Misbinding of color and motion in human early visual cortex: Evidence from event-related potentials

Yanyu Zhang [a,b,c,d], Xilin Zhang [a,b,c,d], Yizhou Wang [e], Fang Fang [a,b,c,d,*]

[a] Department of Psychology and Key Laboratory of Machine Perception (Ministry of Education), Peking University, Beijing 100871, PR China
[b] Beijing Key Laboratory of Behavior and Mental Health, Peking University, Beijing 100871, PR China
[c] Peking-Tsinghua Center for Life Sciences, Peking University, Beijing 100871, PR China
[d] PKU-IDG/McGovern Institute for Brain Research, Peking University, Beijing 100871, PR China
[e] National Engineering Laboratory for Video Technology, School of Electronics Engineering and Computer Science, Peking University, Beijing 100871, PR China

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One of the central tasks for the visual system is to integrate visual features into objects, which is referred to as the binding problem. To study the binding mechanisms, it has been suggested to use phenomena of feature misbinding to separate active feature binding from feature co-occurence. Taking advantage of a steady-state misbinding of color and motion, we performed psychophysical and event-related potential (ERP) adaptation experiments to investigate the neural mechanisms of the misbinding (i.e., the active

1. Introduction

Different visual features (e.g., color, motion, and orientation) of an object are processed to a certain degree by different functional specialized modules of cerebral cortex. For example, some V4 neurons respond selectively to color, and V5 neurons encode various aspects of motion information (Fellaman & Van Essen, 1991;

cortex has been suggested to be involved in the reentrant processes, as evidenced by functional magnetic resonance imaging (fMRI), transcranial magnetic stimulation (TMS), and neuropsychological studies (Colby & Goldberg, 1999; Esterman, Verstynen, & Robertson, 2007; Friedman-Hill, Robertson, & Treisman, 1995; Koivisto & Silvanto, 2012; Robertson, 2003; Shafritz, Gore, & Marois, 2002) showing that this area could modulate feature bind-

the test) as a function of the test speed. For each condition, the psychometric values at the Þve test speeds were Þt with a cumulative normal function. We interpolated the data to Þnd the speed expected to be perceived as stationary. The speed difference between the misbinding condition and the control condition was the CCMAE from adaptation to the color-motion misbinding in the effect part, and the speed difference between the correct binding condition and the control condition was the CCMAE from adaptation to the correct color-motion binding.

2.6. ERP experiment

The ERP experiment aimed to measure the color-contingent motion adaptation effect in the brain. It consisted of 36 blocks of 36 trials, 6 blocks for each adaptor. Similar to the psychophysical experiment, each block started with a 30 s pre-adaptation (Fig. 1C). On a trial, after a 5-sec topping-up adaptation and a 0.2Ð0.4 s blank interval, a test stimulus was presented for 0.4 s. Subjects needed to make a 2-AFC judgment on a near-threshold luminance change (increment or decrement) of the test stimulus for attentional control. The luminance change occurred between 0.2 and 0.4 s after the onset of the test stimulus. It was determined by QUEST staircases (Watson & Pelli, 1983) before the experiment to ensure that subjects performed equally well for all the adapting and test stimuli (75% correct). For each adaptor, each of the two test stimuli was presented on 108 trials. The order of the three adaptation conditions/blocks was randomized across subjects.

2.7. EEG recording

EEG was recorded from 64 scalp sites using Ag/AgCl electrodes mounted in an elastic cap (Brain Products, Munich, Germany) according to the extended international 10Ð20 EEG system. We recorded VEOG (vertical electro-oculogram) from an electrode positioned above the right eye and HEOG (horizontal electro-oculogram) from an electrode at the outer canthus of the left eye. The signals from the 64 scalp electrodes were referenced online to an electrode on the tip of the nose and were re-referenced ofßine to the mean signal from the left and right mastoids. Impedance for all the electrodes was kept below 5 k X. EEG was ampliÞed with a gain of 500 K, band-pass Þltered from 0.05 to 100 Hz, and digitized at a sampling rate of 1000 Hz.

