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Author(s)	Kimura, Motohiro; 木村, 元洋; Katayama, Jun'ichi et al.
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**Independent processing of visual stimulus changes in ventral and dorsal stream features
indexed by an early positive difference in event-related brain potentials**

MOTOHIRO KIMURA, JUN'ICHI KATAYAMA, HARUMITSU MUROHASHI

Graduate School of Education, Hokkaido University, Sapporo 060-0811, Japan

Manuscript correspondence to:

Motohiro Kimura

Graduate School of Education, Hokkaido University

Kita-11 Nishi-7, Kita-ku, Sapporo 060-0811, JAPAN

Tel & Fax: +81-11-706-3113

E-mail: m-kimura@edu.hokudai.ac.jp

Abstract

In event-related brain potential (ERP) studies of brain activity using a visual S1-S2 matching task, change stimuli elicit a posterior positive component with a latency of 100-200 ms. To elucidate the hierarchical organization of the processing of a visual stimulus change based on multiple stimulus features, ERPs were recorded in 12 participants performing an S1-S2 matching task with stimuli defined by color (mediated by the ventral stream) and motion direction (mediated by the dorsal stream). Each trial consisted of two sequentially presented stimuli (S1-S2), where S2 was either (1) the same as S1 (i.e., no-change), (2) different from S1 in color only (color change), (3) different in motion direction only (motion direction change), or (4) different in both color and motion direction (color-motion direction change). These trials were presented in random order with equal probability, and the participants were asked to respond to one of these trials in separate blocks. Relative to the no-change stimulus, the three types of change stimuli elicited posterior positivities. The scalp-topography of change positivities differed according to the feature changed. In addition, the amplitude and scalp-topography of change positivities in response to a conjunction change were the respective sums of those in response to changes in the corresponding single features. These results suggest that the change detection system reflected by the change positivity is separate for each feature dimension, and these operate independently.

Key words: Event-related brain potential (ERP), Visual change detection, Ventral stream feature, Dorsal stream feature.

Independent processing of visual stimulus changes in ventral and dorsal stream features

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1. Introduction

Visual change detection is an important cognitive function that facilitates adaptation to the external environment. The measurement of event-related brain potentials (ERPs) in many psychophysiological studies has provided a powerful means to investigate the timing and hierarchical organization of change detection processing in the human brain (e.g., Wang et al., 2003, 2004). ERP studies using an S1-S2 matching paradigm have reported robust ERP components that are thought to be related to visual change detection. When two sequentially presented visual stimuli (S1-S2) conflict with each other in certain features, a central negative component at around 250-350 ms (N270) is elicited after the onset of S2 (e.g., Cui et al., 2000; Kong et al., 2000; Wang et al., 2001; Wang et al., 2003, 2004; Yang and Wang, 2002). In addition, Kimura et al. (in press) reported that, preceding N270, a posterior positive component with a latency of 100-200 ms ("change-related positive difference, CRPD, or change positivity") is elicited by a visual stimulus change. At present, the change positivity is thought to reflect visual-modality-specific change detection processing (Kimura et al., in press), while N270 is thought to reflect modality-non-specific change detection processing (Wang et al., 2002) in a visual S1-S2 matching task.

The concept of different cortical areas or 'channels' for the processing of specific visual

features has been largely supported by neurophysiological studies on primates (e.g., Merigan and Maunsell, 1993; Wilson et al., 1993), as well as by human functional neuroimaging studies (e.g., Corbetta et al., 1991; Zeki et al., 1991). These studies have confirmed that stimulus features necessary for object identification, such as color and shape, are processed in the occipito-temporal “ventral stream”, whereas stimulus properties such as spatial relationships and movement are processed in the occipito-parietal “dorsal stream” (reviewed in Ungerleider and Haxby, 1994). This form of dissociation was originally identified in the macaque monkey (e.g., Merigan and Maunsell, 1993; Wilson et al., 1993), but further studies also support its presence in the human brain (e.g., Ungerleider and Haxby, 1994).

In previous studies on the change positivity and N270, these notions have been extended to understand the nature of change detection processing. N270 can be elicited by changes in several features of visual stimuli, such as color (Wang et al., 2001; Wang et al., 2003, 2004), shape (Cui et al., 2000; Wang et al., 2003, 2004), position (Yang and Wang, 2002), and digit value (Kong et al., 2000). On the other hand, change positivities can be elicited by changes in color and shape (Kimura et al., in press).

The feature-specificity of the change positivity and N270 has been addressed more directly. Wang et al. (2003, 2004) reported that the N270 elicited by a feature-conjunction change (change in both color and shape) had two consecutive negative peaks. Further, the scalp-topographies of the N270 did not differ according to the feature changed, and had central distributions. The authors interpreted the two negative peaks as an index of the consecutive processing stages for the two-feature comparison. Thus, they concluded that the system reflected by N270 processes

changes in the two features in a serial manner. These results are consistent with the view that the change detection system reflected by N270 is a single system, and is shared for several feature dimensions.

