

Neural mechanisms of unconscious visual motion priming

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Abstract The neural correlates of the motion priming were examined in normal young subjects using event-related brain potentials (ERPs) and functional magnetic resonance imaging (fMRI). Visual motion perception can be unconsciously biased in favor of a particular direction by a preceding motion in that direction. Motion priming first involved an enhancement of ERP amplitude about 100 ms following the onset of motion. The amplitudes of ERP components after 350 ms were also increased. The fMRI results suggest that the early-latency effect reflects modulation of neural responses in extrastriate cortex. Higher-level visual processing areas, including cortical regions MT/MST and the intraparietal cortices were also activated. The findings provide direct evidence that unconscious priming of motion perception is the result of interaction of direction-selective neural responses to motion stimuli. The results cannot be accounted for by refractoriness of neural responses, but instead support a theory of motion priming based on motion opponency, as proposed in computational models.

Keywords: visual motion, unconsciousness, event-related potential, functional MRI.

The perception of a visual event can be biased, or primed, by prior exposure to related visual information. For instance, visual motion perception can be biased in favor of a particular direction by a preceding stimulus moving in that direction^[1,2], even when the priming stimulus is not visible^[3]. Thus, visual motion priming can provide a probe into unconscious processes. However, the neural mechanisms underlying unconscious visual priming are poorly understood. Using brain imaging techniques, we now show that the unconscious biasing of visual motion perception results from the interaction of direction-selective neural responses in early cortical visual processing areas.

We presented observers with sine-wave gratings that moved ambiguously to either the left or the right. When such a target stimulus is preceded by a prime that moves unambiguously in one direction, motion direction is disambiguated^[2,4]. Such motion priming occurs without the observer's awareness and typically decays to a chance level over a prime-target interval of 1 s^[4]. Two possible neural mechanisms could be responsible for this phenomenon. First, priming could reflect neural refractoriness

between the motion signals evoked by the prime and the target^[5,6]. This results in a temporary decrease in sensitivity of detection of the second motion direction. If so, the amplitude of the associated neural signals should decrease as the interval between the two motion stimuli is reduced. Alternatively, motion opponency models postulate that neural signals that favor the same direction combine, whereas those that prefer opposite-motion directions subtract from each other^[4,7–9]. Therefore, motion priming should be associated with larger neural responses as the prime-target interval is reduced. We evaluated these opposing predictions in two experiments using event-related brain potentials (ERPs) and functional magnetic resonance imaging (fMRI).

1 Methods

(i) Subjects. 17 young adults (mean age 22) participated the two experiments using ERPs. Each had vision of at least 20/40. Two of the seventeen subjects performed the same tasks in fMRI experiments.

(ii) Tasks. Subjects judged the apparent motion direction(s) of single (Experiment 1) or double motion jumps (Experiment 2) of sine-wave gratings (4-cycle/degree, visual angle 4.2°). Movement was induced by implementing a phase shift between successive frames—either clearly to the left or the right (phase shift of 90°), or completely ambiguous, sometimes appearing to move to the left and sometimes to the right (phase shift of 180°). When shown rapidly one after another, the sequence produced a vivid impression of leftward or rightward motion. The frame sequences for leftward, rightward, and ambiguous motion are shown in fig. 1(a). In Experiment 1, subjects were required to press the left or right button when they perceived the single motion jump to the left or right. In Experiment 2 they were asked to press the left button if two successive motion jumps were perceived to be in the same direction, and the right button if motion jumps were in opposite directions. The instructions to press the left and right buttons were switched for about half of the subjects.

The interval between the jumps (prime-target interval) was varied between 200, 400, and 1000 ms. For each interval, the control condition consisted of two motion jumps consistently perceived in the opposite directions unambiguously. All the control and priming conditions were presented in a random order. The total number of responses of perceived motions in the same direction is nearly equal to those perceived in the opposite directions.

(iii) ERP Recording. The electroencephalogram (EEG) was recorded from 14 scalp electrodes at Fz, Cz, Pz, Oz, C3, C4, P3, P4, T5, T6, O1, O2, OL, and OR. The EEG was amplified with filter 0.1–100 Hz and continuously sampled (250 Hz/channel) for off-line analysis. ERPs were selectively averaged to the last apparent mo-

tion frame (target). Each ERP component was measured relative to a 200 ms baseline preceding the onset of the stimuli. Peak amplitudes and latencies were computed for the P1 (50—150 ms), N1 (100—200 ms), and P3 (250—550 ms) components.

