

Neural correlates of the eye dominance effect in human face perception: the left-visual-field superiority for faces revisited

Wookyoung Jung,¹ Joong-Gu Kang,^{1,2} Hyeonjin Jeon,¹ Miseon Shim,^{1,3} Ji Sun Kim,¹ Hyun-Sung Leem,² and Seung-Hwan Lee^{1,4}

¹Clinical Emotion and Cognition Research Laboratory, Department of Psychiatry, Inje University, Goyang 10380, Korea, ²Department of Optometry, Eulji University, Seongnam 13135, Korea, ³Department of Biomedical Engineering, Hanyang University, Seoul 04763, Korea, and ⁴Department of Psychiatry, Ilsan Paik Hospital, College of Medicine, Inje University, Goyang 10380, Korea

Correspondence should be addressed to Seung-Hwan Lee, Department of Psychiatry, Ilsan Paik Hospital, College of Medicine, Inje University, Juhwa-ro 170, Ilsanseo-Gu, Goyang 10380, Korea. E-mail: lshps@paik.ac.kr.

Wookyoung Jung and Joong-Gu Kang contributed equally to this work.

Abstract

Faces are processed best when they are presented in the left visual field (LVF), a phenomenon known as LVF superiority. Although one eye contributes more when perceiving faces, it is unclear how the dominant eye (DE), the eye we unconsciously use when performing a monocular task, affects face processing. Here, we examined the influence of the DE on the LVF superiority for faces using event-related potentials. Twenty left-eye-dominant (LDE group) and 23 right-eye-dominant (RDE group) participants performed the experiments. Face stimuli were randomly presented in the LVF or right visual field (RVF). The RDE group exhibited significantly larger N170 amplitudes compared with the LDE group. Faces presented in the LVF elicited N170 amplitudes that were significantly more negative in the RDE group than they were in the LDE group, whereas the amplitudes elicited by stimuli presented in the RVF were equivalent between the groups. The LVF superiority was maintained in the RDE group but not in the LDE group. Our results provide the first neural evidence of the DE's effects on the LVF superiority for faces. We propose that the RDE may be more biologically specialized for face processing.

Key words: eye dominance; face processing; visual field; left-visual-field superiority for faces; event-related potential; N170

Introduction

It is known that bilateral pairs of structures in the body are not symmetrical in either form or function (Porac and Coren, 1976). One of the structures in the pair is often behaviorally or physiologically superior to the other, with the superior side being referred to as dominant. For instance, the dominant eye (DE) refers to the eye that is consistently preferred under monocular viewing conditions (Carey and Hutchinson, 2013). Approximately

two-thirds of the population is reportedly right-eye dominant (RDE) while the other one-third is left-eye dominant (LDE) (Bourassa et al., 1996; Reiss and Reiss, 1997; Ehrenstein et al., 2005; Eser et al., 2008). The higher prevalence of RDE can be observed even in children and is not related to sex (Dellatolas et al., 1998).

During visual processing, each hemisphere processes the information that is presented in the contralateral visual field (VF), i.e. information from the left visual field (LVF) is sent initially to

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the right hemisphere (RH), whereas information from the right visual field (RVF) is sent initially to the left hemisphere (LH). Visual processing is lateralized to a particular hemisphere depending on the type of information being perceived. For example, word processing is strongly lateralized in the LH (Cohen et al., 2000; Dehaene and Cohen, 2011), whereas face processing is strongly lateralized in the RH; this strong lateralization for faces is known as the LVF superiority (De Renzi et al., 1968, 1994; Carey and Diamond, 1980; Moscovitch and Klein, 1980; Gazzaniga and Smylie, 1986; Levine et al., 1988; Gazzaniga, 2000; Le Grand et al., 2003; Kanwisher and Yovel, 2006; Thomas et al., 2008; Yovel et al., 2008). However, it remains unknown how the contralateral presentation of a face affects the hemisphere that is not dominant for face processing. Moreover, it is unclear what effects the DE would have on the lateralization of face perception.

The DE's superiority has been demonstrated in both behavioral and physiological studies, which found that participants tend to perform more accurately when using their DE (Lund, 1932; Freeman and Chapman, 1935; Coren, 1999). Minucci and Connors (1964) reported that the reaction times (RTs) to stimuli presented monocularly were faster during presentations to the DE than they were during presentations to the non-DE. A functional magnetic resonance imaging study showed that the DE activates more of the primary visual cortex (V1) than does the non-DE for visual stimuli (Rombouts et al., 1996). Indeed, a crucial relationship between the DE and the V1 ipsilateral to the DE has been reported for visual stimuli, with the V1 ipsilateral to the DE being larger and more strongly activated than the V1 contralateral to the DE (Erdogan et al., 2002; Shima et al., 2010).

Although interest in eye dominance has a long and rich history, the function of eye dominance remains unclear. In particular, few studies have examined the relationship between eye dominance and face perception in terms of lateralization. To the best of our knowledge, no systematic investigations of the effects of eye dominance on the LVF superiority for faces have been performed.

Initially, faces are perceived through each of the two eyes. The images from each eye are blended into a combined binocular view so that we perceive a single, stable face (Blake, 2004). With both eyes open, people with normal binocular vision have no sense that one eye contributes more than the other to the combined binocular view (Yang et al., 2010). Hence, we wanted to examine how the DE contributes to binocular face perception, even though most people are unaware of the DE's contribution. In particular, we sought to determine whether the neural responses underlying face processing would reflect the influence of the DE, and if so, how the DE (or non-DE) would interact with the RH, which is strongly devoted to face processing, or with the LH, which has limited involvement in face processing.

In this study, we used event-related potentials (ERPs), especially P100 and N170, to investigate the neural asymmetry for face processing. The P100 component is thought to reflect basic visual processing, while the N170 is believed to reflect the structural encoding of human faces (Bentin and Deouell, 2000; Eimer, 2000; Liu et al., 2002; Itier and Taylor, 2004; Lee et al., 2010). Here, we had two main objectives. First, we revisited the LVF superiority for faces. Face stimuli presented in the LVF are initially projected to the V1 in the RH, which has differential relationships to the DE, i.e. the V1 in the RH is ipsilateral to the DE in RDE subjects, whereas the V1 in the RH is contralateral to the DE in LDE subjects. This suggests that the V1 in the RH would be more strongly activated in the RDE group than it would be in

the LDE group (Shima et al., 2010). Thus, we hypothesized that the RDE group would reveal a stronger LVF superiority for faces than would the LDE group; that is, the RDE would provide a more favorable condition for face processing, with the RDE group (vs the LDE group) responding faster and more strongly to face stimuli presented in the LVF.