In relation to the change positivity, Kimura et al. (in press) reported that the amplitude and scalp-topography of the change positivity elicited by a conjunction change (change in both color and shape) were the respective sums of those elicited by changes in the corresponding single features (color change and shape change). In addition, the topographies of the change positivities differed according to the feature changed. Although a precise localization of activation generators based on scalp-recorded ERPs may be difficult (e.g., on the basis of the 'inverse problem'), it is at least possible to infer the involvement of different generators from different ERP topographies (e.g., McCarthy and Wood, 1985). Thus, Kimura et al. (in press) concluded that the change detection system reflected by the change positivity could be separated on the basis of several features, and that the system independently processed changes in multiple visual stimulus features. Taken together, these results suggest that there exists a two-stage change detection system: feature-specific change detection systems operating in parallel, and a higher feature-non-specific change detection system operating in serial.

The feature-specific elicitation of change positivity is likely to be consistent with the notion of feature-specific 'channels' for visual change detection processing. However, such a feature-specific elicitation of change positivity has been examined only for changes in multiple ventral stream features (i.e., color and shape); no study has yet investigated the hierarchical organization of change detection processing between ventral and dorsal stream features.

Although Yang and Wang (2002) used a stimulus change in spatial location, which is thought to be processed mainly in the dorsal stream, the scenario of the combined use of dorsal and ventral stream features is yet to be addressed.

The present study has three principal objectives: first, to determine whether or not early change detection processing for a dorsal stream feature is also reflected by posterior positivity; second, to determine whether the scalp-topography of change positivity differs according to the feature changed; third, to determine whether additivities in amplitude and scalp-topography of change positivity such as those found in the use of multiple ventral stream features can be extended to ventral and dorsal stream features. To answer these questions, we recorded ERPs while participants performed an S1-S2 matching task with multi-feature stimuli representative of both ventral and dorsal stream features. Color was selected as a ventral stream feature and motion direction as a dorsal stream feature. Color has been reported to be processed prominently in ventral stream area V4 (e.g., Corbetta et al., 1991), and motion direction has been reported to be processed in dorsal stream area MT (e.g., Albright, 1984; O'Craven et al., 1997). If the change detection systems for ventral and dorsal stream features have a similar functional organization, then it should be expected that a change in motion direction is also manifested by the change positivity. In addition, if different neural populations are activated by stimulus changes in color and motion direction, the scalp-topography of change positivity should differ according the feature changed. Finally, if these neural populations are activated independently of each other, the amplitude and scalp-topography of change positivities elicited by a conjunction change (i.e., change in both color and motion direction) should be the respective sums of those elicited by

changes in the corresponding single features (color change and motion direction change).

2. Methods

2. 1. Participants

Twelve students (6 women, 6 men; age range = 21-28 years, $M = 22.4$ years) participated in this experiment. All participants were right-handed and had normal or corrected-to-normal vision. Written informed consent was obtained from each participant after the nature of the study was fully explained.

2. 2. Stimuli

Nine types of moving circle were used as stimuli. Each moving circle (visual angle $1.2 \times 1.2^\circ$ from 100 cm view distance) was defined by color (red, blue, or yellow) and motion direction (0.8° leftward, upward, or rightward from the center of the display), and presented at the center of a display against a black background. To make a smooth movement, the location of the circle was changed at each refresh of the computer display (120 Hz): i.e., the location of the circle was changed 12 times within 100 ms. Each trial consisted of two sequentially presented stimuli (Stimulus 1-Stimulus 2; S1-S2; 100 ms each) separated by a brief blank (400 ms), where S2 was either (1) the same as S1 (i.e., no-change; Nc), (2) different from S1 in color only (color change; Cc), (3) different in motion direction only (motion direction change; Mc), or (4) different in both color and motion direction (color-motion direction change; CMc). The intertrial interval between the onset of S1 and the next S1 was 1200 ms.

2. 3. Procedure

The experiment consisted of 16 blocks, each of which had 180 trials in which the four trial types were presented in random order with equal probability ($p = .25$). The participant's task was to respond selectively to one of the four trial types: no-change task (Nc task), color change task (Cc task), motion direction change task (Mc task), or color-motion direction change task (CMc task). All four tasks were performed four times by each participant, with the order randomized across participants.

The participant was seated in a reclining chair in a sound- and electro-shielded room. Each block was initiated with an instruction regarding the target type. Participants were instructed to press a button with the right thumb as quickly and accurately as possible when the target type was presented. Participants were also asked to focus on the center of the display, and to minimize any eye movement during trials. The procedure was repeated for each block.

2. 4. Recordings

An electroencephalogram (EEG) was recorded using an electrocap (Electro-Cap International) fitted with 25 silver-silver chloride cup electrodes placed at positions Fp1, Fp2, F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, T5, P3, Pz, P4, T6, PO7, PO3, POz, PO4, PO8, O1, Oz, and O2 according to the modified International 10-20 System. All electrodes were referenced to the nose tip. Blinks and eye movements were monitored with electrodes above and below the right eye (vertical electrooculogram, V-EOG) and at the right and left outer canthi of the eyes (horizontal electrooculogram, H-EOG). Electrode impedance was kept less than 5 k Ω . EEG and EOG signals were amplified, bandpass-filtered at 0.03-30 Hz, and digitized at 200 Hz.