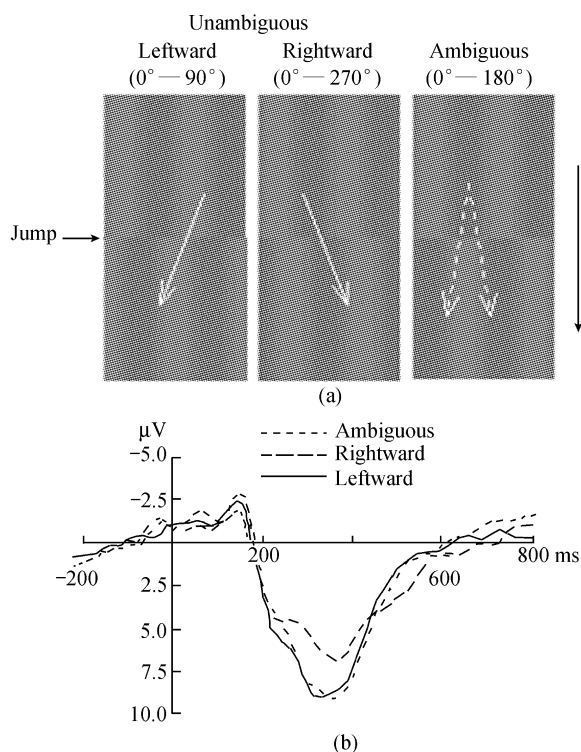


Fig. 1. (a) Sketch map of paradigm of single visual motion; (b) grand average ERP waveform elicited by single motion.

(iv) Functional magnetic resonance imaging. fMRI scans were obtained from two of the subjects who also participated in ERPs. They performed part of the motion tasks used in ERP experiments. One condition includes strong priming (double jumps with a 200 ms prime-target interval) and another the non-priming condition (single jumps, left, right, ambiguous). Between these conditions, subjects view stationary sine-wave gratings. There were eight imaging runs for each subject. A GE 1.5 Tesla magnet was used to obtain T2*-weighted gradient echo echo-planar images with blood oxygen level dependent (BOLD) signals. Twenty-two 5-mm whole brain volumes of axial slices were acquired for each subject (repetition time = 3 s, echo time = 40 ms, flip angle 90°) and analyzed using multiple regression^[10,11]. Brain regions showing significant signal enhancement to motion perception were defined as voxels with $Z > 3.09$ (corrected) for the overall experimental effect.

2 Results

(i) ERPs Experiment 1. Single leftward (right-

ward) motion was consistently perceived within and across subjects (99.3% in the 90° left) phase shift, and 99.3% in the 270° (rightward motion) condition). Thus under these conditions, motion direction was perceptually unambiguous. In the 180° phase shift condition, however, leftward motion was reported 56.6% of the time within and across subjects. This counter-phase condition was perceptually ambiguous.

There were no significant differences in ERP component amplitudes or latencies between the unambiguous leftward and rightward motion conditions. However, the amplitude of the P3 component elicited by ambiguous motion was significantly smaller than that evoked by unambiguous motion, $F_{2,32} = 8.248$, $P < 0.005$ (fig. 1(b)).

(ii) ERPs Experiment 2. ERPs to the target in the motion priming conditions were compared to those in the control motion trials for each of the three prime-target intervals. With an interval of 200 ms between the prime and target motion jumps, relative to the control condition, motion priming was associated with significantly more positive-going ERP activity at both early (approximately 100 ms, $F_{1,16} = 5.898$, $P < 0.05$) and late (350 ms, $F_{1,16} = 11.373$, $P < 0.005$) stages of processing following the onset of the target motion. When the delay interval was increased to 400 ms, P3 components associated with target ERP were significantly more than those in the control condition ($F_{1,16} = 14.408$, $P < 0.005$), but not at the earlier 100 ms latency ($F_{1,16} = 3.698$, $P > 0.05$). At a prime-target interval of 1000 ms, there were no significant differences between the ERPs for motion priming and control conditions at either early or late stages of processing following target onset (fig. 2(b)).

These ERP results were well correlated with the psychophysical findings. The degree of motion priming decayed over the prime-target interval: target motion was perceived to move in the same direction as the prime on 96%, 80% and 54% of trials was at the 200, 400, and 1000 ms prime-target intervals, respectively. (A 100% response proportion of same-direction responses represents perfect priming, whereas 50% correspond to a chance level of same-direction responses, or lack of priming). These results therefore justify labeling of the three prime-target intervals as leading to “priming” (200 ms interval), “weak priming” (400 ms), and “no priming” (1000 ms), respectively. The ERP difference waveforms between the motion priming and control conditions at the three prime-target intervals. The difference waveform represents the neural activity evoked by the target stimulus specifically associated with motion priming. Both the early 80—130 ms ($P < 0.05$) and late 250—500 ms ($P < 0.001$) phases of ERP activities were positively enhanced in the strong priming condition (200 ms prime-target interval) compared to the weak (400 ms) and no priming (1000 ms) conditions.

