FACE GENDER CATEGORIZATION AND HEMISPHERIC ASYMMETRIES: CONTRASTING EVIDENCE FROM CONNECTED AND DISCONNECTED BRAINS

GIULIA PRETE, ** MARA FABRI, *D NICOLETTA FOSCHI *C AND LUCA TOMMASI **

Abstract—We investigated hemispheric asymmetries in categorization of face gender by means of a divided visual field paradigm, in which female and male faces were presented unilaterally for 150 ms each. A group of 60 healthy participants (30 males) and a male split-brain patient (D.D.C.) were asked to categorize the gender of the stimuli. Healthy participants categorized male faces presented in the right visual field (RVF) better and faster than when presented in the left visual field (LVF), and female faces presented in the LVF than in the RVF, independently of the participants' sex. Surprisingly, the recognition rates of D.D.C. were at chance levels - and significantly lower than those of the healthy participants - for both female and male faces presented in the RVF, as well as for female faces presented in the LVF. His performance was higher than expected by chance - and did not differ from controls - only for male faces presented in the LVF. The residual right-hemispheric ability of the splitbrain patient in categorizing male faces reveals an owngender bias lateralized in the right hemisphere, in line with the rightward own-identity and own-age bias previously shown in split-brain patients. The gender-contingent hemispheric dominance found in healthy participants confirms the previously shown right-hemispheric superiority in recognizing female faces, and also reveals a left-hemispheric superiority in recognizing male faces, adding an important evidence of hemispheric imbalance in the field of face and gender perception. © 2016 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: face gender categorization, hemispheric asymmetries, split-brain, own-gender bias.

E-mail address: giulia.prete@unich.it (G. Prete).

Abbreviations: CC, corpus callosum; LVF, left visual field; ORB, own-race bias; OGB, own-gender bias; OAB, own-age bias; RVF, right visual field.

http://dx.doi.org/10.1016/j.neuroscience.2016.10.021 0306-4522/© 2016 IBRO. Published by Elsevier Ltd. All rights reserved.

INTRODUCTION

Humans are social animals, living in a social environment and interacting with each other for individual and group-related reasons. As social individuals, we are sensitive to our conspecifics, and the most informative cue exploited to recognize and categorize our conspecifics is their faces. The evolutionary basis of this extraordinary ability is confirmed by the evidence of a similar bias for conspecifics' face recognition in a number of species besides humans (see Leopold and Rhodes, 2010 for a review).

Decades of research have definitively confirmed a right-hemispheric superiority for face processing (Meadows, 1974), both at a neural level (e.g., Yovel et al., 2008), and at a behavioral level (e.g., Prete et al., 2015b), not only in humans, but also in other animals species (for reviews, see Rosa Salva et al., 2012; Rogers et al., 2013). The most agreed-upon explanation of this evidence is that of a right-hemispheric superiority in global shape processing - faces being processed as a global percept – as opposed to a left-hemispheric superiority in local processing (Yovel et al., 2001). Nevertheless, if the right-hemispheric lateralization for face processing appears unquestionable, hemispheric asymmetries are much more controversial when analyzed separately for the specific features of the face, such as gender, age, ethnical group, and so on. In humans, this issue has been explored by means of behavioral paradigms, neuroimaging studies, and neurological patients. A neurological condition which is still very informative about a possible cerebral imbalance is that of epileptic patients who underwent the surgical resection of the corpus callosum (CC). in an attempt to reduce the spread of epileptic activity between the hemispheres ("split-brain" patients). Although this surgical treatment is rarely used today, thanks to the development of more efficient pharmacological therapies than those available in the past years, the performance of such patients, in whom the left and right cerebral hemispheres are surgically disconnected, constitutes a milestone for the investigation of hemispheric abilities (e.g., Gazzaniga, 2005).

Using a divided visual field paradigm, Mason and Macrae (2004) asked a group of healthy participants and a male split-brain patient (J.W.) to carry out a face gender categorization task, and a face identity recognition task. The results revealed no cerebral asymmetries in gender recognition, but they showed a right-hemispheric

^a Department of Psychological Science, Health and Territory,

[&]quot;G. d'Annunzio" University of Chieti-Pescara, Italy

^b Department of Clinical and Experimental Medicine, Neuroscience and Cell Biology Section, Polytechnic University of Marche, Ancona, Italy

^c Regional Epilepsy Center, Neurological Clinic, "Ospedali Riuniti", Ancona, Italy

^{*}Corresponding author at: Department of Psychological Science, Health and Territory, University of Chieti, BLOCCO A, Via dei Vestini 29, I-66013 Chieti, Italy. Fax: +39-871-35542163.

superiority during identity recognition, both in healthy participants and in the patient. This superiority was also supported by functional magnetic resonance imaging (fMRI) results in healthy participants, showing that the right fusiform gyrus and the right temporal gyrus were more strongly activated in the identity recognition task than in the gender recognition task, during the central presentation of the faces (Mason and Macrae, 2004).