A separate average was computed for each of the 16 conditions defined by the trial type (no-change, color change, motion direction change, and color-motion direction change) and task type (no-change task, color change task, motion direction change task, and color-motion direction change task) for each electrode location. Averaging epochs were 800 ms, starting 100 ms before and ending 700 ms after the onset of S2. Automated artifact rejection was applied to remove data epochs that were contaminated by blinks, saccades, or excessive muscle activity over 100 μ V in amplitude. Epochs with incorrect responses were also excluded. The averaged ERPs were corrected with respect to the mean amplitude baseline over the 100 ms that preceded the onset of S2.

2. 5. Data analysis

Behavioral performance was measured in terms of reaction time, percentage of correct responses (hit rate), and percentage of false alarms (false alarm rate) in the four tasks. Responses were scored as hits if they occurred within 100-700 ms of the onset of target S2. Responses to non-target S2 were classified as false alarms.

Considering possible contamination by stimulus selection effects (e.g., Anllo-Vento and Hillyard, 1999; Kasai et al., 2003; Smid et al., 1999), stimulus change effects were assessed among ERPs with equal task relevance: i.e., ERPs elicited by four S2 types as target and as non-target. In order to counteract the effects of the selection-related effects, the ERP data in response to non-target S2 were pooled according to the four trial types over task types. For the purpose of the present study, ERPs elicited by non-target S2, which were not contaminated by the effects of motor response and had a higher signal/noise ratio, were analyzed in detail. For ERPs elicited by non-target S2, to

estimate the stimulus change effects, the waveform elicited by the no-change stimulus was subtracted from those elicited by the three types of change stimuli (color change, motion direction change, and color-motion direction change). These difference waves were transformed into topographical maps. Based on the results of the topographical maps, electrodes were selected for statistical analysis: the parietal electrodes (Pz) where the posterior positivity to a change in motion direction was of maximum amplitude, and the left occipito-temporal electrodes (PO7) where the amplitude of posterior positivity to a color change was of maximum amplitude. To determine the significant elicitation of change positivities regardless of the change type, the mean amplitudes of ERP waveforms within 120-180 ms (posterior positivity in response to color change had peak amplitudes in this time window) and 180-240 ms time windows (posterior positivity in response to motion direction change had peak amplitudes) from the onset of S2 were quantified and subjected to a three-way analysis of variance (ANOVA) with the following factors: 2 Color change types (Change, No-change) × 2 Motion direction change types (Change, No-change) × 2 Electrodes (Parietal, Left occipito-temporal)¹.

To compare the scalp-distributions of the posterior positivities elicited by the three types of stimulus change, the mean amplitudes of the change – no-change difference waves within 120-180 ms and 180-240 ms were subjected to a two-way ANOVA with the following factors: 3 Change types (Color, Motion direction, Color-motion direction) × 13 Electrodes (T5, P3, Pz, P4, T6, PO7, PO3, POz, PO4, PO8, O1, Oz, O2).

To examine the additivity of the posterior positivity, a comparison was made between the empirical difference wave obtained by subtracting the ERPs elicited by the no-change stimulus

from those elicited by the color-motion direction change stimulus (CMc - Nc difference wave) and the modeled difference wave obtained by summing the difference waves obtained by subtracting the ERPs elicited by the no-change stimulus from those elicited by the color change stimulus and from those elicited by the motion direction change stimulus ((Cc - Nc difference wave) + (Mc - Nc difference wave)). The mean amplitudes of the empirical and modeled difference waves within 120-180 ms and 180-240 ms time window from the onset of S2 were quantified, and subjected to a two-way ANOVA with the following factors: 2 Difference wave types (Empirical, Modeled) x 13 Electrodes (T5, P3, Pz, P4, T6, PO7, PO3, POz, PO4, PO8, O1, Oz, O2).

3. Results

3. 1. Behavioral performance

Table 1 shows mean reaction times, hit rates, and false alarm rates for the four task types. Reaction times were longer when change stimuli were target (color change task, motion direction change task, color-motion direction change task) than when a no-change stimulus was target (no-change task) ($F(3,33) = 26.00, p < .001$). Multiple-comparison tests revealed that the reaction time for the color-motion direction task was longer than those for the no-change and color change tasks, and that the reaction time for the no-change task was shorter than those for the other three tasks. Hit rates were generally high among the four tasks, with no statistically significant differences between the tasks. False alarm rates in the color-motion direction task were higher than those in the other three tasks ($F(3,33) = 7.44, p < .001$).

Insert Table 1 around here.

3. 2. Event-related brain potentials

Fig. 1 shows the grand averaged ERPs elicited by the four types of S2 in four tasks (four midline electrodes: Fz, Cz, Pz, Oz). ERPs in response to all types of S2 were characterized by six components: a P1 at around 120 ms, an N1 at around 180 ms, a P2 at around 220 ms, an N2 at around 280 ms, and a late positive component (LPC) at around 400-500 ms from the onset of S2. The ERPs elicited by each target stimulus were mainly characterized by an enhanced negative component at around 200-300 ms (SN and N2b) and a parietal positive component at around 400-500 ms (P3b). For the purpose of the present study, ERPs elicited by non-target stimuli, which were not contaminated by large effects of target selection and motor response, were analyzed.

Insert Fig. 1 around here.