2.8. ERP data analysis

We used Brain Vision Analyzer (Brain Products, Munich, Germany) to analyze EEG signals induced by the test stimuli. EEG data were Þrst low-pass Þltered at 30 Hz and then epoched from 100 ms before stimulus onset to 250 ms after stimulus onset. EEG epochs were corrected for baseline over the 100 ms interval immediately before stimulus onset. Eye-blink artifacts were semi-automatically corrected using the method proposed by

2.9. Source localization

Estimation of dipole sources was performed using the Brain Electrical Source Analysis (BESA) algorithm (BESA version 5.3). For the misbinding and correct binding conditions, dipole modeling was carried out based on the difference waveforms between the same and opposite trials. We Þrst used one dipole with free location and orientation to Þt the distribution of the difference waveform in the 68Ð110 ms interval for the misbinding condition and in the 57Ð79 ms interval for the correct binding condition, respectively. The four-shell ellipsoidal head model was used. The initial starting position of the dipole was randomly chosen and using different starting locations yielded a highly similar dipole conÞguration. Then, we localized a dipole within area V1 to best account for the distribution of the difference waveform in the 68Ð110 ms interval for the misbinding condition and a dipole within area V2 to best account for the distribution of the difference waveform in the 57Ð79 ms interval for the correct binding condition, respectively.

3. Results

3.1. Psychophysical results

In the psychophysical experiment, we measured the CCMAE from adapting to the correct binding or the misbinding of color and motion in the effect part. After pre-adaptation and topping-up adaptation, a test stimulus (i.e., red or green moving dots) was presented brießy, and subjects made a 2-AFC judgment on the motion direction of the test stimulus (upward or downward) (Fig. 1B).

Because data from the red and green test stimuli showed a similar pattern, they were pooled together for analysis. Fig. 2A shows the psychometric functions in the three adaptation conditions. In the control condition, subjects adapted to the induction part only. Their performance was almost perfect for all the test stimuli (about 50% level for the 0 /s stimulus, good judgment for the 0.3 /s and 0.6 /s stimuli), demonstrating that adaptation to the induction part only generated little CCMAE in the effect part area. However, after adapting to the correct binding of color and motion, the psychometric function showed a leftward shift. This result demonstrated that subjectsÕ perception of the moving direction of the tests was biased opposite to the physical direction of the adapting dots (with the same color as the test). Strikingly, after adapting to the misbinding of color and motion, the psychometric function exhibited a rightward shift, showing that subjectsÕ perception of the direction of the tests was biased opposite to the perceived (rather than the physical) direction of the adapting dots. These results demon-

(68Ð110 ms after stimulus onset). However, for the correct binding condition, the C1 peak phase (57Ð79 ms after stimulus onset) exhibited signiÞcant difference. No signiÞcant difference was found in the control condition.

3.3. Dipole modeling of intracranial source

We carried out dipole modeling of intracranial sources of the C1 component with the BESA algorithm, based on the difference waveforms between the same and opposite trials. We searched for one dipole with free location and orientation that could best explain the distribution of the difference waveform over the 68Ð110 ms interval for the misbinding condition and over the 57Ð79 ms interval for the correct binding condition, respectively. In the misbinding condition (Fig. 4A), a dipole located in V2 (Talairach coordinates: −7, −90, −14, BrodmannÕs area 18) was identiÞed. It could account for 91.1% of the variance in the C1 sch7rg]TJ -2.7867 T1.8365.TD [(ivoltag)-40967(diptribut)ona c

Electrophysiological studies in monkey subjects have found that color and motion are processed in different, yet mutually connected cortical pathways (Fellaman & Van Essen, 1991). It is widely accepted that the color processing pathway consists of the blobs of V1, the thin stripes of V2, and V4, and the motion processing pathway includes the layer 4B of V1, the thick stripes of V2, and V5/MT^{+} (Bartels & Zeki, 2000; Sincich & Horton, 2005). Meanwhile, neurons selective for both color and motion direction were found in V1 (Gegenfurtner et al., 1996). Recently, using fMRI, Seymour, Clifford, Logothetis, and Bartels (2009) applied multivariate pattern analysis (MVPA) to decode subjectsÕ perception when they viewed color-motion conjunctions. It was shown that the physical feature conjunctions could be decoded from fMRI spatial activation

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