Second, we examined the effects of the LDE on face processing. We hypothesized that the LDE would not process a face presented in the RVF to the same degree as the RDE processes a face presented in the LVF, even though the LDE and RVF have an ipsilateral relationship. Regarding the ERPs, we hypothesized that (i) the N170 for face processing would be more strongly activated in the RDE group than it would be in the LDE group and (ii) for the LDE group, the N170 in the LH would not be as strong as the N170 in the RH in the RDE group. Collectively, this study aimed to investigate whether eye dominance is a key factor in the LVF superiority for faces and whether this would intensify or attenuate the LVF superiority.

Materials and methods

Participants

Forty-three right-handed individuals participated in the experiment. Participants were recruited from the local community through the internet, newspapers and fliers. All participants were healthy and had normal or corrected-to-normal vision, as determined by checking their visual acuity with the Snellen chart (Lovie-Kitchin, 1988). None of the participants had any history or signs of neurological dysfunction. Eye dominance was assessed by the hole-in-card test (Miles, 1930), which was repeated three times; this test is the most reliable test for determining eye dominance (Taghavy and Kügler, 1987) and is not influenced by handedness. Twenty participants (10 women) were placed in the LDE group (mean age = 27.00 ± 7.08 years) and 23 participants (11 women) were placed in the RDE group (mean age = 29.32 ± 7.91 years). Handedness was assessed by the Edinburgh Handedness Inventory (Oldfield, 1971), with scores ranging from -100 for strong left-handedness to +100 for strong right-handedness; the participants' mean handedness value was 98.9 (SD = ± 2.75). All participants provided written informed consent, and the protocol was approved by the Institutional Review Board of Ilsan Paik Hospital.

Stimuli

Stimuli were selected from the standardized set of Korean face pictures (Park et al., 2011). All face images showed a frontal view and neutral expression (Figure 1). Two different face images for each sex were used. Each face was 9.4 cm high and 7.5 cm wide (8.27° by 6.60° in visual angle). All faces were equated for luminance, height and width. Each face subtended a visual angle of 14.03° horizontally. The stimuli were presented on a 20-in. cathode-ray tube monitor (85 Hz, 1280×960 pixels) and viewed from a distance of 65 cm (Figure 2).

Procedure

In a dimly lit, sound-attenuated room, participants were comfortably seated in front of a computer screen, and a response key on a keyboard was aligned with their body midline. Participants read the instructions and completed practice trials consisting of 12 faces (six trials for each sex) to ensure they understood the task. A trial began with a fixation dot that was

presented for 500 ms, followed by a black screen with a variable delay (600 – 1200 ms) (Figure 2). The face stimulus was then presented for 200 ms, followed by a black screen for 2000 ms. The experiment consisted of four blocks of 100 trials, in which a stimulus was presented randomly to one VF at a time. All stimuli were viewed binocularly. In addition, five catch trials in which no stimulus appeared were randomly presented in each block in order to increase the reliability of the participants' discrimination.

For the task, participants were asked to press a response key with their index finger as quickly and accurately as possible after the face was presented, regardless of the presentation side (i.e. left or right visual hemifield), while keeping their gaze on the face stimulus. Participants were asked to alternate which hand they used to perform the trials in each block in order to control for the effect of the response hand on face processing. At the beginning of each block, participants were instructed to keep their head still and to only move their eyes side to side during the presentation of stimuli to avoid head movements during the electroencephalography (EEG) recordings. The experimenter observed each of the participants as they performed the task to ensure that their head was centrally fixated. The entire ERP recording session for each participant lasted ~25 min.



Fig. 1. The male and female faces used in the experiment.

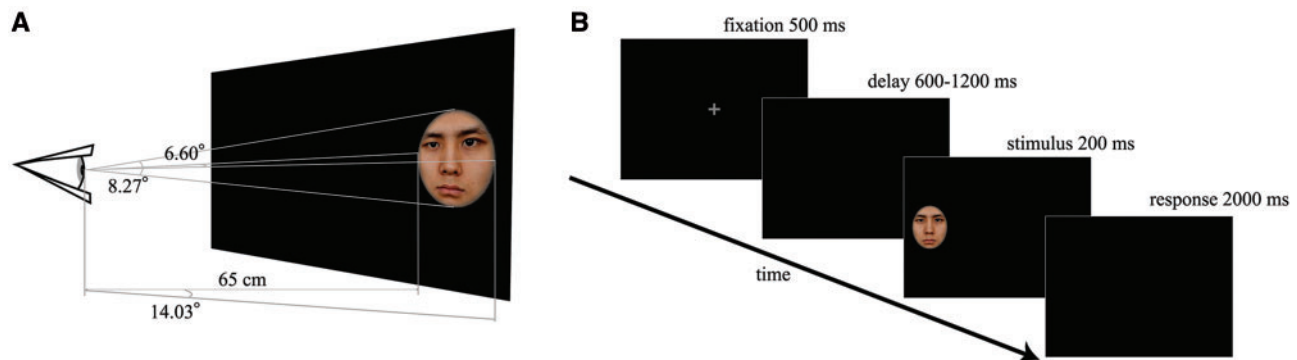


Fig. 2. Depictions of the stimuli and experimental paradigm. (A) Size of the stimuli. (B) The experimental paradigm. The stimulus was randomly presented to one visual field at a time but viewed binocularly.

EEG recording and ERP analysis

The EEG signals were recorded using a NeuroScan SynAmps 2 amplifier (Compumedics, El Paso, TX, USA) from 62 Ag/AgCl surface electrodes. The electrodes were mounted on a Quik-Cap (Compumedics) according to the extended international 10–20 system. As the reference, a linked electrode pair was located at the left (M1) and right mastoid (M2), and the ground electrode was placed on the forehead. Three additional electrodes were placed at the outer canthi of both eyes and below the right eye to register horizontal and vertical eye movements. Electrode impedance was maintained at $< 5 \text{ k}\Omega$. EEG data were recorded with a 0.1–100-Hz bandpass filter at a sampling rate of 1000 Hz, and 60-Hz noise was removed using a notch filter.

