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Attribute-invariant orientation discrimination at an early stage of processing in the human visual system

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Abstract

This study investigated event-related brain potentials (ERPs) during selective attention to the orientation of a bar comprised of two squares, which were defined by only color or motion (intra-attribute conditions) or both (interattribute condition). An early positive potential in association with orientation selection was elicited for all conditions in similar latency ranges but with different scalp distributions. These results suggest that attribute-invariant orientations can be discriminated at an early stage of processing in the human brain, which fills a gap between monkey electrophysiology and human psychophysics, while attribute-specific orientations are also available in a given context.
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1. Introduction

The visual system processes feature dimensions, such as color or motion, in their respective channels or modules (Zeki, 1993), which indicates that the different attributes of an image are separately detected in the initial stage of processing. However, it has been suggested that contour or edge information for different attributes is converged beginning in an early stage of processing. In behavioral studies, tilt effects and illusory contours occur across stimuli defined by luminance, motion, and disparity cues (Poom, 2000, 2001). In addition, orientations defined by different feature dimensions show similar discrimination thresholds (Regan, 2000) and search efficiency (Cavanagh, Arguin, & Treisman, 1990). These results suggest that common attribute-invariant representations are formed and

perception or task performance is then achieved based on these representations. Neurophysiological studies in monkeys have provided neural bases for common form representations: there are neurons that selectively respond to orientation or shape, regardless of the defining attributes, in cortical areas V2 (Leventhal, Wang, Schmolesky, & Zhou, 1998; Marcar, Raiguel, Xiao, & Orban, 2000) and IT (Sary, Vogels, & Orban, 1993; Sary, Vogels, Kovacs, & Orban, 1995).

However, it remains unclear how common representations are involved in shape discrimination processes in the human brain. Although common and distinctive brain regions have been identified in response to forms defined by different feature dimensions (e.g., Dupont et al., 1997; Mendola, Dale, Fischl, Liu, & Tootel, 1999; Orban, Dupont, Bruyn, Vogels, & Vandenberghe, 1995), no overlapping brain regions were activated in the discrimination of color- and motion-defined forms (Gulyas, Heywood, Popplewell, Roland, & Cowey, 1994). Thus, shape discrimination seems to be based on attribute-dependent representations rather than attribute-invariant representations. However, the slow time course of the hemodynamic response in neuroimaging techniques may mask slight transient neural responses, and

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experimental tasks that require common representations have not been examined.

Scalp-recorded, event-related brain potentials (ERPs) are a useful tool for examining fine temporal information in the brain. Previous ERP studies on visual-selective attention have identified several components associated with discrimination or selection processes in separate feature dimensions such as color, motion, and shape/orientation (for reviews, Harter & Aine, 1984; Hillyard & Anllo-Vento, 1998; Näätänen, 1992). Stimuli with an attended feature value (i.e., red or circle) typically evoked selection negativities (SNs) over posterior regions with an onset latency at around 150–300 ms post-stimulus, relative to those with an unattended feature. Earlier selection positivities (SPs) at around 100–200 ms post-stimulus have also been identified for color, motion, and shape/orientation, although these have been reported relatively infrequently because of the small amplitude (Anllo-Vento, Luck, & Hillyard, 1998; Kenemans, Lijffijt, Camfferman, & Verbaten, 2002; Martinez, Di Russo, Anllo-Vento, & Hillyard, 2001; Martin-Loeches, Hinojosa, & Rubia, 1999; Proverbio, Esposito, & Zani, 2002). The selection potentials are clearly distinguished from the early stimulus-evoked P1 and N1 components that are associated with a gain control mechanism of sensory-evoked responses by spatial attention (for a review, see Hillyard & Anllo-Vento, 1998). In contrast, scalp distributions of SPs and SNs can vary according to the feature dimension to be attended, which indicates that these may reflect neural activities in specialized brain regions for processing particular attributes (Anllo-Vento & Hillyard, 1996; Anllo-Vento et al., 1998; Martin-Loeches et al., 1999; Previc & Harter, 1982). Furthermore, the scalp distributions and neural origins of SPs differ from those of SNs, which suggests that the selection potentials reflect a processing sequence in particular feature dimensions (Anllo-Vento et al., 1998): early processing for SPs and later processing for SNs.

In the present study, we examined ERPs during selective attention to the orientation of stimuli similar to those used by Morita, Morita, and Kumada (2003), where the orientation was determined by the spatial arrangement of two squares, as shown in Fig. 1. In the interattribute condition, one of the squares was segregated from the background by

motion and the other was segregated by color. Therefore, the integration of information across these two attributes would be required to discriminate the orientation. Morita et al. (2003) showed that visual search became more difficult as the number of items increased in the interattribute condition relative to when the two squares were defined by the same attribute (intra-attribute conditions), which suggests that attribute-specific representations are involved in visual search processes. In contrast, the present study examined only a single item to elucidate neural substrates of form discrimination processes based on attribute-invariant representations. If common representations found in single-unit studies in the early visual cortex are available for the discrimination of orientation defined by different attributes, orientation SP should be observed in the interattribute condition. In addition, we compared ERPs associated with orientation discrimination in the interattribute condition with those in the intra-attribute conditions to explore how attribute-specific representations are integrated into common representations.

2. Methods

2.1. Participants

Eighteen volunteers (five females; 19–36 years old, mean 23.2 years) participated in this experiment. All had normal or corrected-to-normal visual acuity and color vision. One male was left-handed. Written informed consent was obtained from each participant after the nature of the study had been fully explained.

2.2. Apparatus and stimuli

Stimuli were presented on a color video monitor (NANAO FlexScan 56 T/S) controlled by a computer (GenuineIntel Pentium II) equipped with a Visual Stimulus Generator (Cambridge Research Systems, VSG2/3) at a viewing distance of 57 cm. Schematic illustrations of the stimuli are shown in Fig. 1. A bar was presented at the center in one of the quadrants of the background ($8.14° \times 8.14°$ in visual angle) filled with a yellow-and-black random-dot pattern; each dot ($0.03° \times 0.03°$) was randomly assigned yellow ($26 \, cd/m^2$) or black ($0 \, cd/m^2$). The bar consisted of a pair of squares ($1.49° \times 1.49°$) adjacent to each other with a small gap between them. The size of the gap was $0.75°$ for targets or $0.15°$ for non-targets (standards). The bar appeared with an orientation of $45°$ or $135°$ at a distance of $2.3°$ from a fixation point at the center of the background. The fixation point was a small white circle ($0.2° \times 0.2°$) and was always visible during experimental blocks.
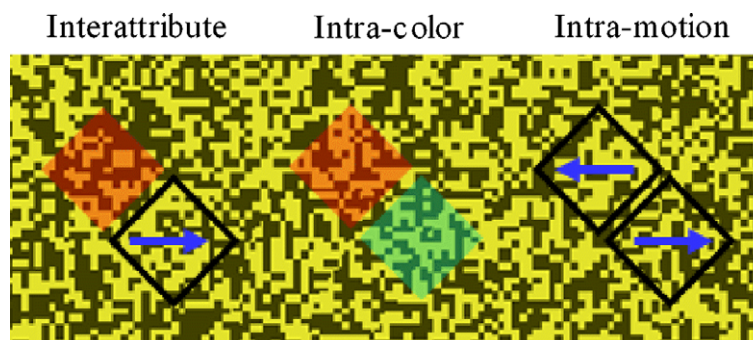

Fig. 1. Schematic illustrations of stimuli used in the present experiment. Black outlines indicate motion-defined contours. Blue arrows indicate directions of motion.