Stimulus change effects. Fig. 2 shows the grand averaged ERPs elicited by the four types of S2 as non-target (In order to counteract the effects of the selection-related effects, task types were pooled). In the 100-250 ms time window, ERPs in response to all types of S2 were characterized

by three components: a P1 component peaking at about 120 ms, an N1 component peaking at about 180 ms, and a P2 component peaking at about 220 ms from the onset of S2. In addition, compared to the no-change stimulus, ERPs elicited by change stimuli (i.e., color change, motion direction change, and color-motion direction change stimuli) shifted to a positive polarity over the P1, N1, and P2 latency range. Fig. 3 shows the topographical maps of the P1, N1, and P2 components elicited by a no-change stimulus. P1 had bilateral peaks in the occipital regions (O1 and O2), N1 had bilateral peaks in the temporal regions (T5 and T6), and P2 peaked in the occipital region (Oz).

Insert Figs. 2 and 3 around here.

Amplitude modulation as a function of stimulus change can be more clearly observed in difference waves (Fig. 4), which were obtained by subtracting the ERP elicited by the no-change stimulus from those elicited by the three types of change stimuli (color change, motion direction change, and color-motion direction change stimuli). A posterior positive component in the 100-250 ms time latency was observed regardless of the change type. The posterior positivity elicited by a color-motion direction change had larger amplitudes than those elicited by a color change or motion direction change. In addition, the peak latencies of the positivities differed according to the feature changed; posterior positivity in response to color change had an earlier peak latency than

that in response to motion direction change. The scalp-topographies of posterior positivities are shown in Fig. 5. The positivity elicited by a color change was bilaterally distributed over the occipito-temporal regions (PO7 and PO8), while that elicited by a motion direction change was maximal over the parietal region (Pz). These topographies of positivity, especially in relation to motion direction change, were different from those of the P1, N1, and P2 components.

Insert Figs. 4 and 5 around here.

The mean amplitude of averaged ERPs at the PO7 electrode where the positivity elicited by color change had a maximum amplitude, and the mean amplitude of averaged ERPs at Pz where the positivity elicited by motion direction change had a maximum amplitude, were compared. Mean ERP amplitudes within the 120-180 ms time window (where the positivity in response to color change was maximal) and 180-240 ms time window (where the positivity in response to motion direction change was maximal) are summarized in Table 2. The mean amplitudes were subjected to three-way ANOVAs (2 Color change types \times 2 Motion direction change types \times 2 Electrodes). For the 120-180 ms time window, significant elicitations of posterior positivity were supported by the main effect of Color change type ($F(1,11) = 6.62, p < .05$) and Motion direction change type ($F(1,11) = 7.44, p < .05$). The interaction of Color change type \times Motion direction change type was not significant. For the 180-240 ms time window, similar results were obtained.

Significant elicitations of posterior positivity were supported by the main effect of Color change type ($F(1,11) = 5.23, p < .05$) and Motion direction change type ($F(1,11) = 17.63, p < .01$). The interaction of Color change type \times Motion direction change type was also not also significant.

Insert Table 2 around here.

Topographical differences among posterior positivities for three change types. The scalp-distributions of the posterior positivities elicited by the three different stimulus changes (color change, motion direction change, and color-motion direction change) were compared more quantitatively by two-way ANOVAs (3 Change types \times 13 Electrodes). For the 120-180 ms time window, the analysis showed a significant interaction of Change type \times Electrode ($F(24,264) = 1.57, p < .05$). For the 180-240 ms time window, the analysis also showed a significant interaction of Change type \times Electrode ($F(24,264) = 3.44, p < .001$). Subsequent analysis revealed that the effects were due to the fact that the positivity in response to color change had bilateral peaks around the occipito-temporal regions (PO7 and PO8), while that in response to motion direction change peaked around the parietal region (P3, PZ, and P4). In addition, to confirm that the interactions did not result solely from a change in source strength, the amplitude values were reanalyzed after the data were normalized by vector length (McCarthy and Wood, 1985). For both time windows, the same analysis showed significant interactions of Change type \times Electrode

($F(24,264) = 1.91, p < .01$ for the 120-180 ms time window; $F(24,264) = 2.94, p < .001$ for the 180-240 ms time window).

Additivity of the posterior positivity. To investigate the extent of additivity of the posterior positivity, empirical difference waves were compared to modeled difference waves. Fig. 6 shows empirical difference waves elicited by a conjunction change (CMc – Nc difference wave) and modeled difference waves calculated as the sum of the difference wave according to each specific feature ((Cc – Nc difference wave) + (Mc – Nc difference wave)). Fig. 7 shows topographical maps of the difference waves. These figures highlight that the waveforms and the scalp-topographies of modeled difference waves are similar to those of empirical difference waves. Two-way ANOVA (2 Difference wave types x 13 Electrodes) on the mean amplitudes of the empirical and modeled difference waves within 120-180 ms and 180-240 ms showed no significant effect of Difference wave type ($F_s < 1$), as well as no significant interaction between the other factors ($F_s < 1$), indicating that the modeled difference waves were not statistically different from the empirical difference waves within these two latency ranges.

Insert Figs. 6 and 7 around here.