The recorded EEG data were pre-processed using Scan 4.3 software (Compumedics). Gross artifacts, including movement artifacts, were rejected via visual inspection by a trained individual who was blind to the data's origin. Eye-blink artifacts and horizontal eye movements were removed using standard blink-correction algorithms implemented in the pre-processing software (Semlitsch *et al.*, 1986). EEG data were re-referenced to the common average reference. Data were filtered using a 0.1–30 Hz bandpass filter and epoched from 200 ms before stimulus onset to 800 ms after stimulus onset. The epochs were subtracted from the average value of the pre-stimulus interval for baseline correction. If any remaining epochs contained significant physiological artifacts (amplitudes exceeding $\pm 75 \mu\text{V}$) at any of the 62 electrode sites, they were excluded from further analysis. Only artifact-free epochs were averaged across trials and participants for the ERP analysis. Among the 200 trials for each VF condition, regardless of hand, the number of epochs after pre-processing was not significantly different between the two groups. The number of remaining epochs for the LDE and RDE groups were 180.70 ± 24.86 and 183.34 ± 20.33 , respectively, for the LVF ($P = 0.694$) and 179.40 ± 33.80 and 180.43 ± 19.96 , respectively, for the RVF ($P = 0.902$).

To compare the peak amplitudes between the two DE groups, the P100 and N170 were measured using the averaged ERP waveforms from each subject. The time windows were determined based on the topographical distribution in each participant. For the P100, we measured the maximum positive peak amplitude in the window from 40 to 160 ms at O1 and O2 after stimulus onset. The N170, which is the face-specific component, is maximal at the lateral posterior (P7 and P8) and occipito-temporal (PO7 and PO8) scalp electrodes (Rossion and Jacques, 2008). Thus, here, the N170 peaks were measured using the averaged signals from P7 and PO7 for the LH and the

averaged signals from P8 and PO8 for the RH between 140 and 240 ms after stimulus onset (Lee et al., 2016).

Statistical analysis

Behavioral data were analyzed by a three-way mixed analysis of variance, with response hand (left vs right) and VF (LVF vs RVF) as the repeated-measures factors and DE group (LDE vs RDE) as the between-subjects factor. For the ERP data, we conducted a four-way mixed analysis of variance, with hemisphere (left vs right), response hand (left vs right), and VF (LVF vs RVF) as repeated-measures factors and DE group (LDE vs RDE) as a between-subjects factor. The *P* values were corrected with the Bonferroni correction for follow-up tests. The significance level was set at $P < 0.05$ (two-tailed).

Results

Data from one participant were excluded from the analysis because his mean RT was substantially above the mean \pm 3SD RT distribution of the remaining participants. Additionally, three participants were excluded following initial horizontal eye movement artifacts reduction if insufficient data for analysis remained (see EEG recording and ERP analysis). Thus, data from 39 participants were analyzed.

Behavioral data

Catch trials and trials with incorrect responses were removed from the analysis (0.5% of the total trials). The median RT for each hand-VF combination in each DE group was computed for each participant. No significant main effects of DE group [$F(1, 37) = 1.695, P = 0.201, \text{partial } \eta^2 = 0.044$] were noted. However, a significant main effect of VF [$F(1, 37) = 29.614, P < 0.001, \text{partial } \eta^2 = 0.445$] was observed, indicating that participants' RTs were significantly longer for stimuli presented in the LVF (mean = 346.22, SD = 55.97) than they were for stimuli presented in the RVF (mean = 330.28, SD = 58.96) group [$F(1, 38) = 30.132, P < 0.001, \text{partial } \eta^2 = 0.442$, also Bonferroni-corrected $P < 0.001$]. The main effect of response hand was not significant ($P = 0.203, \text{partial } \eta^2 = 0.043$). None of the other effects was significant.

ERP data

P100 amplitude. The P100 amplitude revealed no significant main effects of DE group [$F(1, 37) = 1.961, P = 0.170, \text{partial } \eta^2 = 0.050$] (Supplementary Figure S1A). There was a significant interaction between hemisphere and VF [$F(1, 37) = 30.418, P < 0.001, \text{partial } \eta^2 = 0.451$]; specifically, there was a double dissociation between these factors. In the LH (O1), the P100 amplitudes for stimuli presented in the LVF (mean = 4.46, SD = 2.43) were significantly larger than were those for stimuli presented in the RVF (mean = 3.30, SD = 1.99) group [$F(1, 38) = 14.651, P < 0.001, \text{partial } \eta^2 = 0.278$, also Bonferroni-corrected $P < 0.001$]. In the RH (O2), the P100 amplitudes for stimuli presented in the RVF (mean = 4.27, SD = 1.70) were significantly larger than were those for stimuli presented in the LVF (mean = 3.56, SD = 2.28) [$F(1, 38) = 5.850, P < 0.05, \text{partial } \eta^2 = 0.133$, also Bonferroni-corrected $P < 0.05$] (Supplementary Figure S1B). That is, stimuli presented in the ipsilateral VF with respect to the hemisphere elicited P100 amplitudes that were significantly greater than were those elicited by stimuli presented in the contralateral VF.

P100 latency. The P100 latency revealed a marginally significant main effect of DE group [$F(1, 37) = 3.939, P = 0.055, \text{partial } \eta^2 = 0.096$], indicating that the latency in the LDE group (mean = 122.08, SD = 8.17) tended to be longer than in the RDE group (mean = 116.87, SD = 8.17). There was a significant interaction between hemisphere and VF [$F(1, 37) = 196.502, P < 0.001, \text{partial } \eta^2 = 0.842$], revealing a double dissociation between these factors. Specifically, the P100 latency in the RH (mean = 106.42, SD = 14.45) was significantly shorter than in the LH (mean = 134.67, SD = 15.34) for stimuli presented in the LVF, whereas the P100 latency in the LH (mean = 100.36, SD = 10.54) was significantly shorter than in the RH (mean = 135.64, SD = 12.70) for stimuli presented in the RVF. That is, the P100 latency for stimuli presented in the ipsilateral VF with respect to the hemisphere was significantly longer [$F(1, 38) = 138.767, P < 0.001, \text{partial } \eta^2 = 0.785$, also Bonferroni-corrected $P < 0.001$, and $F(1, 38) = 116.360, P < 0.001, \text{partial } \eta^2 = 0.754$, also Bonferroni-corrected $P < 0.001$ for the VF differences in the LH and RH, respectively].