Even in the literature on split-brain patients, however, the evidence of hemispheric dominance is not consistent for different facial characteristics, such as identity. For instance, exploring the cerebral asymmetry for self-face recognition, Turk et al. (2002) found that the left disconnected hemisphere of the patient J.W. was dominant with respect to the right hemisphere, even if both hemispheres were able at recognizing faces. On the other hand. Keenan et al. (2003) found the opposite pattern of results: the right disconnected hemisphere of the patient M.L. was better than the left hemisphere in self-face recognition. This latter result is in line with a previously shown increased galvanic skin response when own face was presented to the right hemisphere of a split-brain patient (Preilowski, 1979). Keenan and Gorman (2007) explained the difference between the results of the patient M.L. (Keenan et al., 2003) and those of the patient J.W. (Turk et al., 2002) as possibly due to "pre-surgical condition, the nature of the surgery, post-operative response, a difference in testing methods, or perhaps an interaction between these variables" (p. 1076). Moreover, a different study in which Turk et al. (2005) exploited a delayed match-to-sample task revealed that the patient J.W. showed a right-hemispheric superiority in recognizing faces of his own ethnicity. Specifically, the results confirmed the expected own-race bias (ORB), and revealed that the disconnected right hemisphere of the patient better recognized Caucasian than Japanese faces, showing that the ORB is right-lateralized. However, by administering the same task to nine healthy participants, the authors confirmed the ORB, but no hemispheric lateralization was found.

As regards cerebral asymmetries for face gender processing, Proverbio et al. (2010) recorded Event-Related brain Potentials (ERPs) in healthy participants during the passive viewing of female and male faces, and found that faces of the opposite gender than the participants' elicited a larger and earlier centro-parietal N400 compared to faces of their own gender (both in female and male participants), whereas a greater occipitoparietal late positive component was elicited when faces of the same-gender as the participants' were presented. Importantly, the results revealed that the N400 (the "marker" of other-gender) mainly involved the left hemisphere, whereas the late positive component (the "marker" of own-gender) was mainly lateralized to the right hemisphere. An unexpected hemispheric imbalance during face gender recognition was found in a behavioral study carried out by Parente and Tommasi (2008): the authors presented healthy participants with either female and male whole faces, or chimeric faces in which the left/ right halves were of the same gender, or chimeric faces composed by two hemifaces of different gender (half

female and half male). They found that male-male chimeric faces were recognized better than female-female faces, independently of the participants' gender. Importantly, they found that female-male chimeric faces were better recognized than male-female stimuli, showing a right-hemispheric superiority for female faces recognition, without differences between female and male observers. The authors explained the right-hemispheric superiority in recognizing female faces by referring to the lateralized bias in maternal cradling, that has been shown to occur preferentially on the left side of the body's midline, possibly attributable to the right-hemispheric superiority for (female) face processing (Todd and Banerjee, 2016). Finally, it has to be highlighted that Wright and Sladden (2003) confirmed the OGB both in female and male healthy participants, but they also showed that part of the bias was attributable to the hairstyle of the faces used as stimuli. In the study by Parente and Tommasi (2008) the hairstyle was hidden by enclosing faces in a white oval-shaped mask, and this could be one reason for the absence of an overall OGB. Moreover, Verdichevski and Steeves (2013) investigated the effect of face age and gender on the face identity recognition: the authors asked healthy participants to carry out a same/different task during the presentation of female/male, young/old faces. The results revealed an own-age bias (OAB), due to the better performance of older participants during the presentation of older faces (also a trend toward the OAB was found in vounger participants for vounger faces), together with an own-gender bias (OGB), at least in females, due to the fact that females outperformed males during the presentation of female faces. Since the results revealed an overall better performance by older than younger participants. the authors concluded that this finding could be ascribed to the more extensive experience that older people have with persons of all ages.

To summarize, the ERPs results by Proverbio et al. (2010) suggest a right-hemispheric superiority in the processing of faces containing the same characteristics as those of the observers, specifically the gender, whereas the behavioral results described by Parente and Tommasi (2008) suggest a right-hemispheric superiority for the recognition of female faces, independently of the participants' gender. Finally, Mason and Macrae (2004) failed in finding any cerebral asymmetry in a gender recognition task, both in healthy observers and in a split-brain patient. Thus, it seems to emerge that face gender is independent of other facial characteristics, such as identity or ethnicity, which appear to be a righthemipsheric domain. In fact, apart from the evidence of a left-hemispheric superiority in the identification of own face found in a split-brain patient by Turk et al. (2002), the other findings reported above seem to suggest a right-hemispheric superiority in categorizing faces having the same characteristic as those of the patients tested (e.g., self-face: Preilowski (1979), Keenan et al. (2003); face ethnicity: Turk et al. (2005)). Results collected with healthy participants lead to a less clear hemispheric imbalance: for example, cerebral asymmetries were not found in the control group tested by Turk et al. (2005) for the ORB; similarly, Mason and Macrae (2004) failed

to find cerebral asymmetries during a gender recognition task in healthy participants. Nevertheless, different – and inconsistent – evidences of hemispheric asymmetry during face gender recognition were described by Proverbio et al. (2010), and by Parente and Tommasi (2008).

The stronger right-hemispheric involvement in recognizing faces having characteristics in common with the observer has been generally explained as coming from the right-lateralized neural substrates of self representation and self consciousness, mainly involving the right temporal and prefrontal areas (e.g., Feinberg and Keenan, 2005; Keenan et al., 2005; Devue and Brédart, 2011).

In an attempt to clarify the relationship between hemispheric abilities and face gender categorization, in the present study we exploited a divided visual field paradigm, in which female and male healthy participants, and a male split-brain patient (D.D.C.) were asked to categorize the gender of female and male faces. Starting from the evidence of a hairstyle influence on face gender recognition (Wright and Sladden, 2003), we hid the hair of the facial stimuli, by using a white oval-shaped mask as that used by Parente and Tommasi (2008). Moreover, besides the lateral presentation of the stimuli, a central presentation condition was also exploited in a separate session, in order to ensure that the stimuli presented briefly and laterally were correctly categorized as female or male when presented centrally and without time limits (i.e. the central presentation being used as a control condition). Starting from the results described above, we expected to find a righthemispheric OGB in the split-brain patient, whereas we have no specific hypotheses concerning the performance of healthy participants.

