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Upright or inverted, entire or exploded: right-hemispheric superiority in face recognition withstands multiple spatial manipulations

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ABSTRACT

Background. The ability to identify faces has been interpreted as a cerebral specialization based on the evolutionary importance of these social stimuli, and a number of studies have shown that this function is mainly lateralized in the right hemisphere. The aim of this study was to assess the right-hemispheric specialization in face recognition in unfamiliar circumstances.

Methods. Using a divided visual field paradigm, we investigated hemispheric asymmetries in the matching of two subsequent faces, using two types of transformation hindering identity recognition, namely upside-down rotation and spatial "explosion" (female and male faces were fractured into parts so that their mutual spatial relations were left intact), as well as their combination.

Results. We confirmed the right-hemispheric superiority in face processing. Moreover, we found a decrease of the identity recognition for more extreme "levels of explosion" and for faces presented upside-down (either as sample or target stimuli) than for faces presented upright, as well as an advantage in the matching of female compared to male faces.

Discussion. We conclude that the right-hemispheric superiority for face processing is not an epiphenomenon of our expertise, because we are not often exposed to inverted and "exploded" faces, but rather a robust hemispheric lateralization. We speculate that these results could be attributable to the prevalence of right-handedness in humans and/or to early biases in social interactions.

Subjects Neuroscience, Psychiatry and Psychology

Keywords Face matching, Exploded faces, Face-inversion effect, Divided visual field paradigm, Hemispheric asymmetries

INTRODUCTION

The ability to recognize conspecifics is crucial for survival, and it has been demonstrated in a variety of species that visual cues are very important to this purpose, especially for social animals (i.e., *Gronenberg, Ash & Tibbetts, 2007; Parr, 2011; Dahl et al., 2013; Somppi et al., 2014*). One of the most useful visual cues for recognizing conspecifics is the face: a great amount of evidence has been collected on the ability to identify faces (e.g., *Ramon, 2015*), also indicating that the tendency to gaze at faces rather than other

Submitted 1 October 2015 Accepted 9 November 2015 Published 1 December 2015

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Academic editor Giorgio Vallortigara

Additional Information and Declarations can be found on page 11

DOI 10.7717/peerj.1456

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objects is an innate skill, not only in humans but also in other animals (*Johnson et al.*, 1991; Sugita, 2008; Rosa Salva, Regolin & Vallortigara, 2010; Rosa Salva et al., 2011). Proof of the importance of facial recognition is the evidence of specific cerebral areas involved in face processing. A number of studies have shown that the fusiform gyrus, particularly in the right hemisphere, is the brain area specifically involved in face processing (*Gross, Rocha-Miranda & Bender, 1972; Bruce, Desimone & Gross, 1981; McCarthy et al., 1997*), so that this area has been named "fusiform face area" (*Kanwisher, McDermott & Chun, 1997; Kanwisher & Yovel, 2006*). Neuroscientists agree in identifying the right hemisphere as mostly involved in face processing (i.e., *Rizzolatti, Umiltà & Berlucchi, 1971; Yovel, in press*), a right-hemispheric—but not left-hemispheric—lesion causing prosopagnosia, that is the inability to recognize the identity of faces (*Barton et al., 2002*).

Several studies investigated the possibility that the right-hemispheric advantage in face processing is really specific for this type of stimuli, as opposed to a specialization in processing all stimuli that demand acquired expertise. In other words, some authors have cast doubts on the real face-specific superiority of the right hemisphere, favoring the alternative view according to which the right hemisphere would be superior in the processing of familiar stimuli, faces being a sub-category of this class (e.g., *Diamond & Carey, 1986; Gauthier & Tarr, 1997*).

However, a compromise between these two hypotheses is that the right-hemispheric superiority in face processing could be considered as advantageous specifically because of the high frequency of exposure to this familiar class of stimuli: it is reasonable, in fact, to hypothesize that because we are continuously exposed to conspecific faces in everyday life, our brain has evolved a specific neuronal circuit in order to selectively process these frequent stimuli in terms of both rapidity and accuracy. Some evidence in this regard have shown that humans are more capable to recognize own-race and own-gender faces than other-race and other-gender faces (*Wright & Sladden, 2003*; *Wiese, Kaufmann & Schweinberger, 2014*). This evidence agree with the hypothesis of a specialized neural circuit evolved because of the high frequency of exposure to faces.

The "face inversion effect" (*Yin*, 1969) is referred to the impaired performance of observers who are asked to recognize upside-down faces. In this circumstance, it was shown that the right hemisphere maintained its superiority in face processing with respect to the left hemisphere, even if its performance worsened with respect to the processing of upright faces. Moreover, the fusiform face area has been shown to process faces presented both in upright and upside-down orientation (*Kanwisher, Tong & Nakayama, 1998*).