N170 amplitude. The N170 amplitude revealed a significant main effect of DE group [$F(1, 37) = 5.852, P < 0.05, \text{partial } \eta^2 = 0.137$], with the RDE group (mean = -3.92, SD = 1.97) having N170 amplitudes that were significantly more negative than those in the LDE group (mean = -2.39, SD = 1.97) (Bonferroni-corrected $P < 0.05$; Figure 3A). A significant interaction was found between the DE group and VF [$F(1, 37) = 7.896, P < 0.01, \text{partial } \eta^2 = 0.176$], suggesting that the face stimuli presented in the LVF elicited amplitudes that were significantly more negative in the RDE group (mean = -4.15, SD = 2.59) than they were in the LDE group (mean = -1.66, SD = 2.16) (Figures 3B and 4A). However, the amplitudes elicited by stimuli presented in the RVF were not significant in both groups (LDE: mean = -1.39, SD = 2.24; RDE: mean = -2.74, SD = 2.28; Figures 3B and 4B). Critically, a significant difference was only noted between the VFs in the RDE group (Figure 3B). For the RDE group, compared with faces presented in the RVF (mean = -2.74, SD = 2.28), faces presented in the LVF (mean = -4.15, SD = 2.59) elicited amplitudes that were significantly more negative [$F(1, 20) = 16.625, P < 0.01, \text{partial } \eta^2 = 0.454$, also Bonferroni-corrected $P < 0.01$], which is consistent with the LVF superiority for faces. For the LDE group, there was no significant difference in VFs (LVF: mean = -1.66, SD = 2.16, RVF: mean = -1.39, SD = 2.24). Furthermore, a significant interaction was observed between hemisphere and VF [$F(1, 37) = 14.928, P < 0.001, \text{partial } \eta^2 = 0.287$], indicating a double dissociation between these factors. Specifically, stimuli presented in the contralateral VF with respect to the hemisphere elicited N170 amplitudes that were significantly more negative than were those elicited to stimuli presented in the ipsilateral VF [$F(1, 38) = 6.791, P < 0.05, \text{partial } \eta^2 = 0.152$, also Bonferroni-corrected $P < 0.05$ and $F(1, 38) = 14.436, P < 0.01, \text{partial } \eta^2 = 0.275$, also $P < 0.01$ for the VF differences in the LH and RH, respectively].

N170 latency. The N170 latency revealed a marginally significant main effect for the DE group [$F(1, 37) = 3.753, P = 0.060, \text{partial } \eta^2 = 0.092$], suggesting that the latency in the LDE group (mean = 187.19, SD = 18.86) tended to be longer than that in the RDE group (mean = 177.94, SD = 10.31). There was also a significant interaction between the hemisphere and VF [$F(1, 37) = 86.820, P < 0.001, \text{partial } \eta^2 = 0.701$], suggesting a double dissociation relationship between them. Specifically, the N170 latency in the hemisphere contralateral to the VF in which the stimuli were presented was significantly shorter than the latency in the ipsilateral hemisphere [$F(1, 38) = 72.430, P < 0.001, \text{partial } \eta^2 = 0.656$, also Bonferroni-corrected $P < 0.001$ and $F(1, 38) = 50.956, P < 0.001, \text{partial } \eta^2 = 0.573$, also Bonferroni-corrected $P < 0.001$ for the VF differences in the LH and RH, respectively].

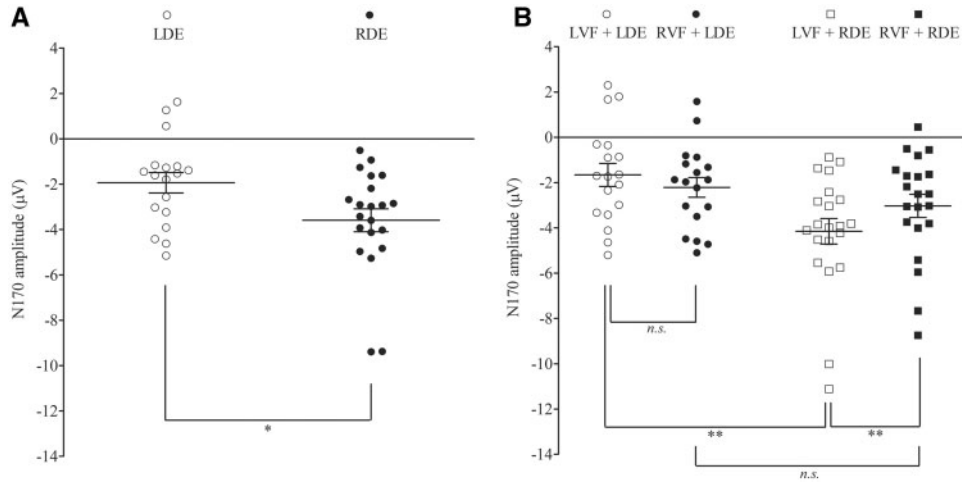


Fig. 3. Results of N170 amplitudes (μV). The graphs show the mean N170 amplitude over electrodes P7, PO7, P8 and PO8. (A) The open circles indicate the LDE group, while the filled circles indicate the RDE group. A scatter plot showing the amplitudes of the N170 responses in the two DE groups. (B) Circles indicate the LDE group, while squares indicate the RDE group. Open shapes indicates the LVF, while filled shapes indicate the RVF. Scatter plots showing the amplitudes of the N170 responses for the different DE and VF combinations. The error bars indicate SE.