EXPERIMENTAL PROCEDURES

Participants

The experiment was administered to D.D.C., a patient with a total resection of the CC, and to 60 healthy participants.

D.D.C. is an Italian man, 38-year-old at the time of the test, who underwent a two-stages callosotomy in an attempt to reduce the spread of epileptic activity between the hemispheres (a partial resection of the CC was carried out in 1994 and the complete callosal resection was carried out in 1995). Also the anterior commissure was partially sectioned (Fig. 1). D.D.C.'s postoperative IQ was 83, as measured by means of the Wechsler Adult Intelligence Scale (WAIS), and his laterality quotient was +40, according to the Edinburgh Handedness Inventory (Oldfield, 1971), in which a score of -100 corresponds to a complete left preference, and +100 corresponds to a complete right preference.

D.D.C. had no visual impairments or psychiatric symptoms and was tested at the Epilepsy Center of the Polytechnic University of Marche (Torrette of Ancona), during a pause between routine neurological examinations.

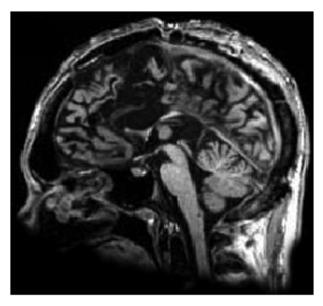


Fig. 1. Midsagittal MRI of patient D.D.C., showing the complete absence of callosal fibers.

A sample of 60 healthy participants took part in the test (30 females; mean age: 22.35 ± 0.31). All participants were right-handed (mean: 67.85 ± 2.45), as measured by the Edinburgh Handedness Inventory (Oldfield, 1971), and they had normal or corrected-to-normal vision. They were tested as volunteers at the Psychobiology Laboratory of the University of Chieti.

Stimuli

Stimuli were 26 photographs of faces in frontal view chosen from the database Karolinska Directed Emotional Faces (Lundqvist et al., 1998): 13 photos were of female individuals and 13 photos were of male individuals; all of them were converted into gray scale images by means of the software Photoshop (Adobe Systems Inc., San Jose, U.S.A.). Stimuli were presented individually against a white background and they were covered by an oval-shaped white mask, leaving visible a portion of the face measuring 150×205 pixels in its minor and major axes, respectively (visual angle: $3.43^{\circ} \times 5.46^{\circ}$, seen at a distance of 56 cm). The mask was used in order to hide hair so as to prevent it from being a diagnostic cue (see Fig. 2).

Procedure

Participants were tested in isolation, and they carried out two experimental sessions, in both of which stimuli were presented laterally and tachistoscopically, and a third control session in which stimuli were presented centrally and without time limits. Each experimental session comprised the presentation of 104 trials: each of the 13 female and the 13 male faces was presented twice in the left visual field (LVF) and twice in the right visual field (RVF). In one of the experimental sessions participants were required to respond using the left hand, and in the other session they were required to

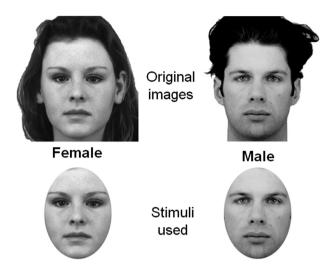


Fig. 2. Upper panel: examples of original female and male faces. Lower panel: examples of stimuli used in the study (in which original images are enclosed in an oval-shaped mask).

respond using the right hand. The order of the two sessions was balanced among participants. The patient D.D.C. started with the right hand session.

In each trial of the experimental sessions, a black fixation cross was presented in the center of the white screen (resolution: 1280×768 pixels). After 1000 ms during which only the cross was present, a face was presented either in the LVF or in the RVF, lasting 150 ms, while the cross remained visible. The presentation time of 150 ms should ensure that the stimulus presented in one hemifield is processed by the contralateral hemisphere. To this aim, some expedients were used: (1) participants were instructed to keep their gaze in the center of the screen; (2) a small central fixation cross was presented in the center of the screen to facilitate fixation; (3) the presentation order of the stimuli was completely randomized (so that participants did not know whether the stimulus would be presented in the LVF/RVF). The center of each stimulus was positioned at 5.1° of visual angle to the left or to the right from the center of the fixation cross. As soon as the stimulus disappeared the screen became blank until the participant gave the response, at which time the next trial started. After the two experimental sessions, each participant carried out a brief final session in which each of the 26 stimuli was presented centrally, without time limits, and participants were asked to take all the time needed to categorize the stimulus as accurately as possible. In each trial of this final session, the central fixation cross was presented for 1000 ms and it was replaced by the presentation of a face in the center of the screen. The image remained visible until the participant gave the response (using the same hand as that used in the last experimental session, so that 50% of participants used the left/right hand), at which time the next trial started. The presentation order of the stimuli was randomized across and within participants in both the experimental and the control sessions. All of the participants were asked to categorize faces

presented both centrally and laterally, in order to obtain a within-subject measurement. In this way any interindividual difference between those conditions was excluded. Moreover, the central condition was not presented before the lateralized condition in order to exclude a possible effect of familiarization with the stimuli. Thus, we avoided the a priori exclusion of the stimuli which were not correctly categorized as female or male in the control condition, carrying out an a posteriori exclusion of these stimuli. For this reason, in the statistical analysis the recognition rates were transformed in percentage of correct recognition, instead of being considered as raw data, in order to make them proportional to the number of stimuli considered in each category.