A biological advantage would have led to evolve specific neural circuits devoted to processing faces as special stimuli, both at the phylogenetic and at the ontogenetic level (*Vallortigara, 2012*), due to the crucial role of this category of stimuli for survival. The assumption of a "cerebral social predisposition" is confirmed by a fast, subcortical route devoted to the processing of face-like stimuli in humans (*Johnson, 2005*), as well as in other species (*Rosa Salva, Mayer & Vallortigara, 2015*). Starting from this premise, we could hypothesize that the right-hemispheric superiority might also turn out to be resistant to other kinds of manipulations besides face inversion (*Leder et al., 2001*), as already demonstrated

by means of geometric distortions (*Hole et al., 2002*), face caricaturing (*Schulz et al., 2012*), and so on. In this regard, Pichler and colleagues (2012) investigated the role of first-order versus second-order structure of faces in adaptation mechanisms: they used the so-called "exploded faces," created by dividing faces into parts which were spaced apart from each other preserving the whole facial configuration (thus destroying the second-order structure), and "scrambled faces," in which the facial configuration was destroyed by swapping face parts with each other (thus destroying the first-order structure). The authors found that exploded upright and upside-down faces generated identity after-effects on intact upright test faces, whereas scrambled faces did not, concluding that the face-like configuration (first-order structure) is necessary to activate face representations, and that the second-order structure of faces was contained in both orientations. These results were somehow in contrast with the idea according to which inverted faces should be processed as a mere collection of local features rather than as a global percept. The classical view on hemispheric competence about global/local processing is that of a right-hemispheric dominance for global analysis and a left-hemispheric dominance for local analysis (see Karim & Kojima, 2010 for a review). By means of inverted exploded faces, however, Pichler and colleagues (2012) showed that these stimuli allowed to sidestep this distinction and to investigate face processing by considering both global and local aspects altogether. In fact, in exploded faces, the spatial relationships among parts remain unaltered (i.e., the eyes are presented above the nose) and the local features are always present (the details of each part of the image remain intact), differently, for example, from blurred or scrambled images. Another study in which exploded faces were used (Moscovitch & Moscovitch, 2000, who referred to these stimuli as "fractured faces"), showed a "super face-inversion effect": upside-down fractured faces were recognized worse than both upright fractured and upside-down whole faces (see also Moscovitch, Winocur & Behrmann, 1997).

A right-hemispheric superiority in matching the identity of famous faces has been shown by Cooper and colleagues (2007), in a divided visual field paradigm, in which a prime face was centrally shown and then followed by a lateral target face. The authors found that the right hemisphere was superior to the left hemisphere in the matching of prime and target faces when the two stimuli were identical, whereas the authors did not find any lateralized bias when the stimuli were different images of the same face, or when they depicted two different familiar faces. Despite these behavioral results, electroencephalographic recordings showed a similar right temporal N250 modulation for the first two conditions (prime and target being the same image or different images of the same face). Cooper and colleagues concluded that a behavioral left visual field advantage (right-hemispheric superiority) in matching prime and target stimuli occurred only when they were the same image, but the event-related potentials revealed that the right hemisphere processed in the same way prime and target faces both when they were the same image and two different images of the same face (thus, confirming the ability to recognize a face, beyond a specific image).

In an attempt to link the possible right-hemispheric superiority in face recognition with the processing of configural aspects of face stimuli, we investigated hemispheric abilities in the processing of upright, inverted, entire and exploded faces (and the combinations of these conditions), by means of a divided visual field paradigm. The hypothesis of the study was that, starting from the well-established right-hemispheric dominance in face processing, the right hemisphere should appear dominant also in the processing of exploded faces, confirming the cerebral asymmetry also for faces undergoing different spatial manipulations. To investigate this issue, in a same/different forced choice task we presented a sample face in the center of the screen, followed by the presentation of a lateralized target face, exploiting the tachistoscopic unilateral visual field paradigm. By manipulating the spatial orientation (upright/inverted) and the global configuration (different degrees of explosion) of the stimuli, we aimed to confirm that the right-hemispheric superiority in face processing would withstand to multiple spatial manipulations.

