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Facilitation of face recognition through the retino-tectal pathway

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ABSTRACT

Humans can shift their gazes faster to human faces than to non-face targets during a task in which they are required to choose between face and non-face targets. However, it remains unclear whether a direct projection from the retina to the superior colliculus is specifically involved in this facilitated recognition of faces. To address this question, we presented a pair of face and non-face pictures to participants modulated in greyscale (luminance-defined stimuli) in one condition and modulated in a blue–yellow scale (S-cone-isolating stimuli) in another. The information of the S-cone-isolating stimuli is conveyed through the retino-geniculate pathway rather than the retino-tectal pathway. For the luminance stimuli, the reaction time was shorter towards a face than towards a non-face target. The facilitatory effect while choosing a face disappeared with the S-cone stimuli. Moreover, fearful faces elicited a significantly larger facilitatory effect relative to neutral faces, when the face (with or without emotion) and non-face stimuli were presented in greyscale. The effect of emotional expressions disappeared with the S-cone stimuli. In contrast to the S-cone stimuli, the face facilitatory effect was still observed with negated stimuli that were prepared by reversing the polarity of the original colour pictures and looked as unusual as the S-cone stimuli but still contained luminance information. These results demonstrate that the face facilitatory effect requires the facial and emotional information defined by luminance, suggesting that the luminance information conveyed through the retino-tectal pathway is responsible for the faster recognition of human faces.

1. Introduction

Humans can discriminate and orient to human faces in only 100 ms, which is significantly faster than they can orient to non-face targets (other animals, vehicles, and various other objects encountered in everyday life) in tasks in which they are required to choose between face and non-face targets (Crouzet, Kirchner, & Thorpe, 2010; Girard & Koenig-Robert, 2011). However, the neural mechanisms that underlie this facilitated recognition of human faces remain unknown.

It is well known that facial stimuli evoke an event-related potential with a peak latency of approximately 170 ms (N170 in electro-encephalography, and M170 in magneto-encephalography) (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Watanabe, Kakigi, Koyama, & Kirino, 1999). The source of the N170/M170 signal has been localised to the fusiform gyrus in humans (Deffke et al., 2007), which shows a selective increase of blood flow in response to facial stimuli (Kanwisher, McDermott, & Chun, 1997). The fusiform gyrus clearly plays a central role in face recognition, but the N170/M170 component occurs too late to be directly involved in the rapid face recognition.

In addition to the N170/M170 component, facial stimuli elicit an early positive component with a peak latency of 100 ms (P100) or less (Braeutigam, Bailey, & Swithenby, 2001; Liu, Harris, & Kanwisher, 2002; Rossion & Caharel, 2011). This fast brain response might be involved in the fast recognition of human faces because it was enhanced during a task in which participants were required to judge whether a visual stimulus was a face or an object (Liu et al., 2002).

To determine the origin of the fast component, we considered the signals conveyed through the retino-geniculo-cortical pathway. Because fast recognition can be achieved in the absence of fine details of facial information (Crouzet & Thorpe, 2011; Girard & Koenig-Robert, 2011; Honey, Kirchner, & VanRullen, 2008), the fast and coarse magnocellular pathway is likely to be involved. However, the shortest visual response latency in V1 is 56 ms and these latencies in V3 and V4 are 70–80 ms in humans (Yoshor, Bosking, Ghose, & Maunsell, 2007). As it takes 20–30 ms to generate a saccade with electrical stimulation of the frontal eye fields (FEF) in monkeys (Bruce, Goldberg, Bushnell, & Stanton, 1985; Robinson & Fuchs, 1969), the retino-geniculo-cortical pathway seems to be too slow to play a role in the fast face-selective responses that occur within 100 ms. This issue raises the possibility that the fast face recognition depend on the retino-tectal pathway, which conveys

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visual information to the cerebral cortex through the superior colliculus and the pulvinar.