Prior to the beginning of the task, written instructions were presented, followed by four trials, used to allow participants to familiarize with the task. In the instructions, participants were informed that photographs of faces would be shown to the left or to the right with respect to the central fixation cross. They were asked to maintain their gaze on the central cross for the duration of the entire task, and to categorize the sex of each stimulus by pressing two different keys ("M" for male and "N" for female), taking care of being as accurate and rapid as possible. They were also instructed that the presentation of the stimuli would be very rapid and that they had to carry out two sessions, using the left/right hand, followed by a last session with a central presentation of the stimuli and without time limits. The paradigm was controlled by means of E-Prime software (Psychology Software Tools Inc., Pittsburgh, PA, U.S. A.), and lasted about 15 min. The experimental procedures were conducted in accordance with the guidelines of the Declaration of Helsinki.

RESULTS

Control group

Recognition rates. In a first step of the analysis, the percentage of correct responses in the control session (central presentation) was calculated for each stimulus in the whole sample. The results showed that stimuli were correctly categorized as female and male, with a mean accuracy higher than 95%, with the exception of 3 female faces for which the accuracy in central presentation was very low (43.33%, 55%, and 58.33%). A stimulus-wise binomial distribution analysis was carried out on the recognition percentage, and the results showed that for two of these female faces the recognition rates did not differ with respect to chance level (50%, p = 0.061, and p = 0.076), and for the third face the difference from chance was barely significant (p = 0.045). Considering the great difference between these recognition rates and those of all of the other stimuli, the responses for the 3 female faces were excluded from further analyses.

After the exclusion of the three female faces, the percentages of correct recognition for female faces (computed out of 10 stimuli) and for male faces

(computed out of 13 stimuli) were calculated for the control session. These percentages were used as the dependent variable in a 2×2 analysis of variance (ANOVA), in which Sex of face (female, male) was used as within-subject factor, and Sex of participant (female, male) was used as between-subject factor. Only the main effect Sex of participants was significant ($F_{(1.58)}=5.4$, MSE=156, p=0.024, $\eta_p^2=0.08$), showing a better performance of female participants (99.11 \pm 0.46) than male participants (96.83 \pm 0.78). The interaction between the two factors was not significant ($F_{(1.58)}=0.11$, p=0.74), showing the absence of an OGB when stimuli were presented centrally.

The percentage of correct responses for female and male faces in the experimental sessions was computed for stimuli presented in the LVF and in the RVF. These percentages were used as the dependent variable in a repeated measures ANOVA, in which Starting session (left hand, right hand) and Sex of participant (female, male) were used as between-subject factors, and Hand used to respond (left, right), Hemifield of presentation (LVF, RVF), and Sex of face (female, male) were used as within-subject factors. The results revealed that the interaction between Starting session and Hand was significant $(F_{(1,56)} = 7.82, MSE = 994, p = 0.007,$ $\eta_0^2 = 0.12$), and post hoc comparisons – carried out by means of Duncan test - showed that there was a learning effect: the performance was better when participants used the left hand, but only for participants who had carried out the first session using the right hand (p = 0.016). The same trend was present for participants who carried out the first session using the left hand: their performance was better when they used the right hand (in the second session) than the left hand, even if the difference did not reach statistical significance (p = 0.148).

Thus, in order to exclude the learning effect, the results were analyzed considering only the first session carried out by each participant, and thus considering Hand used to respond and Sex of participant as between-subject factors, and Hemifield of presentation and Sex of face as within-subject factors. The main effect Sex of face was significant ($F_{(1,56)} = 25.24$, MSE = 7507, p < 0.001, $\eta_p^2 = 0.31$): male faces were better recognized than female faces (male = 84.1% \pm 1.37%, female = 72.92% \pm 1.89%). The interaction between Sex of face and Hemifield of presentation was significant $(F_{(1,56)} = 22.12, MSE = 7812, p < 0.001,$ $\eta_{\rm p}^2 = 0.28$; Fig. 3). Post-hoc comparisons revealed that female faces were better recognized when presented in the LVF (78.75% \pm 2.28%) than in the RVF (67.08% \pm 2.83%, p = 0.002), whereas male faces were better recognized when presented in the RVF (89.68% \pm 1.04%) than in the LVF (78.52% \pm 2.34%, p = 0.003). Moreover, there was no difference between female and male faces presented in the LVF (p = 0.948), but when presented in the RVF, male faces were better recognized than female faces (p < 0.001). The other main effects and interactions failed to reach statistical significance.

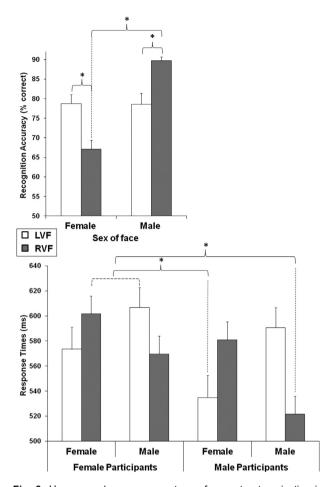


Fig. 3. Upper panel: mean percentage of correct categorization in healthy participants. The graph represents the interaction between Sex of face and Hemifield. Lower panel: mean response times (in ms) for the stimuli correctly categorized by healthy participants. The graphs represent the interaction among Sex of face, Hemifield, and Sex of participant (all of the comparisons within each levels of Sex of participant are significant). Asterisks show significant comparisons; bars represent standard errors.