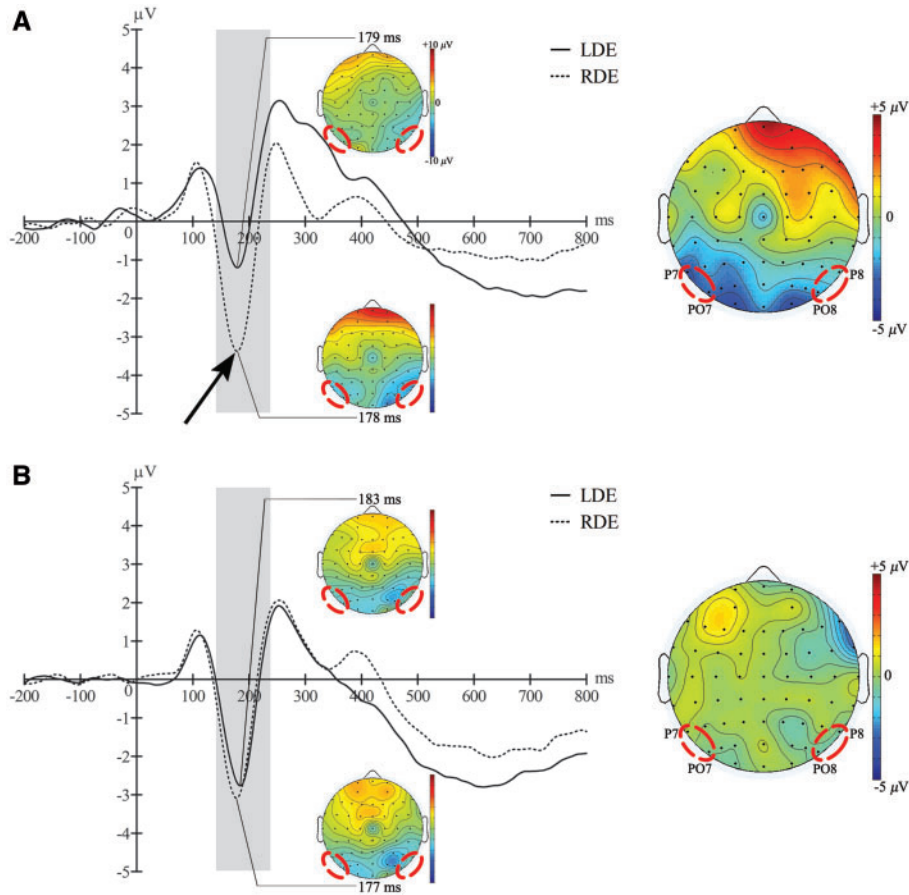


Fig. 4. The N170 waveform and topography. The graphs show the averaged signals over electrodes P7, PO7, P8 and PO8. The solid line represents the LDE group, while the dotted line represents the RDE group. (A) Waveforms and topographies of the N170 components elicited by each DE group in the LVF. (B) Waveforms and topographies of the N170 components elicited by each DE group in the RVF. The gray area represents the range of the N170 component (140–240 ms).

Discussion

Our study provides the first neural evidence of the DE's role in face processing. We found that the LVF superiority phenomenon is highly dependent on eye dominance. Specifically, LVF

superiority was robustly observed when the RDE group responded to face stimuli presented in the LVF; this phenomenon was significantly diminished when the LDE group responded to stimuli presented in the LVF. Moreover, the LVF phenomenon in the LDE group was significantly decreased compared with the

response for stimuli presented in the RVF. Collectively, our results suggest that the well-established LVF superiority phenomenon depends on the participants' DE.

Here, the N170 amplitudes in the RDE group were considerably larger than were those in the LDE group, and the N170 latency tended to be delayed in the LDE group relative to that in the RDE group. The delayed N170 latency reflects that face processing was more difficult for participants in the LDE group than it was for those in the RDE group (Rossion *et al.*, 1999). Consistent with the strengthened response to stimuli presented in the LVF in the RDE group, we also found that the RH, which was ipsilateral to the RDE, was more actively involved in face perception (Figure 5B).

A double dissociation between the VF and hemisphere was consistently observed in the amplitude and latency of both the P100 and N170. The amplitude and latency of the P100 component were larger and longer, respectively, in the hemisphere ipsilateral to the VF in which the face stimuli were presented, whereas the amplitude and latency of the N170 component were larger and shorter, respectively, in the hemisphere contralateral to the VF in which the face stimuli were presented. The P100 component's maximal response occurs in the hemisphere ipsilateral to the hemifield being stimulated, a phenomenon known as the paradoxical effect, in which visual evoked potentials do not show the anatomically predicted amplitude asymmetry (Barrett *et al.*, 1976). In particular, the double dissociation in the N170 amplitude implies that the intensity of the LVF superiority varies depending on the DE (Figure 6). In the present study, the LDE group did not show significantly reduced N170 amplitudes in either hemisphere relative to the total group

($P=0.076$ and 0.379 for the LH and RH, respectively), whereas the RDE group showed larger N170 amplitudes across both hemispheres ($P=0.029$ and 0.032 for the LH and RH, respectively). These results indicate that the LVF superiority was intensified in the RDE group relative to the total group. In addition, the intensity of the LVF superiority consistently increased as it moved towards the RDE group (LDE to total group to RDE). However, no significant interactions were observed among the factors of DE, hemisphere and VF. In sum, the LVF superiority identified in the RDE group was based on the RH dominance.

On the basis of our results, we propose that RDE individuals might have a biological mechanism that is more favorable for face processing compared with LDE individuals. This proposal is consistent with abundant literature arguing that human facial processing is pre-dominantly served by the RH (De Renzi *et al.*, 1968, 1994; Carey and Diamond, 1980; Moscovitch and Klein, 1980; Gazzaniga and Smylie, 1986; Levine *et al.*, 1988; Gazzaniga, 2000; Le Grand *et al.*, 2003; Kanwisher and Yovel, 2006; Thomas *et al.*, 2008; Yovel *et al.*, 2008). Importantly, our proposal helps elucidate the brain hemisphere and eye that are specialized for face processing. Several neuropsychiatric disorders support our proposal. For example, individuals with autism show deficits in attending to faces and in their face-processing abilities. Hernandez *et al.* (2009) showed that healthy adults begin to explore the face by looking at the eye in the VF contralateral to their DE, whereas RDE patients with autism begin to explore the face by looking at the eye in the VF ipsilateral to their DE. Such findings suggest that face processing is more closely related to innate factors such as eye dominance (Reiss and Reiss, 1997)