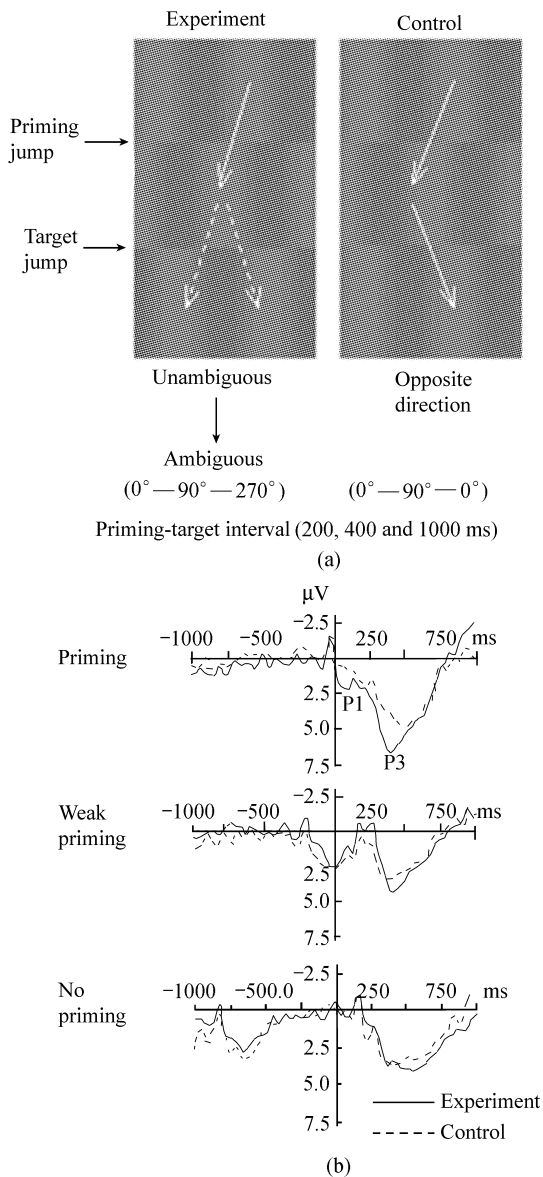


Fig. 2. (a) Sketch map of paradigm of double motion; (b) grand average ERP waveform elicited by double motion.

Fig. 3(a) shows topographic maps of the difference ERP waveforms partitioned by different time epochs of ERP activity. 98 ms following the target motion, there was significant priming-related enhancement in activity in posterior scalp electrode sites. 386 ms following the target motion, the difference appeared more extensively in posterior sites, but included more anterior areas as well. Because of the limited spatial resolution of scalp ERPs, no strong claims can be made for the spatial localization of these neural effects. However, the P1 component in the visual ERP has been localized to extrastriate cortex^[12]. Thus the observed regional distribution of priming-related

ERP activity suggests that motion priming has its first effect in extrastriate cortical areas associated with relatively early stages of visual processing.

(iii) fMRI experiment. In a further attempt of the spatial localization of such an effect, we examined the fMRI responses to the same motion priming condition. Because of the limited temporal resolution of the fMRI method, neural responses associated with prime and target motions cannot be separated reliably. In addition, the strongest motion priming effect only lasts about 200 ms. Thus, having the ERPs subjects performed the same tasks inside of the MR scanner, we were mainly interested in activation location during the perceptual judgment of motion directions. We compared MR signals associated with perceptual judgments of motion direction with the perception of stationary sine-wave gratings. Fig. 3(b) shows the resulting activation patterns of a subject overlaid on a high-resolution structural MRI of the subject's brain. Significant ($P < 0.001$) voxels associated with processing motion direction were found in ventral occipital, MT/MST, superior temporal, and intraparietal cortices.

3 Discussion

The perceived direction of motion of a target stimulus that moves ambiguously to the left or the right can be disambiguated by an immediately preceding prime that moved consistently in only one direction. This form of visual motion priming, which occurs outside of awareness, is fast acting, lasting about 1000 ms. Our ERP results reveal that visual priming of 2D motion direction was associated with enhanced positivity of neural responses at posterior scalp sites at both early (100 ms) and late (350 ms) stages of processing following the onset of target motion. This enhancement was the greatest at a short prime-target interval of 200 ms. The ERP positive enhancement associated with motion priming decayed at longer intervals, and was eliminated at 1000 ms. Judgments of the perceived direction of motion of the target showed a similar time course.