4. Discussion

In a previous study on visual change detection using an S1-S2 matching paradigm, change stimuli elicited a posterior positivity (“change-related positive difference, CRPD, or change positivity”) (Kimura et al., in press). It was shown that the scalp-topography of change positivities differed according to the feature changed, and the visual stimulus conjunction change in ventral stream features (i.e., color and shape) elicited change positivities that had an additive amplitude and scalp-topography made up of the values of the corresponding single features. In the present study, we recorded ERPs elicited by an S1-S2 matching task with stimuli defined by ventral and dorsal stream features (color and motion direction), and investigated whether or not a stimulus change in a dorsal stream feature is manifested by the change positivity, and whether or not different scalp-topographies according to the feature changed and the additivity of the change positivity are observed between the ventral and dorsal stream features.

4. 1. Change positivity elicited by stimulus change in ventral and dorsal stream features

We found here that posterior positivities with a latency range of 100-250 ms were elicited by stimulus changes in both color and motion direction. Although the peak latency of the posterior positivities appeared to be earlier in response to a color change than to a change in motion direction, statistical analysis of amplitudes in two time windows (120-180 ms and 180-240 ms) revealed a significant elicitation of posterior positivities in response to color change and motion direction change in both time windows. The scalp distribution of the posterior positivity also differed depending on the feature changed, and was also different from those of the P1, N1, and

P2 components. Thus, we concluded that the positivities did not reflect the modulation of exogenous components, but rather an overlapping component associated with feature-specific change detection processing. A difference in scalp topographies according to the feature changed also suggests that the locus of generator of the change positivity varies according to the feature changed. The observation of different topographies according to the feature changed is similar to that obtained in a S1-S2 matching task with ventral stream features (color and shape) (Kimura et al., in press). Thus, our results indicate that the visual system may include a feature-specific change detection mechanism regardless of ventral and dorsal stream features. This conclusion was also supported by the results of the additivity of change positivities (see next session).

4. 2. Additivity of change positivity for dorsal and ventral stream feature conjunction

The amplitude of change positivities elicited by a conjunction change (i.e., change in both color and motion direction) was larger than those elicited by a single feature alone (color change or motion direction change). The empirical difference wave (CMc - Nc difference wave) could be modeled by adding the individual difference waves obtained with color change and motion direction change (modeled difference wave; $(C_c - N_c) + (M_c - N_c)$ difference wave). With regard to the scalp-topographies, change positivities had a different distribution depending on whether they were elicited by a color change or a motion direction change. Change positivities elicited by a conjunction change had a scalp-topography that was the sum of those elicited by the corresponding single features. These results support the notion of independent brain activity emanating from separate generators. Thus, the visual change detection systems reflected by the

change positivity process multi-feature changes in parallel. These results are consistent with previous results obtained using stimulus changes of ventral features (color and shape), which indicate the existence of feature-specific change detection systems in the human visual system (Kimura et al., in press).

Feature-independent elicitation is a well-known property of auditory mismatch negativity (MMN) (Näätänen et al., 1978). MMN is an ERP component that can be elicited by any discriminable change in the auditory environment, and is thought to reflect auditory-modality-specific change detection processing. The feature-specific elicitation of auditory MMN has been observed for various kinds of features such as frequency and stimulus onset asynchrony (SOA) (Levänen et al., 1993; Paavilainen et al., 2001), intensity and SOA (Paavilainen et al., 2001), frequency and duration (Levänen et al., 1993; Wolff and Schröger, 1995, 2001), duration and intensity (Paavilainen et al., 2001; Wolff and Schröger, 1995, 2001), frequency and location (Schröger, 1995), and location and the conjunction between frequency and intensity (Takegata et al., 1999) (but see also, e.g., Winkler et al., 1990). Although the counterpart of MMN in the visual modality has been discussed over the past few decades, it is still unclear whether a comparable MMN component exists in the visual modality (for review, see Pazo-Alvarez et al., 2003). In addition, visual MMN studies have not reported a feature-specific auditory MMN counterpart (Heslenfeld, 2003). However, our results suggest that the basic feature-specific change detection mechanism underlies both the auditory and visual systems.

5. Conclusions

In summary, posterior change positivities at around 120-240 ms were elicited by a stimulus change in a dorsal stream feature as well as in a ventral stream feature. These change positivities had different scalp-topographies according to the changing feature. In addition, additivity of amplitudes and scalp-topographies of change positivity for concurrent changes in ventral and dorsal stream features was noted. These results suggest that feature-specific change detection systems, operating in parallel, exist in the human visual system.

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Foot Note

¹ When the amplitudes of ERPs elicited by target stimuli and non-target stimuli were tested by a four-way ANOVA (2 Color change types (Change, No-change) × 2 Motion direction change types (Change, No-change) × 2 Electrodes (Parietal, Left occipito-temporal) × 2 Task relevance (Target, Non-target)), the significant elicitation of three types of change positivities regardless of task relevance was supported by the main effect of Color change type and Motion direction change type without their interaction (main effect of Color change type: $F(1,11) = 38.12$, $p < .001$ for 120-180 ms, $F(1,11) = 6.29$, $p < .05$ for 180-240 ms; main effect of Motion direction change type: $F(1,11) = 24.48$, $p < .001$ for 120-180 ms, $F(1,11) = 30.14$, $p < .001$ for 180-240 ms). In addition, although a main effect of Task relevance was obtained ($F(1,11) = 7.38$, $p < .05$ for 120-180 ms, $F(1,11) = 71.90$, $p < .001$ for 180-240 ms), there were no significant interactions between the other factors for two time windows. The main effects of Task relevance was due to the fact that ERPs elicited by four types of S2 as a target were generally shifted to a more negative polarity than those elicited by the four S2 types as a non-target. The effect could be interpreted as the overlapping of the selection-related negative component (e.g., SN and N2b) (e.g., Anllo-Vento and Hillyard, 1996; Kasai et al., 2003; Smid et al., 1999). For the purpose of this study, detailed analyses for the posterior positivities were conducted only for ERPs in response to S2 as a non-target.