In order to further explore the interaction between Sex of face and Hemifield, single sample t-tests were carried out to compare the percentages of correct recognition in each level of the interaction with the chance level of 50%. Applying the Bonferroni correction for multiple comparisons, the significant threshold was set at p=0.0125. All the results were significant $(6.03 < t_{(59)} < 38.29, p < 0.001$ for all comparisons), confirming that participants correctly categorized both female and male faces, in both visual fields.

Response times. Similar analyses as those carried out for the recognition rates were also carried out on response times (RTs), only for the correct responses. RTs were excluded from the analysis when they exceeded two standard deviations in a condition, and the remaining RTs were used as the dependent variable in a repeated measures ANOVA, in which Starting session (left hand, right hand) and Sex of participant (female, male) were used as between-subject factors, and Hand used to respond (left, right), Hemifield of

presentation (LVF, RVF), and Sex of face (female, male) were used as within-subject factors. The results confirmed a significant interaction between Starting session and Hand ($F_{(1,55)} = 19.87$, MSE = 96,203, p < 0.001, $\eta_p^2 = 0.26$): correct responses were faster when participants used the right hand, but only for participants who had carried out the first session with the left hand (p = 0.001); moreover, correct responses were faster when participants used the left hand, but only for participants who had carried out the first session with the right hand (p = 0.012).

Thus, data were analyzed considering only the first session carried out by participants, with Hand used to respond and Sex of participant as between-subject factors, and Hemifield and Sex of face used as withinsubject factors. The interaction between Sex of face and Hemifield was significant $(F_{(1,56)} = 54.58,$ $MSE = 121,962, p < 0.001, \eta_p^2 = 0.49), and post hoc$ tests showed that all comparisons were significant (p < 0.001 for all comparisons). In particular, the responses were faster for female faces presented in the LVF (554.14 \pm 12.43) than in the RVF (591.27 \pm 11.1), and they were faster for male faces presented in the RVF (545.6 \pm 10.41) than in the LVF (598.64 \pm 11.16). Moreover, the responses were faster for female compared to male faces in the LVF, and they were faster for male faces compared to female faces in the RVF.

Finally, the three-way interaction including Sex of face, Hemifield, and Sex of participant reached statistical significance ($F_{(1,56)}=4.16$, MSE=9295, p=0.046, $\eta_p^2=0.07$; Fig. 3). Post-hoc comparisons confirmed that all of the comparisons between Sex of face and Hemifield were significant, both for female and male participants (p < 0.037 for all comparisons). Moreover, RTs were longer for female participants who recognized male faces in the LVF, with respect to male participants who recognized both female faces in the LVF (p = 0.033) and male faces in the RVF (p = 0.012); similarly, RTs were longer for female participants who recognized female faces in the RVF, with respect to male participants who recognized both male faces in the RVF (p = 0.017), and female faces in the LVF (p = 0.049). The other main effects and interactions did not reach significance.

D.D.C. The recognition rates in the control session revealed that the patient D.D.C. correctly categorized the sex of all of the male stimuli, whereas he failed at categorizing the sex of two out of the 13 female stimuli presented centrally. Thus these two female stimuli were excluded from further analyses.

A binomial analysis on the correct responses was carried out for each of the 4 conditions (female and male faces presented in the LVF and in the RVF), for each session (left hand, right hand). The results showed that the responses were given at a chance level, except for male faces presented in the LVF, which were recognized at a higher rate than expected by chance in both sessions (left hand: p = 0.003; right hand: p < 0.001; see Table 1).

Moreover, a series of ${\rm chi}^2$ tests were carried out, comparing the results of the left/right hand sessions, but none of the comparisons were significant, revealing the absence of a difference due to the hand used by D.D.C. (female-LVF: ${\rm chi}_{(1)}^2=0.04$, p=0.847; female-RVF: ${\rm chi}_{(1)}^2=0.66$, p=0.414; male-LVF: ${\rm chi}_{(1)}^2=0.02$, p=0.876; male-RVF: ${\rm chi}_{(1)}^2=0.36$, p=0.548). Thus, the responses of both sessions (left and right hand) were considered together, and the frequencies of correct responses between hemifields were compared for female and male faces. Only the comparison for male faces was significant (${\rm chi}_{(1)}^2=3.88$, p=0.048), showing that D.D.C. better recognized male faces when presented in the LVF than in the RVF (female faces: ${\rm chi}_{(1)}^2=0.18$, p=0.674).

Control group vs D.D.C. The percentages for each category of response collected from the control group were compared with those by D.D.C. Starting from the absence of significant differences between the left and the right hand sessions, both in healthy participants and in D.D.C., the responses recorded in the two sessions were collapsed. The percentage of correct responses by D.D.C. was considered as a reference value to be compared to the mean percentage of correct responses by the control group, by means of single sample t-tests. We used exact t-tests, instead of exploiting some specific measures for the comparison between a single case and a group of healthy participants (i.e., Crawford and Garthwaite, 2005), capitalizing on the large sample size of the study (for similar comparisons between a single case and a control group see also Prete et al., 2015a). Applying the Bonferroni correction for multiple comparisons, the significant threshold was set at p = 0.0125.

The results of the t-tests revealed that the performance of the healthy participants was better than that by D.D.C. for female faces presented in the LVF ($t_{(59)} = 9.7$, p < 0.001) and in the RVF ($t_{(59)} = 6.35$, p < 0.001), as well as for male faces presented in the RVF ($t_{(59)} = 41.46$, p < 0.001). The result was not significant for male faces presented in the LVF ($t_{(59)} = 0.6$, p = 0.55).

DISCUSSION

A divided visual field paradigm was used in order to investigate the possible hemispheric asymmetries for face gender categorization in female and male healthy participants and in the male split-brain patient D.D.C. Starting from the evidence collected in previous studies with split-brain patients, showing a right-hemispheric dominance in processing facial stimuli belonging to the same ethnicity of the patient (Turk et al., 2005), and in processing self-face (Preilowski, 1979; Keenan et al., 2003), we expected to find an OGB lateralized to the right hemisphere in D.D.C., thus resulting in a higher accuracy in categorizing male faces presented in the LVF. On the other hand, starting from inconsistent results collected in healthy participants concerning hemispheric asymmetries in the processing of different characteristics of facial stimuli, we did not have specific hypotheses on the performance of the control group. The results of the present study confirmed a right-hemispheric OGB in D.D.C.,

Table 1. Number (and percentage) of correct categorizations by D.D.C., for female and male faces presented in the left visual field (LVF) and in the Right Visual Field (RVF), and *p*-values of the binomial distribution analyses, for the Left hand session and for the Right hand session separately (italic values represent the significant results)

D.D.C.	Female faces (22 stimuli)		Male faces (26 stimuli)	
	LVF	RVF	LVF	RVF
Left hand	13 (59.09%)	10 (45.45%)	20 (76.92%)	11 (42.31%)
Binomial left hand	0.118	0.154	0.003	0.115
Right hand	14 (63.64%)	14 (63.64%)	21 (80.77%)	14 (53.85%)
Binomial right hand	0.076	0.076	< 0.001	0.144

showing that his recognition rate was higher than that expected by chance for male faces presented in the LVF, and that it did not differ statistically from the recognition rate of the healthy participants, whereas the results of D.D.C. were at chance level for female faces presented both in the LVF and in the RVF, as well as for male faces presented in the RVF, and they were also significantly lower than those of healthy participants in all of these conditions. These data could be considered as in line with the results found with split-brain patients by Preilowski (1979), and by Keenan et al. (2003) showing a righthemispheric superiority in self-face recognition, as well as with those by Turk et al. (2005) showing a righthemispheric superiority in the processing of faces of the same ethnicity as a patient's. A similar right-hemispheric dominance has also been shown in healthy participants for self-voice recognition (Rosa et al., 2008; Gainotti, 2015), as well as for self-body parts recognition (Frassinetti et al., 2008), further supporting the righthemispheric involvement in self-representation and selfconsciousness (e.g., Feinberg and Keenan, 2005; Keenan et al., 2005; Devue and Brédart, 2011).

On the other hand, the results of the healthy participants did not confirm the right-hemispheric superiority in recognizing faces of their-own gender: both accuracy and RTs revealed a right-hemispheric superiority in categorizing female faces, and a lefthemispheric superiority in categorizing male faces, independently of the sex of the participants. The righthemispheric superiority in the processing of female faces confirmed the results already shown by Parente and Tommasi (2008) by means of chimeric faces, whereas the left-hemispheric superiority for male faces adds a new evidence in the field of cerebral specialization for face gender processing. Concerning the hypothesis of a righthemispheric superiority in the processing of facial stimuli containing characteristics in common with the observers', we might speculate that it is due to the exposure frequency to faces having these characteristics, and in this view the gender could be considered as a "special" dimension: own-face characteristics seem to have a righthemispheric lateralized neural substrate possibly due to a more frequent exposure - for instance - to persons (and thus faces) belonging to our-own ethnicity, and thus possibly attributable to right-lateralized substrates of selfrepresentation, whereas we are not selectively exposed to persons of our own gender. From this point of view, we speculate that specialized neural circuits - lateralized in the right hemisphere - might have evolved for the processing of some facial characteristics, and specifically for those to which we are more often exposed (e.g., our ethnicity). However, gender is a dimension cutting across ethnicity and age, and thus it could have a specialized neural substrate, disregarding the sex of the observer. Anyway, our results reveal that a crossed hemispheric specialization for the processing of face gender is present also in healthy brains, with a right-hemispheric superiority in categorizing female faces, and a left-hemispheric superiority in categorizing male faces. Parente and Tommasi (2008) explained their finding of a right-hemispheric superiority in processing female faces by referring to maternal cradling, which has been shown to preferentially occur on the left side of the mother's body, so that the face of the newborn is directly projected to the right hemisphere of the mother, and vice versa. Congruent with this speculation is the absence of a laterality preference during cradling as carried out by males (Bourne and Todd, 2004), and the absence of a right-hemispheric superiority for male faces. In this view, Quinn et al. (2002) found that infants aged 3-to-4 months better recognized faces of the same sex of their primary caregiver, who often is a female (the mother). Moreover, a similar bias toward own ethnicity was found by Kelly et al. (2005) starting from the same age (4 months), but not in newborns. All these evidences support the notion according to which a preference toward specific facial characteristics develops at about 3 months of age and it depends on the exposure to these facial characteristics. Tham et al. (2015) have recently found that 4-month olds correctly recognized female faces of their own ethnicity, whereas 8-9-month-olds lost the gender preference but showed the ORB. Finally, a further support for the present speculation comes from the study by Gaither et al. (2012) who tested Caucasian, Asian, and Caucasian-Asian 3-month olds with both Caucasian and Asian faces. They found the expected ORB both in Asian and Caucasian children, but not in biracial babies, showing that the exposure to a specific face category is the reason for the development of facial specific perceptual bias.