The viewpoint of neural refractoriness predicted reduced temporal interaction between the motion signals evoked by prime and target as the prime-target interval^[5,6], and should express as reduction in amplitude of ERP components. In fact, the opposite was observed in the present experiment. Motion priming was associated with higher amplitude of the P1 and P3 at the short 200 ms prime-target interval compared to the 400 ms interval. On the other hand, computational models of human vision propose motion opponency as a mechanism for processing motion direction^[7,8]. These models assume that the neural responses of leftward or rightward motion-detecting neurons subtract from those of opposite-motion direction neurons, resulting in a net response whose strength and sign determine the direction of motion perception. However, direct neural evidence for motion opponency

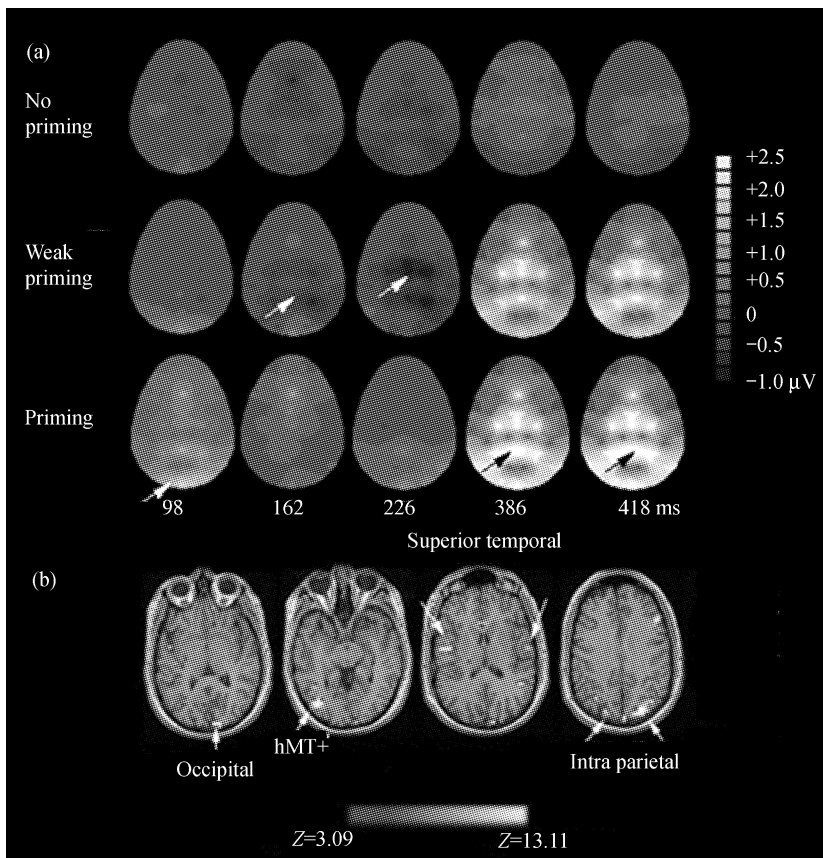


Fig. 3. (a) Topography of ERP difference wave was obtained by subtracting control group from experimental group; (b) fMRI map in the double visual motion condition.

has been demonstrated in monkey's single-unit recording^[13,14], and human fMRI^[15]. Consistent with previous findings, our ERPs associated with perceptual decisions of motion directions can be better explained as a result of combined directional-selective neural responses. We found that ambiguous motion perception (e.g. either left or right motion) was associated with lower-amplitude ERP activity than was unambiguous motion direction. This is consistent with the view that an ambiguous motion percept (left/right by chance) is the result of the combined neural responses to opposing motion directions, which is reduced due to subtraction. The ERP results from Experiment 2 support a temporal interaction model of motion priming based on motion opponency or motion energy^[4,9]. In the priming conditions, the neural response to the priming motion favoring one particular motion direction was combined with a weak neural response associated with ambiguous motion. Such a summation of neural signals is weakened as the time interval between the two motion stimuli increases, consistent with our finding of

reduced ERP amplitudes (fig. 3(a)). In contrast, the control condition motion occurred in opposite directions, resulting in a subtraction of neural responses, as reflected in smaller ERP amplitudes (fig. 2).

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