017.25 Hz and low-pass filtered (400 Hz cutoff) during acquisition. The state of three buttons was sampled at the same rate as the MEG data (at 1,017.25 Hz) and was incorporated directly into the MEG data file to ensure correct time alignment. The data were preprocessed as follows. First, the cardiac artifact was removed by the method of event synchronous subtraction (15). A representative heartbeat from the data was used as a template. This template was then slid through the data, sample by sample, and the correlation between the template and the overlapping data segment was cal-

culated at each point. Sharp peaks in the resulting correlation output reflected heartbeat detections. For each cortical MEG channel, the beats were averaged to obtain a clean averaged waveform. The averaged beat was then subtracted from the raw data at each occurrence of the cardiac artifact. After cardiac correction, environmental noise was removed using 4D Magnes software. The 4D Magnes acquisition system uses a combination of magnetometer and gradiometer reference coils to monitor environmental noise (16). These coils were positioned sufficiently above the head to receive little brain signal, but close enough to receive similar environmental noise to what is seen by the cortical channels. Environmental noise was removed from the cortical channel recordings by subtracting a weighted sum of the reference recordings from each cortical channel. After environmental noise reduction, the data were then high-pass filtered using a 0.1-Hz cutoff.

Analysis. Analyses of neural data were performed on average MEG signal from individual channels. We first divided the time course into periods of clockwise motion perception, counter-clockwise motion perception, and no motion perception (Fig. 2A), which we define as epochs. From each unique epoch that lasted at least 1 s, we took the average MEG activity of each sensor from the middle 500 ms of the period (Fig. 2B). No data were used from epochs lasting less than 1 s.

To find sensors whose activity differed between periods of motion perception and no motion perception, we performed an analysis of covariance, using these mean MEG signals as the dependent variable, perception of motion (a binary variable) as the factor, and time of recording as a control covariate. This analysis was performed across subjects and across motion coherences.

We then used a stepwise linear discriminant analysis (17) to test how well patterns of MEG signals could classify periods of motion perception. To do this, we used the mean MEG signals from the epochs described above. Each sensor's data were treated as an independent variable in the discriminant analysis. This analysis was performed using the stepwise discriminant analysis in the SPSS statistical package (Version 17; SPSS Inc.), using the default *F* values (*F* to enter = 3.84, *F* to remove = 2.71), and leave-one-out cross validation.

To determine how neural activity varied with motion coherence, we performed an analysis of covariance on the activity of each sensor, using motion coherence as the factor, and time of recording as a control covariate. This analysis was performed across all five subjects who viewed stimuli with coherent motion, and was repeated separately for epochs in which motion was perceived and epochs during which no motion was perceived. We then used a similar stepwise linear discriminant analysis (as above) to classify epochs based on their motion coherence (based on the pattern of MEG data, each epoch could be classified as 0%, 5%, 10%, or 30% coherent). This analysis was performed separately for each subject, and separately for groups of epochs in which motion was perceived and for which motion was not perceived.

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