Putting together all these findings, we can conclude that our brain is specifically prone to processing the faces of our conspecifics (e.g., Leopold and Rhodes, 2010), and in particular specific categories of faces depending on exposure (e.g., Morton and Johnson, 1991). In the first 3 months of life, humans do not have a specific preference for the ethnicity or the gender of faces, but starting from this age children become more efficient in the processing of faces having the characteristics to which they are more often exposed (female faces

and faces of their ethnicity). In this view, the ORB becomes stronger with age, due to the prolonged exposure to faces of the same ethnicity as the infant's, but the gender bias tends to weaken with age, due to the substantially comparable exposure to both female and male faces. Concerning the hemispheric lateralization for female/male categorization, the right-hemispheric superiority for female faces could be attributable to maternal cradling (as already proposed by Parente and Tommasi, 2008), and we can speculate that the complementary left-hemispheric superiority found in the present study for male faces could be the result of a compensatory distribution of functions between the hemispheres (e.g. Badzakova-Trajkov et al., 2015).

The difference between the results of D.D.C. and the participants has to be ascribed to the hemispheric disconnection in the patient. From this point of view, it is not the first time in which hemispheric asymmetries for facial characteristics differ between connected and disconnected brains. For example, Turk et al. (2005) found a right-hemispheric lateralized ORB in the split-brain patient J.W., but they did not find hemispheric asymmetries in the control group. It has to be noted that the right-hemispheric superiority found in D. D.C. for recognizing male faces is due to the poorer performance in the other conditions (male faces in the RVF and female faces in both visual fields), rather than to a supernormal ability of the right hemisphere in recognizing male stimuli. From this perspective, it could be concluded that the surgical hemispheric disconnection prevents the processing of face gender by the left hemisphere, and it leaves intact a right-hemispheric ability in recognizing male faces. Thus, the right-hemispheric residual ability in categorizing male faces could be due either to a specific right-hemispheric superiority with respect to the left hemisphere in recognizing male faces (independently of the patient's gender), or to a specific OGB (D.D.C. being a male). In this latter case, a right-hemispheric superiority in categorizing female faces should be found in female split-brain patients. The extreme rareness of such neurological patients, however, did not allow us to further investigate this hypothesis, and thus we cannot exclude any of these possibilities, but future studies should explore cerebral asymmetries in face processing also in female callosotomized patients. Importantly, however, we have shown that the hemispheric disconnection upsets the balance between the hemispheres in categorizing the gender of faces, revealing a left-hemispheric performance at chance level with both female and male faces and a right-hemispheric random performance only for female faces. Starting from the frame described above, we can conclude that in case of total hemispheric disconnection the "normal" skills distribution between the hemispheres for female/male facial categorization disappears, and only a residual right-hemispheric superiority in recognizing male faces remains evident.

CONCLUSIONS

The results of the present study have shown that (i) in healthy participants the right hemisphere is superior in

categorizing female faces, whereas the left hemisphere is superior in categorizing male faces; but (ii) in case of hemispheric disconnection this asymmetry is abolished or partially reversed, with the left hemisphere becoming unable at categorizing face gender, and the right hemisphere revealing a residual ability in correctly categorizing male faces.

Acknowledgments—We thank Professor Gabriele Polonara for providing us with the MRI images of the patients, and Claudia D'Avanzo for helping us in recruiting and testing healthy participants. We also thank very much D.D.C. for his willingness to collaborate in the tasks.

REFERENCES

- Badzakova-Trajkov G, Corballis MC, Häberling IS (2015) Complementarity or independence of hemispheric specializations? A brief review. Neuropsychologia. http://dx.doi.org/10.1016/ji.neuropsychologia.2015.12.018.
- Bourne VJ, Todd BK (2004) When left means right: an explanation of the left cradling bias in terms of right hemisphere specializations. Dev Sci 7(1):19–24.
- Crawford JR, Garthwaite PH (2005) Testing for suspected impairments and dissociations in single-case studies in neuropsychology: evaluation of alternatives using monte carlo simulations and revised tests for dissociations. Neuropsychology 19(3):318. http://dx.doi.org/10.1037/0894-4105.19.3.318.
- Devue C, Brédart S (2011) The neural correlates of visual self-recognition. Conscious Cogn 20(1):40–51. http://dx.doi.org/10.1016/j.concog.2010.09.007.
- Feinberg TE, Keenan JP (2005) Where in the brain is the self?

 Conscious Cogn 14(4):661–678. http://dx.doi.org/10.1016/j.concog.2005.01.002.
- Frassinetti F, Maini M, Romualdi S, Galante E, Avanzi S (2008) Is it mine? Hemispheric asymmetries in corporeal self-recognition. J Cogn Neurosci 20(8):1507–1516.
- Gainotti G (2015) Implications of recent findings for current cognitive models of familiar people recognition. Neuropsychologia 77:279–287. http://dx.doi.org/10.1016/j.neuropsychologia.2015.09.002.
- Gaither SE, Pauker K, Johnson SP (2012) Biracial and monoracial infant own-race face perception: an eye tracking study. Dev Sci 15(6):775–782. http://dx.doi.org/10.1111/ji.1467-7687.2012.01170.x.
- Gazzaniga MS (2005) Forty-five years of split-brain research and still going strong. Nat Rev Neurosci 6(8):653–659.
- Keenan JP, Gorman J (2007) The causal role of the right hemisphere in self-awareness: it is the brain that is selective. Cortex 43 (8):1074–1082.
- Keenan JP, Rubio J, Racioppi C, Johnson A, Barnacz A (2005) The right hemisphere and the dark side of consciousness. Cortex 41 (5):695–704.
- Keenan JP, Wheeler M, Platek SM, Lardi G, Lassonde M (2003) Selfface processing in a callosotomy patient. Eur J Neurosci 18 (8):2391–2395. http://dx.doi.org/10.1046/j.1460-9568.2003.02958.x.
- Kelly DJ, Quinn PC, Slater AM, Lee K, Gibson A, Smith M, Pascalis O (2005) Three-month-olds, but not newborns, prefer own-race faces. Dev Sci 8(6):F31–F36.
- Leopold DA, Rhodes G (2010) A comparative view of face perception. J Comp Psychol 124(3):233. http://dx.doi.org/10.1037/a0019460.
- Lundqvist D, Flykt A, Öhman A (1998) The Karolinska Directed Emotional Faces (KDEF). Stockholm: Department of Neurosciences Karolinska Hospital.
- Mason MF, Macrae CN (2004) Categorizing and individuating others: the neural substrates of person perception. J Cogn Neurosci 16 (10):1785–1795.

- Meadows JC (1974) The anatomical basis of prosopagnosia. J Neurol Neurosurg Psychiatry 37(5):489–501.
- Morton J, Johnson MH (1991) CONSPEC and CONLERN: a two-process theory of infant face recognition. Psychol Rev 98(2):164. http://dx.doi.org/10.1037/0033-295X.98.2.164.
- Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh Inventory. Neuropsychologia 9:97–113. http://dx.doi.org/10.1016/0028-3932(71)90067-4.
- Parente R, Tommasi L (2008) A bias for the female face in the right hemisphere. Laterality 13(4):374–386. http://dx.doi.org/10.1080/13576500802103495.
- Preilowski B (1979) Self-recognition as a test of consciousness in left and right hemisphere of "split-brain" patients. Act Nerv Super (Praha) 19(2):343–344.
- Prete G, Fabri M, Foschi N, Brancucci A, Tommasi L (2015a) The "consonance effect" and the hemispheres: a study on a split-brain patient. Laterality 20(3):257–269. http://dx.doi.org/10.1080/1357650X.2014.959525.
- Prete G, Marzoli D, Tommasi L (2015b) Upright or inverted, entire or exploded: Right-hemispheric superiority in face recognition withstands multiple spatial manipulations. PeerJ 3:e1456. http://dx.doi.org/10.7717/peerj.1456.
- Proverbio AM, Riva F, Martin E, Zani A (2010) Neural markers of opposite-sex bias in face processing. Front Psychol 1:169. http://dx.doi.org/10.3389/fpsyg.2010.00169.
- Quinn PC, Yahr J, Kuhn A, Slater AM, Pascalis O (2002) Representation of the gender of human faces by infants: a preference for female. Perception 31(9):1109–1121. http://dx.doi.org/10.1068/p3331.
- Rogers LJ, Vallortigara G, Andrew RJ (2013) Divided brains: the biology and behaviour of brain asymmetries. Cambridge University Press.
- Rosa C, Lassonde M, Pinard C, Keenan JP, Belin P (2008) Investigations of hemispheric specialization of self-voice recognition. Brain Cogn 68(2):204–214. http://dx.doi.org/10.1016/j.bandc.2008.04.007.

- Rosa Salva O, Regolin L, Mascalzoni E, Vallortigara G (2012) Cerebral and behavioural asymmetries in animal social recognition. Comp Cogn Behav Rev 7(10):110–138. http://dx.doi.org/10.3819/ccbr.2012.70006.
- Tham DSY, Bremner JG, Hay D (2015) In infancy the timing of emergence of the other-race effect is dependent on face gender. Infant Behav Dev 40:131–138. http://dx.doi.org/10.1016/j.infbeh.2015.05.006.
- Todd BK, Banerjee R (2016) Lateralization of infant holding by mothers: a longitudinal evaluation of variations over the first 12 weeks. Laterality 21(1):12–33. http://dx.doi.org/10.1080/1357650X.2015.1059434.
- Turk DJ, Handy TC, Gazzaniga MS (2005) Can perceptual expertise account for the own-race bias in face recognition? A split-brain study. Cogn Neuropsychol 22(7):877–883. http://dx.doi.org/10.1080/02643290442000383.
- Turk DJ, Heatherton TF, Kelley WM, Funnell MG, Gazzaniga MS, Macrae CN (2002) Mike or me? Self-recognition in a split-brain patient. Nat Neurosci 5(9):841–842. http://dx.doi.org/10.1038/nn907.
- Verdichevski M, Steeves JK (2013) Own-age and own-sex biases in recognition of aged faces. Acta Psychol 144(2):418–423. http://dx.doi.org/10.1016/j.actpsy.2013.06.005.
- Wright DB, Sladden B (2003) An own gender bias and the importance of hair in face recognition. Acta Psychol 114(1):101–114. http://dx.doi.org/10.1016/S0001-6918(03)00052-0.
- 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(13):3061–3068. http://dx.doi.org/10.1016/j.neuropsychologia.2008.06.017.
- Yovel G, Yovel I, Levy J (2001) Hemispheric asymmetries for global and local visual perception: effects of stimulus and task factors. J Exp Psychol Hum Percept Perform 27(6):1369. http://dx.doi.org/10.1037/0096-1523.27.6.1369.

(Accepted 5 October 2016) (Available online 13 October 2016)