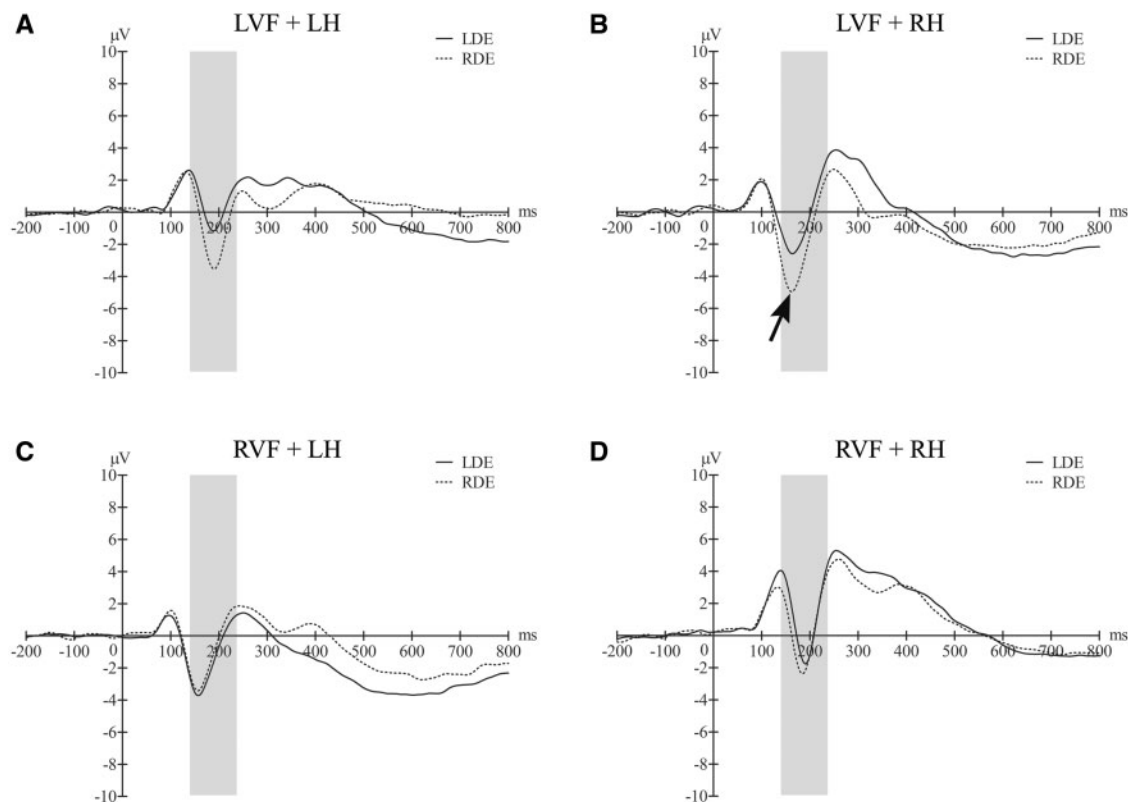


Fig. 5. N170 waveforms from each hemisphere and VF in the two DE groups. The graphs show the averaged signals over electrodes P7 and PO7 for the LH (A and C), and P8 and PO8 for the RH (B and D). The solid line represents the LDE group, while the dotted line represents the RDE group. (A) N170 amplitudes in the LH for stimuli presented in the LVF. (B) N170 amplitudes in the RH for stimuli presented in the LVF. (C) N170 amplitudes in the LH for stimuli presented in the RVF. (D) N170 amplitudes in the RH for stimuli presented in the RVF.

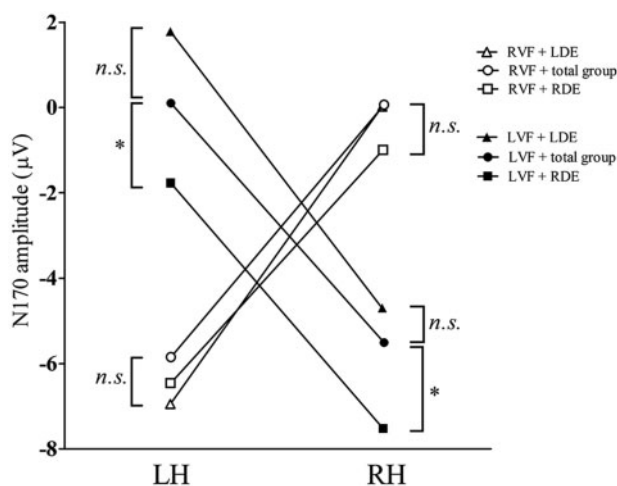


Fig. 6. The intensity of the LVF superiority depending on the DE. The graphs show the averaged signals over electrodes P7 and PO7 for the LH and P8 and PO8 for the RH. Shapes indicate the LDE group (triangles), total group (circles) and RDE group (squares). Open shapes indicate N170 amplitudes in the RVF, while filled shapes indicate N170 amplitudes in the LVF.

than to acquired factors, and that malfunctions in these innate factors could result in disorders such as autism. Additionally, patients with schizophrenia reportedly employ different visual scanning strategies for facial stimuli. Specifically, while healthy adults prefer to view the left side of the face first, patients with schizophrenia prefer to view the right side of the face first (Phillips and David, 1997), suggesting RH dysfunction in schizophrenia (Barnett et al., 2005; see also Cutting, 1990).

Here, we showed that the LVF superiority for faces was intensified by the RDE. However, it remains unclear how the LVF superiority would be induced in a real population comprised of RDE and LDE individuals. To examine this, we generated an artificial population by randomly extracting the N170 amplitudes from seven subjects in the LDE/LVF group and 14 subjects in the RDE/LVF group (one-third for the LDE and two-thirds for the RDE according to the ratio of eye dominance in the general population; the total number of subjects 21 matched the total number of subjects in the RDE group) and performing 5000 permutations of the sampling process. The permutation results were compared with those from our LDE and RDE groups (LDE vs general population vs RDE = $-1.42 \mu\text{V}$ vs $-2.71 \mu\text{V}$ vs $-4.64 \mu\text{V}$). These results indicate that the LVF superiority based on only either LDE or RDE individuals may be different from that based on general population samples. Hence, future studies should collect more-detailed information on the subject population in order to perform face-processing research that is more precise.

We also investigated whether the visual cortex ipsilateral to the LDE would be strongly activated by a face presented in the RVF, as the RDE processes a face better when it is presented in the LVF. Our analysis (Figure 3B) showed that the N170 amplitudes in the LDE group were equivalent to those in the RDE group for stimuli presented in the RVF, suggesting that the visual cortex ipsilateral to the LDE was activated as much as the visual cortex contralateral to the RDE. Thus, the RDE elicits strong activation to faces presented in both the LVF and RVF.