MATERIALS AND METHODS

Participants

Thirty-seven volunteers (32 females) took part in the experiment (mean age: 24.73 ± 0.29 years). As in previous studies investigating the effects of face perception, the gender of participants was not controlled for (e.g., *Ramon & Rossion, 2012; Cattaneo et al., 2014; Bourne & Hole, 2006*), starting from the evidence that females and males did not differ in recognizing lateralized presented faces (*Hirnstein, Hausmann & Güntürkün, 2008; Godard & Fiori, 2010*). All participants had normal or corrected-to-normal vision and were naïve about the purpose of the experiment. Two participants were left-handed and the other 35 were right-handed, as self-reported (left-handed participants were not excluded from the sample, as in previous studies in which lateralized faces were used as stimuli, e.g., *Ramon & Rossion, 2012*). The present study did not involve patients, children or animals, as well as drugs, genetic samples or invasive techniques, thus it was not subject to ethical review by the academic medical research board. Nevertheless, informed consent was obtained from all participants and the experiment was conducted in accordance with the ethical standards prescribed by the Declaration of Helsinki.

Stimuli

Stimuli were created from photographs contained in the Karolinska Directed Emotional Faces (*Lundqvist, Flykt & Öhman, 1998*), a database of female and male faces depicted in emotional and neutral poses. Photographs of 3 female and 3 male Caucasian actors in neutral pose and in frontal view were selected and rendered in gray scale. In order to make the gender of faces well-distinguishable, all female actresses had long hair and all male actors had short hair. From each original photograph, a total of 4 images were obtained by means of the software Photoshop (Adobe Systems Inc., San Jose, CA, USA). Specifically, in order to create the "exploded faces," 3 more images were created based on each original photograph, by cutting the original image into 9 parts having the same size, according to a virtual 3×3 grid. From the original image measuring 192×132 pixels (height \times width, visual angle: $5.07^{\circ} \times 2.21^{\circ}$, seen at a distance of 72 cm), 9 parts were thus obtained, each



Figure 1 Example of Stimuli preparation. Example of a stimulus at each level of explosion created for illustrative purpose (these images are not included in the database used in the study): (A) level 0 (the face is shown in its entirety); (B) level 1 (the parts of the image are spaced 8 pixels from one another); (C) level 2 (the parts of the image are spaced 32 pixels from one another); (D) level 3 (the parts of the image are spaced 64 pixels from one another).

measuring 64×44 pixels $(1.69 \times 0.74^{\circ})$. In order to create the exploded stimuli, the 8 external parts in the image were displaced away from the central part. The distance of the external parts from the central one determined the "level of explosion": at level 0, the face was presented in its entirety—since all the pieces were juxtaposed to each other (original photograph); at level 1, each part was orthogonally spaced 8 pixels away from the neighboring parts; at level 2, each part was orthogonally spaced 32 pixels away from the neighboring parts; at level 3, each part was orthogonally spaced 64 pixels away from the neighboring parts (distances are intended from side to side, see Fig. 1). Stimuli were first created in canonical orientation (upright orientation), and a second set was then obtained rotating each stimulus 180° (inverted orientation).

Procedure

The task was controlled by means of E-Prime software (Psychology Software Tools Inc., Pittsburgh, PA, USA) and presented on a screen with a resolution of $1,280 \times 1,024$ pixels. Participants were tested individually, in a darkened room, sitting at a distance of 72 cm from the computer screen.

Participants were randomly assigned to one of three experimental conditions, which had a similar structure, but differed for the spatial manipulations of sample and target stimuli (see Fig. 2). In all conditions the level of explosion of the sample face was blocked among trials, whereas the target face was presented at each of the four levels of explosion.

A trial started with a sample face shown for 500 ms in the center of the screen; then a fixation cross was centrally presented for 1000 ms, and in the following 100 ms a target



Figure 2 Schematic representation of the procedure. Schematic representation of the paradigm: a sample face was centrally presented for 500 ms, followed by a fixation cross lasting 1,000 ms, then a target face was presented for 100 ms in either the left visual field (LVF) or in the right visual field (RVF). (A) Condition 1 (sample: upright and entire; target: upright and entire or exploded); (B) Condition 2 (sample: upright and exploded; target: upside-down and entire or exploded); (C) Condition 3 (sample: upside-down and exploded; target: upright and entire or exploded).

face was presented on the left side of the screen (50% of trials) or on the right side of the screen (50% of trials), the central fixation cross remaining visible (the center of the stimuli was placed at a distance of 5.37° of visual angle to the left or to the right of the central fixation cross). Then the screen became blank until the participant gave her/his response and—1,000 ms after the response—the next trial started. Target stimuli were presented for 100 ms in order to reduce the possibility of eye movements, starting from the evidence that not less than 110–120 ms are needed to carry out a saccadic movement (i.e., *Trottier & Pratt, 2005*).