Several studies have suggested that the subcortical pathway is involved in processing facial information (Johnson, 2005). Patients with V1 lesions were still able to discriminate the gender and expressions of human faces, although they were unaware of their ability (Morris, DeGelder, Weiskrantz, & Dolan, 2001). Neuroimaging studies have indicated that facial stimuli with emotional expressions evoked responses in these subcortical regions (Morris, Ohman, & Dolan, 1999; Vuilleumier, Armony, Driver, & Dolan, 2003). In addition, neurons in the pulvinar of the monkey responded to face-like patterns with a latency as short as 50 ms (Nguyen et al., 2013).

In the present study, we aimed to elucidate whether the retino-tectal pathway is involved in the fast process of face recognition. To answer this question, we presented a pair of face and non-face pictures to participants modulated in greyscale (luminance-defined stimuli) in one condition and modulated in blue–yellow scale in another. The latter condition was designed so that the stimuli would exclusively activate the short-wave-sensitivity cone (S cone) out of three cones in the retina (S-cone-isolating stimuli; (Sumner, Adamjee, & Mollon, 2002; Wandell et al., 1999)). The luminance-defined stimuli are conveyed through both retino-tectal and retino-geniculate pathways, but the S-cone-isolating stimuli are exclusively conveyed through the retino-geniculate pathway. In fact, S-cone signals do not reach the superior colliculus (Marrocco & Li, 1977; Schiller & Malpeli, 1977; White, Boehnke, Marino, Itti, & Munoz, 2009) but do reach both the ventral and dorsal visual pathways in the visual cortices (Chatterjee & Callaway, 2002; Seidemann, Poirson, Wandell, & Newsome, 1999; Wandell et al., 1999).

In Experiment 1, we examined whether the facilitatory effect on choosing a face that was observed for the luminance stimuli disappeared for the S-cone stimuli. The facilitatory effect was measured by comparing the reaction time of a saccade performed to choose a face with one performed to choose a butterfly. If the retino-tectal pathway is essential for the fast processing of facial information, the facilitatory effect observed for the luminance stimuli should disappear for the S-cone stimuli.

In Experiment 2, we compared the facilitatory effect observed for fearful faces to that observed for neutral faces. Because saccadic latency is shorter for fearful faces than for neutral faces (Bannerman, Hibbard, Chalmers, & Sahraie, 2012), we speculated that the facilitatory effect would be larger for emotional faces than for neutral faces when the stimuli were modulated in greyscale, whereas the effect of emotional expressions would disappear for the S-cone stimuli.

Even if the face facilitatory effect disappears with the S-cone stimuli, it may still be argued that the disappearance has nothing to do with the retino-tectal pathway but was simply due to the unusual appearance of the S-cone stimuli that is conveyed through the retino-geniculate pathway. To address this issue, we prepared "negated stimuli" (Russell, Sinha, Biederman, & Nederhouser, 2006) in Experiment 3 by reversing the polarity of the original colour pictures. It is worth noting that the face colours of negated stimuli looked as unusual as the S-cone stimuli but still contained luminance information. If the face facilitatory effect is still observed with the negated stimuli, we may exclude the possibility that natural appearance conveyed through the reticulo-geniculate pathway is essential for the face facilitatory effect and suggest that the retino-tectal pathway is involved in the fast processing of facial information.

2. Material and methods

2.1. Participants

Fifteen volunteers participated in Experiment 1 (8 females; mean age 20.7 years, age range 20–23 years), thirteen volunteers participated in Experiment 2 (7 females; mean age 20.1 years, range 20–22 years), and eleven volunteers participated in Experiment 3 (1 female; mean age 21.7 years, age range 20–23 years). All of the participants had normal or corrected-to-normal vision and gave written informed consent to participate in the experiments. The study was approved by the ethical committee of Osaka University.

2.2. Apparatus and general task procedures

Participants viewed visual stimuli presented on a gamma-corrected CRT 17-inch monitor (Trinitron Multiscan G200, Sony) with their heads resting on a chin rest and a forehead rest to maintain a viewing distance of 60 cm. The screen refresh rate was 100 Hz (VSG 2/2, Cambridge Research System), and the spatial resolution was 1024×768 pixels ($32^\circ \times 24^\circ$). Eye movements were recorded using a camera-based eye tracker (SR research, Eyelink1000) with a temporal resolution of 1000 Hz. Participants performed a saccadic choice task that followed a protocol similar to the previous study (Crouzet et al., 2010). The participants had to fixate on a cross in the centre ($0.5^\circ \times 0.5^\circ$) for a randomly determined duration between 1.2 and 1.8 s, until the cross disappeared (Fig. 1b). After a gap period of 0.2 s, one face picture and one butterfly picture, each subtending $10^\circ \times 12^\circ$ (width × height), were presented simultaneously, one on the left and the other on the right side of the screen for 2 s. Each picture appeared on its respective side (right or left) at a distance of 8° from the centre. The participants were instructed to move their eyes as quickly and accurately as possible toward the stimulus that belonged to the target category (face or butterfly), which had been pre-determined before the session began. Each session consisted of 100 choice trials. The apparatuses were controlled using house-made programs run on Matlab software (Mathworks, Natick, MA) with the Psychophysics toolbox and the Eyelink Toolbox (Brainard, 1997; Cornelissen, Peters, & Palmer, 2002).

2.3. Stimuli

The visual stimuli consisted of 100 neutral and 100 fearful face pictures taken from the Karolinska Directed Emotional Faces set (Lundqvist, Flykt, & Öhman, 1998) and the NimStim set of facial expressions (Tottenham et al., 2009), as well as 100 butterfly pictures taken from a commercial photo album. We used butterfly pictures because both butterflies and human faces have a symmetrical structure. All of the images were converted to greyscale (0–255, mean = 127, s. d. = 60) and resized to 330×400 pixels ($10^\circ \times 12^\circ$). These greyscale images were used as the luminance-defined stimuli (Fig. 1a, luminance). To prepare the S-cone-isolating stimuli, the spectral emissions of the red (R), green (G), and blue (B) phosphors of the CRT monitor were measured by using a spectral colorimeter (CS-2000, Konica Minolta). Then, 9 dot products were calculated between the spectral absorptions of the L, M, and S cones (Smith & Pokorny, 1975) and the spectral emissions of the R, G, and B phosphors to yield a 3-by-3 matrix that transformed the R, G, B levels linearly into the excitation levels of the L, M, S cones. The inverse of the matrix, which transforms (L, M, S) to (R, G, B), was then used to determine the line (S-cone-isolating line) along which the (R, G, B) levels were modulated to keep the excitation levels of the L and M cones constant while modulating the S-cone excitation level in isolation (see the Visual System Engineering Toolbox provided by Brain Wandell, https://github.com/wandell/vset). The screen background was set to grey ($x = 0.29$, $y = 0.3$) in the CIE colour space at a luminance of 33.1 cd m^{-2}, and the S-cone-isolating line was prepared around this point. The S-cone-isolating stimuli were prepared by mapping the value of each pixel (0–255) linearly onto the S-cone-isolating line over the range of S-cone excitation levels that the CRT monitor was capable of producing.

The negated visual images were created by inverting the polarity of the original colour pictures of faces and butterflies that were used in Experiment 1 (Fig. 3a).

2.4. Experiments

In Experiment 1, each participant performed 4 sessions, one for each of two-by-two conditions: two object categories (face and butterfly) by two stimulus types (luminance and S-cone stimuli). Therefore, the total number of trials was 400 (4 sessions of 100 trials each). The order of the four sessions was counterbalanced across the participants.

In Experiment 2, each participant performed 4 sessions, two for each of the two stimulus types (luminance and S-cone stimuli). The face target category was used across all of the sessions. In this experiment, we presented fearful faces in half of the 100 trials in each session, in addition to the neutral faces used in Experiment 1. The order of the two facial expressions was randomly shuffled.

In Experiment 3, each participant performed 2 sessions with the negated stimuli, one for each of the two object categories (face and butterfly). Therefore, the total number of trials was 200. The order of the two sessions was counterbalanced across the participants. In all experiments, each session was preceded by a training session of 10 trials.