For the RT data, a pattern opposite to that for the ERP results was observed, as faster RTs were noted for stimuli presented in the RVF than for stimuli presented in the LVF. Sergent and Bindra (1981) found that the LVF advantage may be boosted under certain conditions, such as when highly distinguishable

faces or unfamiliar faces are used. Faces are highly discriminable if the distinguishing dissimilarities, like the jaw or hairline contours, are salient. In this regard, our face stimuli (Figure 1) were not highly discriminable or unfamiliar; we only used four faces, and the salient external features were removed from each face, which may have made it difficult for participants to discriminate among the faces. Additionally, familiar faces (e.g. famous faces or experimentally familiarized faces) are known to induce the RVF advantage (Marzi et al., 1974; Marzi and Berlucchi, 1977; Bruyer and Stroop, 1984). During the course of our experiment, the participants likely became familiarized with the face stimuli, since the RT in the first block (mean = 358.76 ms) was significantly longer than the RT in the last block (mean = 316.48 ms).

Our study has limitations. We only included right-handed individuals, thus any conclusions based on these findings should be interpreted with caution. However, our subjects were asked to alternate their response hand in each block to control for the effect of the response hand; we did not observe any significant effects of the response hand. It should be also noted that we did not use a chin rest or other types of head stabilization during the experiment because it is very important for the subjects to be seated in a comfortable position to avoid possible muscle artifacts and noises in the ERP experiments. It was reported that chin rests become uncomfortable after 15 min (Luck, 2014). Instead, we thoroughly supervised whether the participant's head was positioned in the middle during the course of the experiment. A further limitation is that our study lacked a control condition consisting of non-face stimuli. Therefore, the DE's effects on the LVF superiority may extend to all visual stimuli presented in the LVF, not just face stimuli. To rule out this possibility, we performed the experiment with an additional control condition (i.e. Fourier phase-scrambled faces; Supplementary Figure S2). The results showed that for scrambled faces, neither the main effect of DE ($P=0.368$) (Supplementary Figure S3A) nor the interaction effect between DE and VF was significant ($P=0.184$) (Supplementary Figures S3B and S4), implying that the effects of the DE on the LVF superiority phenomenon are specific for faces.

In summary, our findings demonstrate the first neural evidence of the DE's effects on the LVF superiority for faces. Importantly, we found that the DE might mediate the LVF superiority phenomenon for face processing. Furthermore, the DE with a contralateral relationship to the LVF was better able to represent the face images. We hope that our findings will be helpful to future studies, particularly with regard to determining whether neural asymmetry is associated with other lateralized cognitive functions in healthy and patient populations.

Supplementary data

Supplementary data are available at SCAN online.