There were 32 trials for each of the 6 identities (3 female and 3 male): in 16 of such trials, the target face was the same as the sample face (i.e., female 1), in the other 16 trials the identity of the target face was different with respect to the identity of the sample face (i.e., in 8 of the unmatched trials in which the sample face was female 1, the target face was female 2, and in the other 8 trials the target face was female 3). The resulting 192 trials in each experimental condition were repeated three times.

In the first experimental condition the sample face was presented upright and entire (level of explosion 0), and the target face was presented upright and at each of the 4 levels

of explosion (levels: 0, 1, 2 and 3). This condition, in which sample and target stimuli are presented upright (from now on condition "Upright–Upright"), was administrated to 11 participants (7 females). In the second condition a further element of spatial manipulation was added, presenting the stimuli upside-down, as well as exploded: sample faces were presented upright and at level of explosion 2, and target faces were presented upside-down and at each of the 4 levels of explosion. This condition, in which the sample face was presented upright and the target face was presented in inverted spatial orientation (from now on condition "Upright-Inverted"), was administrated to 13 participants (12 females). In the third condition, the spatial orientation of the sample stimuli was also manipulated, in order to investigate the possibility to alter the expected right-hemispheric superiority when the initial coding was more difficult, due to face inversion: sample faces were presented upside-down and at level of explosion 2, and target faces were presented upright and at each of the 4 levels of explosion. This condition, in which the sample face was presented in inverted spatial orientation and the target face was presented in canonical spatial orientation (from now on condition "Inverted-Upright"), was administrated to 13 participants (all females).

Written instructions were presented at the beginning of the task, in which participants were required to maintain their gaze on the central fixation cross and half of them were asked to press either a keyboard button with the left hand when the identity of the target face was the same as that of the sample face, or a button with the right hand when the identity of the sample and target faces differed, whereas the other half received the instructions with the opposite association between hand and response. Prior to the beginning of the task, participants were informed that stimuli could be presented as upright or upside-down, entire or exploded and they were shown some examples in order to familiarize with the stimuli. They were also informed that the gender of faces remained the same between sample and target stimuli in each trial.

The presentation order of the trials was randomized within and across participants, and the task lasted about 25 minutes.

RESULTS

Results were analyzed by means of the Statistica 8.0.550 software (StatSoft. Inc., Tulsa, OK, USA). In a first step, the frequencies of correct responses of the whole sample were transformed in percentages and the mean was compared to the 50% chance threshold by means of exact *t*-tests. This first analysis showed that participants did not respond by chance, since the *t*-test was significant ($t_{(36)}=12.79$; p < .001), indicating that participants matched the identity of sample and target faces at a higher rate than chance (mean accuracy \pm SEM: 61.71% \pm 0.91%). The results were significant also considering each of the 3 groups separately (Upright–Upright: $t_{(10)} = 17.92$; p < .001; Upright–Inverted: $t_{(12)} = 5.73$; p < .001; Inverted-Upright: $t_{(12)} = 7.6$; p < .001).

A split-plot analysis of variance (ANOVA) was carried out, using Sex of faces (female, male), Hemifield of presentation of the target face (left visual field: LVF, right visual field: RVF) and Level of explosion of the target face (0, 1, 2, 3) as within-subject factors,

Condition (Upright–Upright, Upright–Inverted, Inverted-Upright) as between-subject factor, and the percentage of correct responses as the dependent variable. Since we did not have specific hypotheses concerning the effect of gender and handedness of participants, these factors were not controlled for, and thus they were not included in the analysis. Post-hoc comparisons were computed by means of Duncan tests.

All main effects were significant. The effect of Hemifield ($F_{(1,34)} = 99.99, p < .001$, $\eta_p^2 = .746$), revealed that the target faces were correctly recognized more frequently when presented in the LVF (66.32 \pm 0.67) than in the RVF (57.10 \pm 0.51). The main effect of Sex of faces ($F_{(1,34)} = 91.61$, p < .001, $\eta_p^2 = .729$) showed that Female faces were correctly recognized more frequently than Male faces (female faces: 65.73 ± 0.67 ; male faces: 57.68 \pm 0.55). Post-hoc comparisons on the main effect of the Level of explosion $(F_{(3,102)} = 10.65, p < .001, \eta_p^2 = .238; \text{level } 0:67.14 \pm 0.94; \text{level } 1:63.00 \pm 0.97; \text{level}$ 2: 61.20 \pm 0.90; level 3: 59.49 \pm 0.87) showed that the correct matching rates were higher when target faces were presented at Level of explosion 0 with respect to Levels of explosion 2 (p = .017) and 3 (p < .001), and at Level of explosion 1 with respect to Levels of explosion 2 (p = .020) and 3 (p < .001). There were no differences between Levels 0 and 1, and between Levels 2 and 3. Finally, also the effect of Condition was significant $(F_{(2,34)} = 7.43, p = .002, \eta_p^2 = .304)$, and post-hoc comparisons showed that target faces were correctly recognized more frequently in Upright–Upright condition (65.89 ± 0.72) than in Upright–Inverted (58.34 \pm 0.76; p < .001) and in Inverted-Upright (61.53 \pm 0.82; p = .031) conditions.