Table 1*Behavioral performance for each task condition (mean \pm SD)*

Task	Nc	Cc	Mc	CMc
Reaction time (ms)	375.2 \pm 28.6	408.9 \pm 37.1	418.9 \pm 41.5	431.6 \pm 42.0
Hit rate (%)	97.8 \pm 2.2	96.0 \pm 5.2	96.2 \pm 4.1	96.9 \pm 2.8
False alarm rate (%)	1.5 \pm 1.9	1.7 \pm 1.2	1.9 \pm 1.5	3.6 \pm 2.9

Note: Nc = no-change, Cc = color change, Mc = motion direction change, CMc = color-motion direction change.

Table 2

Mean amplitudes of averaged ERPs (μV) in posterior positivity latency range (120-180 ms and 180-240 ms) for non-target stimuli (mean \pm SD)

Trial type	Nc	Cc	Mc	CMc
120-180 ms				
Left occipito-temporal (PO7)	-1.43 \pm 2.02	-1.03 \pm 2.03	-0.86 \pm 2.22	-0.41 \pm 2.42
Parietal (Pz)	-2.24 \pm 2.75	-2.02 \pm 2.62	-1.63 \pm 2.92	-1.32 \pm 3.06
180-240 ms				
Left occipito-temporal (PO7)	-2.09 \pm 2.46	-1.60 \pm 2.83	-0.48 \pm 2.77	0.26 \pm 3.12
Parietal (Pz)	-1.56 \pm 3.73	-1.47 \pm 3.54	0.33 \pm 3.86	0.79 \pm 3.94

Note: Nc = no-change, Cc = color change, Mc = motion direction change, CMc = color-motion direction change.

Figure Captions

- Fig. 1.** Grand averaged ERPs elicited by four types of S2 in four task types. P1, N1, P2, N2 and LPC were elicited for all S2s. ERPs elicited by target stimuli showed enhanced negativity at around 200-300 ms (SN + N2b) and large positivity at around 400-500 ms (P3b). Nc = no-change, Cc = color change, Mc = motion direction change, CMc = color-motion direction change.
- Fig. 2.** Grand averaged ERPs elicited by four types of S2 as non-target (task types were pooled). P1, N1, and P2 components were clearly elicited for all S2 types. Relative to a no-change stimulus, ERPs elicited by change stimuli were shifted to a positive polarity in the 100-250 ms latency range. Nc = no-change, Cc = color change, Mc = motion direction change, CMc = color-motion direction change.
- Fig. 3.** Topographical maps of P1, N1, and P2 components elicited by the no-change stimulus as non-target. P1 was distributed bilaterally in the occipital regions (O1 and O2). N1 had a more lateral distribution, and was bilaterally distributed in the temporal regions (T5 and T6). P2 had an occipital distribution (Oz).
- Fig. 4.** Difference waves obtained by subtracting ERPs elicited by a no-change stimulus from those elicited by change stimulus (color change, motion direction change, and color-motion direction change) as non-target. A posterior positivity ("change positivity") can be clearly observed for the three types of change. Nc = no-change, Cc = color change, Mc = motion direction change, CMc = color-motion direction change.

- Fig. 5.** Topographical maps of difference waves (120-180 ms and 180-240 ms time windows). The posterior positivities (“change positivity”) elicited by color change and motion direction change show different scalp-topographies. Nc = no-change, Cc = color change, Mc = motion direction change, CMc = color-motion direction change.
- Fig. 6.** Empirical (CMc - Nc; black line) and modeled difference waves ((Cc - Nc) + (Mc - Nc) difference wave; gray line). Modeled difference waves are similar in appearance to empirical difference waves. Nc = no-change, Cc = color change, Mc = motion direction change, CMc = color-motion direction change.
- Fig. 7.** Topographical maps of empirical and modeled difference waves. The modeled change positivity and empirical change positivity exhibit similar topographical distributions. Nc = no-change, Cc = color change, Mc = motion direction change, CMc = color-motion direction change.

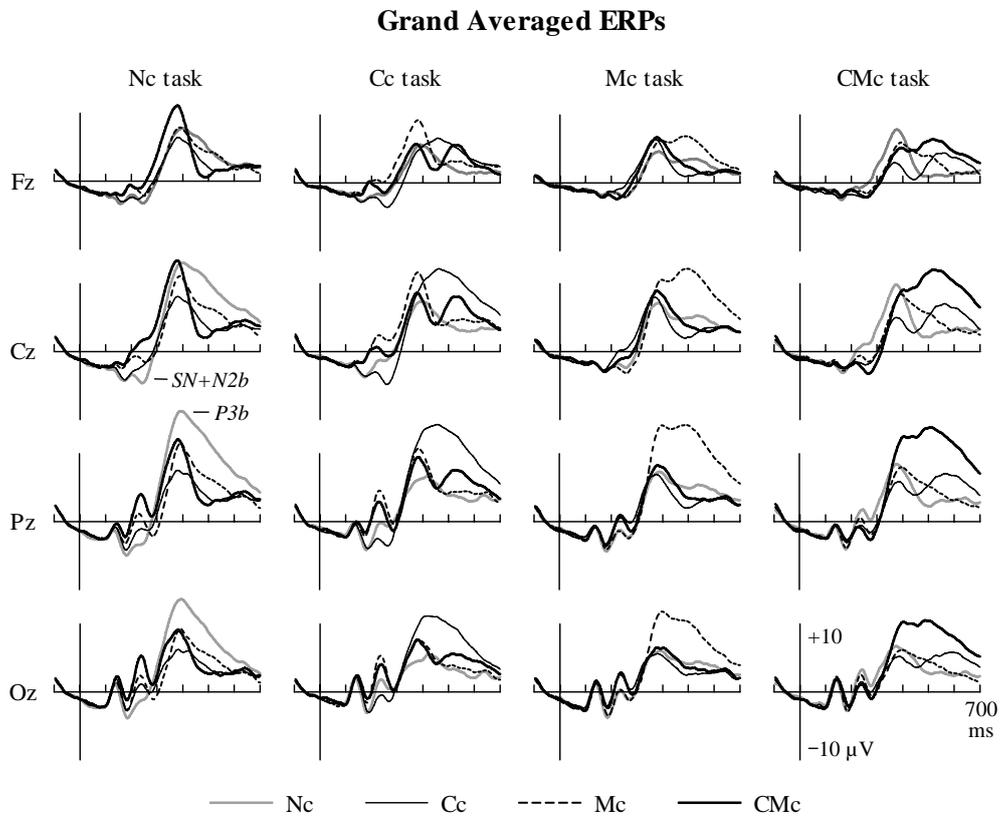


Fig. 1

Grand Averaged ERPs to Non-target Stimuli

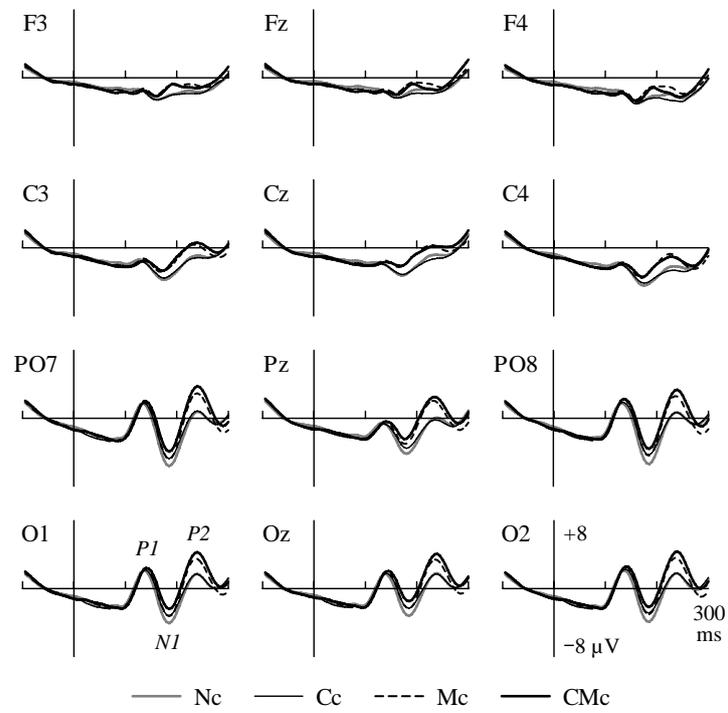


Fig. 2

Maps of Grand Averaged ERPs to No-change S2

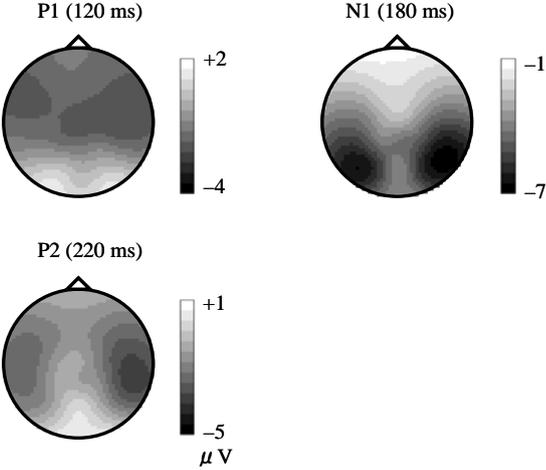


Fig. 3

Change - No-change Difference Waves

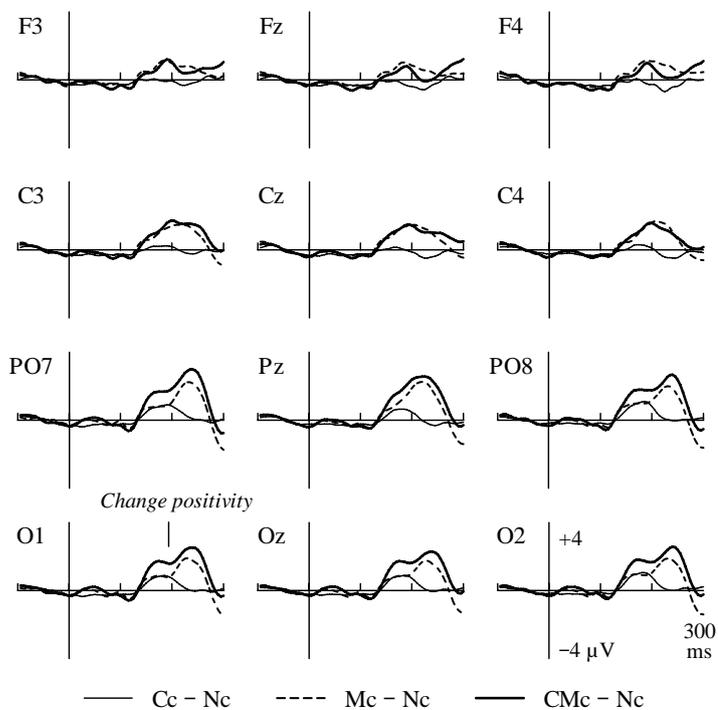


Fig. 4

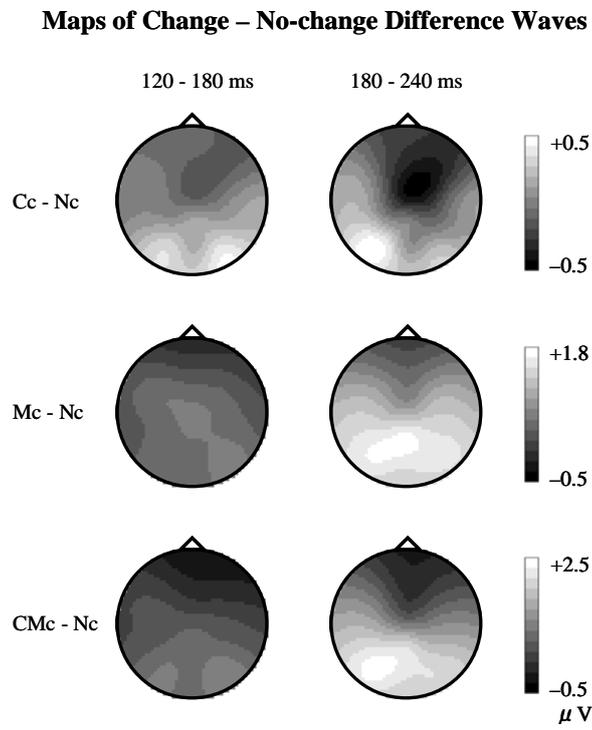


Fig. 5

Modeled vs. Empirical Difference Waves

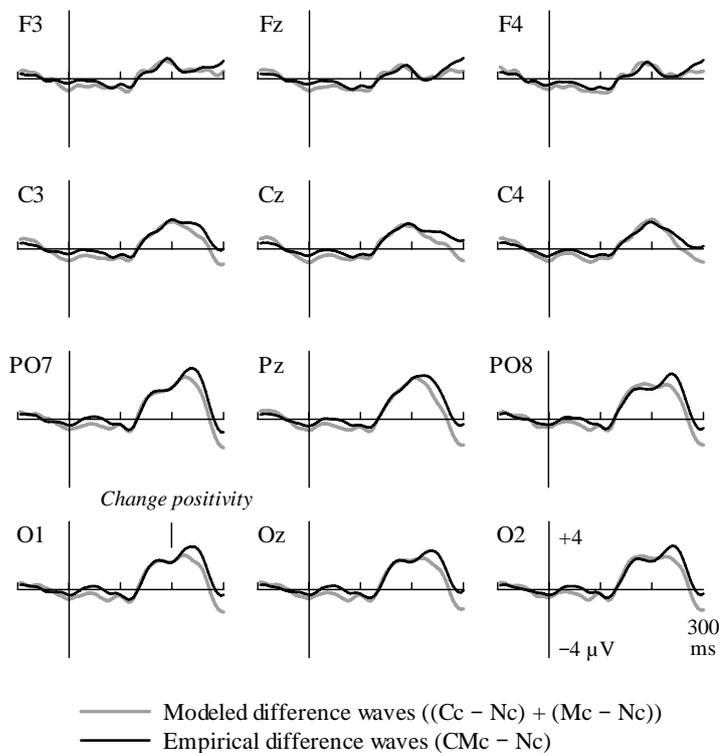


Fig. 6

Maps of Modeled vs. Empirical Difference Waves

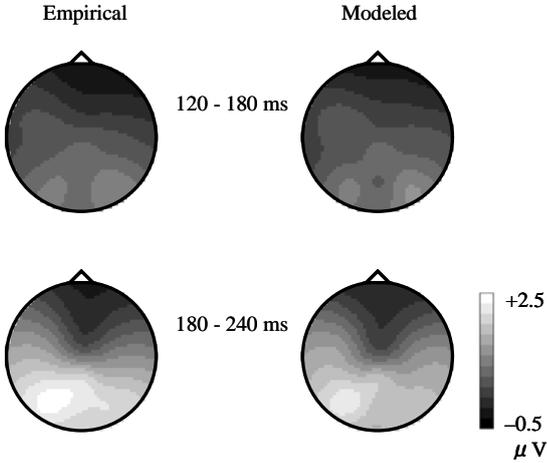


Fig. 7