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References

- Barnett, K., Kirk, I., Corballis, M. (2005). Right hemispheric dysfunction in schizophrenia. *Laterality, Asymmetries of Body, Brain, and Cognition*, *10*, 29–35.
- Barrett, G., Blumhardt, L., Halliday, A., Halliday, E., Kriss, A. (1976). A paradox in the lateralisation of the visual evoked response. *Nature*, *261*, 253–5.
- Bentin, S., Deouell, L.Y. (2000). Structural encoding and identification in face processing: ERP evidence for separate mechanisms. *Cognitive Neuropsychology*, *17*, 35–55.
- Blake, R. (2004). Binocular rivalry. In: L. M. W. Chalupa, J. S., editors. *The Visual Neurosciences*, MIT Press: Cambridge, MA.
- Bourassa, D.C., McManus, I.C., Bryden, M.P. (1996). Handedness and eye-dominance: a meta-analysis of their relationship. *Laterality*, *1*, 5–34.
- Bruyer, R., Stroot, C. (1984). Lateral differences in face processing: Task and modality effects. *Cortex*, *20*, 377–90.
- Carey, D.P., Hutchinson, C.V. (2013). Looking at eye dominance from a different angle: is sighting strength related to hand preference? *Cortex*, *49*, 2542–52.
- Carey, S., Diamond, R. (1980). Maturation of the developmental course of face encoding. *Biological Studies of Mental Processes* 60–93.
- Cohen, L., Dehaene, S., Naccache, L., et al. (2000). The visual word form area. *Brain*, *123*, 291–307.
- Coren, S. (1999). Sensorimotor performance as a function of eye dominance and handedness. *Perceptual and Motor Skills*, *88*, 424–6.
- Cutting, J. (1990). *The Right Cerebral Hemisphere and Psychiatric Disorders*, Oxford University Press: Oxford.
- De Renzi, E., Faglioni, P., Spinnler, H. (1968). The performance of patients with unilateral brain damage on face recognition tasks. *Cortex*, *4*, 17–34.
- De Renzi, E., Perani, D., Carlesimo, G.A., Silveri, M., Fazio, F. (1994). Prosopagnosia can be associated with damage confined to the right hemisphere—an MRI and PET study and a review of the literature. *Neuropsychologia*, *32*, 893–902.
- Dehaene, S., Cohen, L. (2011). The unique role of the visual word form area in reading. *Trends in Cognitive Sciences*, *15*, 254–62.
- Dellatolas, G., Curt, F., Dargent-Pare, C., De Agostini, M. (1998). Eye dominance in children: a longitudinal study. *Behavior Genetics*, *28*, 187–95.
- Ehrenstein, W.H., Arnold-Schulz-Gahmen, B.E., Jaschinski, W. (2005). Eye preference within the context of binocular functions. *Graefes' Archive for Clinical and Experimental Ophthalmology*, *243*, 926–32.
- Eimer, M. (2000). Event-related brain potentials distinguish processing stages involved in face perception and recognition. *Clinical Neurophysiology*, *111*, 694–705.
- Erdogan, A.R., Özdikici, M., Aydin, M.D., Aktas, Ö., Dane, S. (2002). Right and left visual cortex areas in healthy subjects with right- and left-eye dominance. *International Journal of Neuroscience*, *112*, 517–23.
- Eser, I., Durrie, D.S., Schwendeman, F., Stahl, J.E. (2008). Association between ocular dominance and refraction. *Journal of Refractive Surgery*, *24*, 685–9.
- Freeman, G., Chapman, J. (1935). Minor studies from the psychological laboratory of Northwestern University. *American Journal of Psychology*, *47*, 146–51.
- Gazzaniga, M., Smylie, C. (1986). Right hemisphere superiorities: more apparent than real? *Society for Neuroscience Abstracts*, *12*(2), 1449.
- Gazzaniga, M.S. (2000). Cerebral specialization and interhemispheric communication. *Brain*, *123*, 1293–326.
- Hernandez, N., Metzger, A., Magné, R., et al. (2009). Exploration of core features of a human face by healthy and autistic adults analyzed by visual scanning. *Neuropsychologia*, *47*, 1004–12.
- Itier, R.J., Taylor, M.J. (2004). N170 or N1? Spatiotemporal differences between object and face processing using ERPs. *Cerebral Cortex*, *14*, 132–42.
- Kanwisher, N., Yovel, G. (2006). The fusiform face area: a cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *361*, 2109–28.
- Le Grand, R., Mondloch, C.J., Maurer, D., Brent, H.P. (2003). Expert face processing requires visual input to the right hemisphere during infancy. *Nature Neuroscience*, *6*, 1108–12.
- Lee, S.-H., Kim, D.-W., Kim, E.-Y., Kim, S., Im, C.-H. (2010). Dysfunctional gamma-band activity during face structural processing in schizophrenia patients. *Schizophrenia Research*, *119*, 191–7.
- Lee, S.-H., Kim, S., Shim, M.-S., Kim, D.-W., Im, C.-H. (2016). Dysfunctional patterns of gamma-band activity in response to human faces compared to non-facial stimuli in patients with schizophrenia. *Psychiatry Investigation*, *13*, 349–59.
- Levine, S.C., Banich, M.T., Koch-Weser, M.P. (1988). Face recognition: a general or specific right hemisphere capacity? *Brain and Cognition*, *8*, 303–25.
- Liu, J., Harris, A., Kanwisher, N. (2002). Stages of processing in face perception: an MEG study. *Nature Neuroscience*, *5*, 910–6.
- Lovie-Kitchin, J.E. (1988). Validity and reliability of visual acuity measurements. *Ophthalmic and Physiological Optics*, *8*, 363–70.
- Luck, S.J. (2014). *An Introduction to the Event-Related Potential Technique*, MIT Press: Cambridge, MA.
- Lund, F.H. (1932). The dependence of eye-hand coordinations upon eye-dominance. *The American Journal of Psychology*, *44*, 756–62.
- Marzi, C., Berlucchi, G. (1977). Right visual field superiority for accuracy of recognition of famous faces in normals. *Neuropsychologia*, *15*, 751–6.
- Marzi, C., Brizzolara, D., Rizzolatti, G., Umiltà, C., Berlucchi, G. (1974). Left hemisphere superiority for the recognition of well known faces. *Brain Research*, *66*, 358.
- Miles, W.R. (1930). Ocular dominance in human adults. *The Journal of General Psychology*, *3*, 412–30.
- Minucci, P.K., Connors, M.M. (1964). Reaction time under three viewing conditions: binocular, dominant eye, and nondominant eye. *Journal of Experimental Psychology*, *67*, 268.
- Moscovitch, M., Klein, D. (1980). Material-specific perceptual interference for visual words and faces: implications for models of capacity limitations, attention, and laterality. *Journal of Experimental Psychology: Human Perception and Performance*, *6*, 590.
- Oldfield, R.C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, *9*, 97–113.
- Park, J.Y., Oh, J.M., Kim, S.Y., et al. (2011). *Korean Facial Expressions of Emotion (KOFEE)*, Seoul, Korea: Section of Affect & Neuroscience, Institute of Behavioral Science in Medicine, Yonsei University College of Medicine.
- Phillips, M., David, A. (1997). Viewing strategies for simple and chimeric faces: an investigation of perceptual bias in normals and schizophrenic patients using visual scan paths. *Brain and Cognition*, *35*, 225–38.
- Porac, C., Coren, S. (1976). The dominant eye. *Psychol Bull*, *83*, 880–97.
- Reiss, M., Reiss, G. (1997). Ocular dominance: some family data. *Laterality: Asymmetries of Body, Brain and Cognition*, *2*, 7–16.

- Rombouts, S.A., Barkhof, F., Sprenger, M., Valk, J., Scheltens, P. (1996). The functional basis of ocular dominance: functional MRI (fMRI) findings. *Neuroscience Letters*, **221**, 1–4.
- Rossion, B., Delvenne, J.-F., Debatisse, D., et al. (1999). Spatio-temporal localization of the face inversion effect: an event-related potentials study. *Biological Psychology*, **50**, 173–89.
- Rossion, B., Jacques, C. (2008). Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. *Neuroimage*, **39**, 1959–79.
- Semlitsch, H.V., Anderer, P., Schuster, P., Presslich, O. (1986). A solution for reliable and valid reduction of ocular artifacts, applied to the P300 ERP. *Psychophysiology*, **23**, 695–703.
- Sergent, J., Bindra, D. (1981). Differential hemispheric processing of faces: methodological considerations and reinterpretation. *Psychological Bulletin*, **89**, 541.
- Shima, H., Hasegawa, M., Tachibana, O., et al. (2010). Ocular dominance affects magnitude of dipole moment: an MEG study. *Neuroreport*, **21**, 817–21.
- Taghavy, A., Kügler, C. (1987). Pattern reversal visual evoked potentials (white-black-and colour-black-PVEPs) in the study of eye dominance. *European Archives of Psychiatry and Neurological Sciences*, **236**, 329–32.
- Thomas, C., Avidan, G., Humphreys, K., Jung, K.-J., Gao, F., Behrmann, M. (2008). Reduced Structural Connectivity in Ventral Visual Cortex in Congenital Prosopagnosia.
- Yang, E., Blake, R., McDonald, J.E. (2010). A new interocular suppression technique for measuring sensory eye dominance. *Investigative Ophthalmology & Visual Science*, **51**, 588–93.
- Yovel, G., Tambini, A., Brandman, T. (2008). The asymmetry of the fusiform face area is a stable individual characteristic that underlies the left-visual-field superiority for faces. *Neuropsychologia*, **46**, 3061–8.