The significant interaction between Hemifield and Sex of faces ($F_{(1,34)} = 28.82$, p < .001, $\eta_p^2 = .459$) confirmed that Female faces were correctly recognized more frequently than Male faces in both the LVF and the RVF, and that both Female and Male faces were correctly recognized more frequently when presented in the LVF than in the RVF (p < .001 for all comparisons).

Finally, also the three-way interaction concerning Hemifield, Sex of faces and Condition was significant ($F_{(2,34)} = 5.01$, p = .012, $\eta_p^2 = .228$; Fig. 3). Post-hoc comparisons showed a LVF advantage in all cases (p < .001 for all comparisons between LVF and RVF), with the exception of male faces in Upright–Inverted condition. Moreover, female faces were correctly recognized more frequently than male faces in both visual fields and in any condition (p < .001 for all comparisons), with the exception of faces presented in the RVF in the Upright–Inverted condition.

DISCUSSION

The present study confirms the right-hemispheric superiority in face processing, extending this evidence to the unusual situation constituted by exploded and inverted faces. Indeed, the effect of the visual field was highly significant, showing that the identity of two faces was better matched when target stimuli were presented in the left visual field (right hemisphere) than in the right visual field (left hemisphere). This evidence is in line with a number of studies (*Bourne & Hole, 2006; Cattaneo et al., 2014*), strengthening the hypothesis of a right-hemispheric superiority in face processing, that goes beyond the





idea of expertise with a specific class of stimuli: in fact, if this latter case can be applicable to the identification of an upright and entire face-a class of stimuli to which we are continuously exposed—it is not applicable to exploded and/or inverted faces. The results of the present study are also in line with those of Cooper and colleagues (2007), who found a similar right-hemispheric N250 modulation during the recognition of a target face that followed a prime face of the same identity, both when prime and target were the same image and when they were different images (even if the authors lacked to find a behavioral LVF advantage when prime and target were different images of the same person). These results showed that the right-hemispheric superiority in face recognition is not just based on a match-to-sample processing due to a pure mnemonic encoding of the perceptual characteristics of the stimuli, but it is based on higher-order processes, which seem to be resistant to perceptual changes (spatial manipulations or different views of the face). In line with this view, in a facial identity adaptation paradigm during fMRI, Verosky & Turk-Browne (2012) found that adaptation mechanisms occurred in the left fusiform face area only when a face had previously been processed by the RH, whereas they did not occur when the face had only been processed by the LH. The authors concluded that facial identity information is mainly processed by the RH, and then it can be transferred from the right to the left hemisphere. As regard the spatial manipulation of the stimuli, in a PET study Rossion and colleagues (2000) showed that cerebral asymmetries for part-based *versus* whole-based processing of faces take place in the fusiform gyrus, more activated in the LH for part-based processing, and in the RH for whole-based processing.

The present study also showed that exploded faces were recognized with more difficulty than entire faces, and specifically that the entire or almost entire stimuli (levels of explosion 0 and 1) were better recognized than the exploded stimuli (levels of explosion 2 and 3), independently of their spatial orientation (i.e., upright/upside-down). We also found that the performance of the participants were lower when either the sample or the target face were presented exploded and in inverted orientation (Conditions 2 and 3) than when they were presented exploded and upright (Condition 1), in accordance with the "super face-inversion effect" (*Moscovitch & Moscovitch, 2000*). The results of the present study showed that female faces were better recognized than male faces. Importantly, however, as regard the hemispheric bias in interaction with the gender of the stimuli, the only occurrence in which the right-hemispheric superiority was not evident was that concerning male faces in condition "upright-inverted," in which after the upright sample face, an upside-down target face was presented.

An alternative explanation for the right-hemispheric superiority in face analysis is linked to a leftward spatial bias possibly attributable to the prevalence of right-handedness in humans and the higher likelihood of scanning the left side of others in face-to-face interactions (for a detailed review, see Marzoli, