Perceptual asynchrony: motion leads color

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It is widely accepted that motion and color are processed in separate brain areas of primates. Numerous studies on monkeys suggest that neural mechanisms responsible for motion processing respond faster than those for color. Recent studies on humans, however, provide contradictory evidence. Is this discrepancy due to a gap between species (animal vs. human), or between measures (neurophysiological vs. behavioral)? To help resolve this issue, event-related potentials were acquired as human participants viewed motion and color stimuli. Results indicated that the physiological response evoked by motion arose earlier than that by color, which is consistent with previous findings in animals. This temporal precedence of motion signal processing over color was corroborated in a parallel behavioral experiment. *NeuroReport* 17:1159–1163 © 2006 Lippincott Williams & Wilkins.

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Introduction

Physiological research in primates suggests that different attributes, especially motion and color, are processed by different parts of the visual system [1,2]. Motion and color travel from the retina to the cortex primarily through the magnocellular and parvocellular pathway, respectively. In the cortex, motion receives specialized processing in area MT whereas color processing occurs in area V4 (V8) [3–5].

Given the fact that motion and color information processing have different and relatively independent pathways, it would not be surprising if they also demonstrate different temporal properties. Indeed, single-unit studies in animals suggested that neurons specialized for motion processing respond earlier and faster than those for color in both the retina and lateral geniculate nucleus [6,7]. At the cortical level, it was found that neurons specialized for motion signals in V2 activate earlier than those for color [8]. It was also reported that area V4 activates later than MT and MST [9].

This motion-led–color asynchrony can, however, be reversed or eliminated when human observers perceive joint occurrences of motion and color. A striking phenomenon, motion–color asynchrony, was recently demonstrated by Moutoussis and Zeki [10]. Participants viewed moving squares with oscillating changes in both the color and the direction of motion, the temporal phase of which varied in different trials. Participants had to indicate the combined perception of color and direction (e.g. green up, red down or green down, red up). Results showed that observers tended to associate the change in direction of motion together with the color change that occurred about 60–80 milliseconds (ms) later. This kind of 'miss-binding' was interpreted as color being processed faster than motion. Similar phenomena were observed in other paradigms [11,12]. Nishida and Johnston [13], however, used a different response mode and showed that motion and color were perceived without asynchrony. Bedell and colleagues [14] also proposed a two-stage model to account for the different observations on color–motion asynchrony, with the first stage dependent on the sensory processing and the second stage dependent more on task.

Clearly, there is a discrepancy between monkey neurophysiological data and human perception regarding the temporal processing properties of color and motion. This discrepancy could be the result of either an interspecies difference or the different variables measured. To better understand and hopefully resolve this discrepancy, it is imperative to obtain both neurophysiological and behavioral data from the same species (monkey or human), using the same stimuli. This is what we did in the current study. We investigated the temporal properties of motion and color processing using both event-related potentials (ERPs) (neurophysiological data) and psychophysical (behavioral data) measures in human participants.

Methods

Participants

All participants were paid volunteers (age: 20–28 years) with normal or corrected to normal visual acuity and normal color vision. Nineteen (6 women) participated in the ERP test; 15 (seven women) participated in the behavior test, and among them six (1 woman) had also participated in the ERP test.

Stimuli and paradigm

Event-related potential experiment

The stimuli were displayed on a 17-inch cathode-ray tube color monitor, with a refresh rate of 60 Hz. As depicted in Fig. 1, two checkerboards were presented symmetrically to the left and right of the blue fixation cross (0.33° in diameter) at a viewing distance of 86 cm. Both checkerboards were $4^\circ \times 4^\circ$ and their centers were 4° away from the fixation cross. The check size was $0.4^\circ \times 0.4^\circ$. The checkerboards were made of light gray (Commission Internationale de l'Eclairage coordinate: [0.287, 0.325]; luminance: 10.5 cd/m^2) and dark gray ([0.292, 0.245], 1.62 cd/m^2) checks. In the standard condition, either of the two checkerboards could move toward the fixation cross, at a speed of 12°/s; or change its color: from light gray to green [0.291, 0.587] and from dark gray to red [0.623, 0.330] without a luminance change. (The equiluminant parameters were selected for each participant at the beginning of the experiment with the minimum flicker procedure.) Each of the four standard conditions described above occupied 21.5% of the total trials; and the remaining 14% were for the target condition in which the fixation cross could change to a 0.67° blue-filled circle without any change in the checkerboards. The five types of stimuli were presented in a pseudo-random order. In each trial, the stimuli were presented for 50 ms, followed by a random interstimulus interval (ISI), ranging from 450 to 850 ms. During the ISI, the static light/dark gray checkerboards in both visual fields were continuously visible.

Participants were seated comfortably on a sofa in a dim and quiet room. They were trained to focus on the fixation cross during the experiments. The participants' task was to press a button in the response pad accurately and rapidly with the thumb of their dominant hand when they detected the fixation change. There were 40 runs, each containing 70 trials for each participant in the experiment.

Behavioral experiment

In the behavioral test, stimuli were the same as that in the ERP experiment except that the ISI was lengthened to 950–1350 ms. In addition to the primary task of detecting the fixation target, a secondary task was added: participants pressed another button on the response pad with the nondominant hand when they detected any change in either visual field. Each participant had four runs, each containing 70 trials.

Electroencephalogram recording

The electroencephalogram (EEG) data were acquired by a 32-channel EEG system (NeuroScan Inc., El Paso, Texas, USA). The signal was recorded with tin electrodes mounted in an elastic cap according to the '10–10' system (see Fig. 2b). The electrode placed in the left mastoid served as the physical reference (the data were re-referenced with the algebra average of signals from the left and right mastoid electrodes offline). EEG activity within the band range of 0.01–100 Hz was amplified 20 000 times and digitized at 500 Hz in a sampling resolution of 12 bit. EEG and electrooculogram traces were monitored on line and runs with discernible eye movements and muscle activity were aborted and re-acquired.

The EEG data recorded were digitally band-pass filtered within 0.1–40 Hz. ERP epochs were extracted from the original EEG within the span of 200 ms before and 800 ms after the trigger signal, which was sent by the stimuli program and time-locked with the onset of the stimulus for each trial. The baseline for amplitude measurement was defined as the mean voltage of the 200 ms prestimulus period. Artifact rejection was performed and the epochs were averaged for the five conditions separately.

As the P1 in motion condition was much smaller and may be contaminated with noise, we removed the noise with a

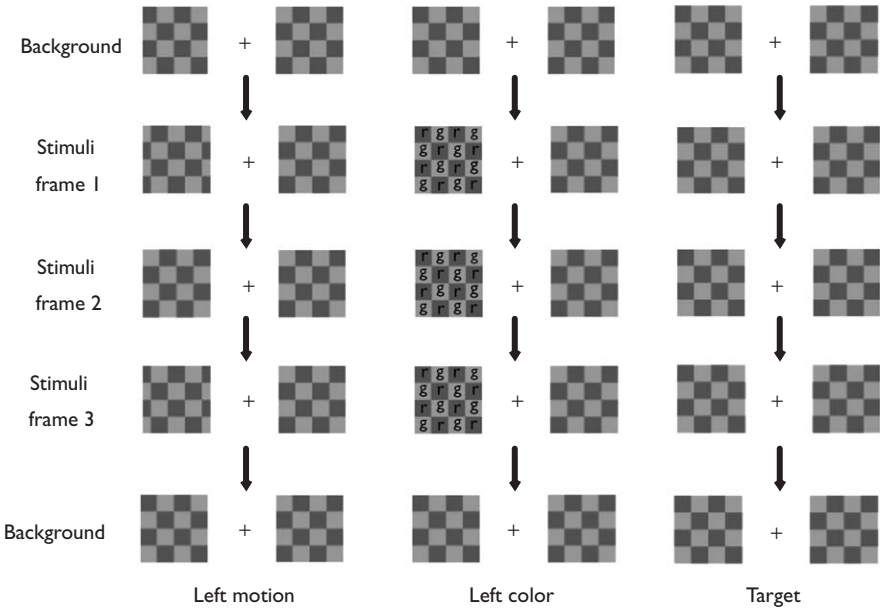

Fig. 1 Schematic depiction of the experimental conditions. Shown here are two example stimuli with color and motion changes occurring in the left visual field and the target detection condition. Different colors were represented by different letters (r or g) here.

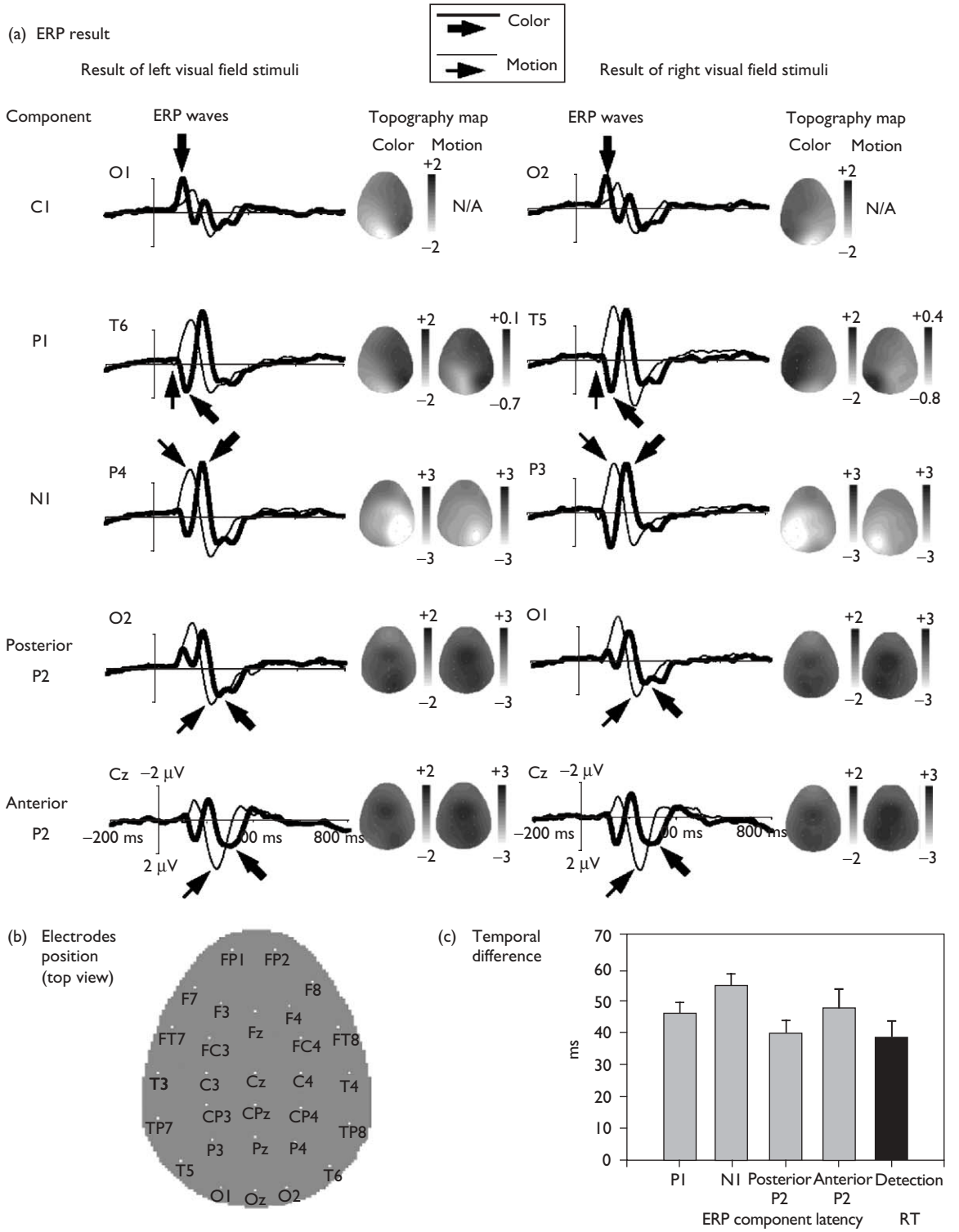

Fig. 2 Experiment results. (a) Grand average event-related potential (ERP) waveforms and top-view topographical maps. (b) Position of the electrodes, seen from the top. (c) Latency differences between motion and color generated ERP components. Difference in reaction times to motion and color changes in the behavioral test are also plotted here for comparison.

high-pass filter (0.5 Hz, 24 dB, in all electrodes for both color and motion) in the topographical map. A zero temporal shift option was used to keep the temporal information intact.

Data analysis

In the ERP experiment, the latency and amplitude of component C1 was compared by paired *t*-tests between the left and right visual field. For other components, peak

latencies and amplitudes were analyzed by repeated-measures analysis of variance with two factors: visual field (left vs. right) and visual attribute (color vs. motion). The contralateral electrodes that had the most salient signal for certain components were chosen for the analysis (see Fig. 2a).

In the behavioral experiment, correct responses between 150 and 850 ms were treated as hits; all others were taken as false alarms. Accuracy was corrected according to the signal detection theory. Accuracies and reaction times of the secondary task were submitted to repeated-measures analysis of variance with two factors: visual field and visual attribute.

Results

Event-related potential

Participants performed well in the fixation task (percent of hit: 98.2%, SE 0.5%) during the ERP recording.

In the color change conditions, a C1 negativity peaking at 120 ms (SE 2.3 ms) could be observed in the ERP waves, which was distributed mainly in the middle and ipsilateral (relative to the visual field of the stimuli) part of the occipital areas (Fig. 2a). Neither the latency nor the amplitude of C1 had significant difference between left and right visual field stimuli. No corresponding component could be observed in the motion conditions. The C1 component is believed to reflect activities from V1 [15]. As the ERP signal often reflects the summation of multiarea activity, however, the lack of a C1 does not always mean no V1 activation [16]. Although it has been argued that motion can bypass V1 [17–19], it will not be further discussed in this paper because it is not critical to our main topic.

Component P1 was observed in both the motion and color conditions (Fig. 2). It was distributed mainly in the scalp area contralateral to the stimuli in both conditions. No significant difference was observed between the left and right visual field in either peak amplitude or latency. The peak amplitude of P1 in the motion condition was significantly smaller than that in the color condition [0.521 ± 0.112 vs. $2.189 \pm 0.228\,\mu V$; $F(1,18)=52.83$, $P<10^{-5}$]. The peak latency of P1 for the motion condition was significantly shorter [98 ± 3.0 vs. 144 ± 2.4 ms; $F(1,18)=205.37$, $P<10^{-10}$]. Component P1 is believed to reflect activity in the extrastriate cortex [20]. In our experiment, the signal from motion was faster than the color signals by about 46 ms (SE 3.2 ms) (Fig. 2). This ERP result is consistent with neurophysiological findings of shorter response latencies of MT neurons than those of V4 neurons [9].

N1 components were also observed in both the motion and the color conditions (Fig. 2a). In both conditions, it was distributed mainly in the contralateral posterior area. The peak amplitude of N1 was not significantly different between motion and color conditions. Like P1, however, the peak latency of N1 was significantly shorter for the motion condition than the color condition [156 ± 3.0 vs. 212 ± 3.1 ms; $F(1,18)=201.47$, $P<10^{-10}$]. The peak latency difference was a little more pronounced in N1 than that in P1 (54 ± 3.8 vs. 46 ± 3.2 ms; $F(1,18)=6.38$, $P=0.021$; see Fig. 2).

Two peak distributions of P2 components in both the motion and color conditions exist: a posterior one and an anterior one (Fig. 2a). The posterior P2 was contralateral to the stimulated visual field while the anterior P2 was situated along the midline. The motion condition generated a larger amplitude than the color condition in anterior P2 [3.284 ± 0.280 vs. $2.188 \pm 0.339\,\mu V$; $F(1,18)=17.68$, $P<10^{-3}$], whereas no significant difference was found in the amplitude of posterior P2. For both components, the peak latencies of the motion condition were shorter than those of the color condition [posterior P2, 240 ± 3.3 vs. 280 ± 4.5 ms; $F(1,18)=76.82$, $P<10^{-7}$; anterior P2, 246 ± 3.6 vs. 288 ± 5.5, $F(1,18)=70.94$, $P<10^{-6}$].

Behavioral results

In the separate behavioral detection task, the percent of hits was quite high (all above 90%) and did not differ across conditions. For reaction time, observers responded faster to motion than to color [388 ± 17.1 vs. 427 ± 16.2 ms; $F(1,15)=51.991$, $P<10^{-5}$]. The mean difference was 38 ms (SE 5.3 ms), which is close to the peak latency differences observed in the ERP signals (Fig. 2c). No interactions were found between the visual field and attributes.

Discussion

In all ERP components generated by both motion and color changes, the latencies were consistently shorter for motion than for color stimulation. This suggests that in human observers, the neural processing of motion information precedes that of color. Does the discrepancy between different studies [9–14,21] mentioned earlier reflect different type of measures? Why does the timing of neural events and perceptual temporal judgments suggest a different order of operations? One proposal is that motion is processed faster but perceived slower [10]. Here, perception time was defined as the end result of processing of the system as a whole. It is true that single neuron properties do not always equal the whole perceptual procedure. ERP data given here, however, gave a holistic evaluation of brain activity, and even the last component in the ERP data suggested that motion leads color. What is more, the 'end result' could be highly dependent on the tasks, which had been noted by some researchers [13,14,22]. Naturally, because speed in the physical sense can be derived on the basis of time and distance, if we measure the speed of the signal processing via time, then the implicit assumption is that the two signals go the same 'distance'. This assumption may not be correct when different tasks were employed in comparing the temporal properties of color and motion processing. It may be responsible for the inconsistencies in the literature, which were designed for various research purposes. If we want to get a general consequence of the temporal order in neural information processing for motion and color, we need another standard that favors neither of the two. Simple detection would be a good candidate: it is the basic initial process for either motion or color perception and a comparison at this stage would be most straightforward. The behavioral task used here was designed with this criterion in mind. The task required only the detection of the color or motion signal. It examined early processing and avoided further bias caused by various high-level task demands. With this simple task, the motion signal leads the color signal by about the same magnitude in RT of the perceptual task as in the ERP measures. As participants needed to respond on the basis of their perceptual experience, we may say motion was perceived faster than color in humans in a general sense.

Evolutionarily speaking, rudimentary motion processing is probably most important for the survival of an animal, be

it a predator or prey. Color information is also important, but may be less immediate than that of motion. There has been no neurophysiological data to show color's precedence over motion processing in animals. In the case of human observers, because of the frequent exposure to colors and color names, it is possible that color enjoys an advantage when the task requires semantic association and representation. This idea needs further investigation.

We used ERP as the neurophysiological tool of choice because it can measure signals from multiple cortical areas simultaneously with excellent temporal resolution, especially when the activation sequence does not always follow a hierarchical arrangement [16]. Although ERP does not provide precise localization of neural activity, it can provide a distribution of the signals. The topographical maps (see Fig. 2) show that each component of P1, N1 or P2 had a similar distribution in the color and motion conditions. It is suggested that the corresponding components in the two conditions have similar neural sources, and a temporal comparison is reasonable. In a separate behavioral test, similar temporal differences in RT are also consistent with the ERP result. A similar comparison has been found in other studies [23]. In previous ERP studies, there have been debates on the components of chromatic and achromatic stimuli (for a review see [24]). Some researchers observed that certain components of chromatic stimuli would invert compared with their achromatic counterpart, using gratings as stimuli, while others did not see this using checkerboard stimuli.

Another concern is in reference to spatial frequency – is the temporal difference observed here unique to the spatial frequency used in the study? To address that concern, we performed a control ERP experiment in which we varied the fundamental frequency of the stimuli. The new stimulus could have a higher (3.75 c/deg) or lower (0.25 c/deg) fundamental frequency than the original test (1.25 c/deg). The results showed that for both frequencies the motion signal still leads color.

To rule out the possible asymmetrical attention effects in the two conditions, observers performed a fixation task irrelevant to the color or motion change in our ERP study. If the observers attended the color or motion stimuli, the ERPs could be different. It is not very likely that attention to the color or motion stimuli would, however, change the ERP signals at the early stages of processing. Evidence exists that attention modulation of motion and color processing occurs at relatively late stages [20], and attention primarily affects the amplitude of the ERP signal rather than the latency. In a recent study by Armstrong and colleagues [23], ERPs initiated by motion and color stimuli were measured in both hearing and deaf participants whereas their responses were relevant to the perception of motion or color of the stimuli. Although motion–color asynchrony was not the focus of their study, their results did show an earlier onset for motion than for color stimulus in N1 component. Similar results were also shown in a study on visual development by Mitchell and Neville [25].

Conclusions

With direct ERP measurements and behavioral studies of signal processing, the temporal asynchrony of motion and color processing was evaluated. Results show that motion information leads color information in time in human perception at the early stages of visual processing.

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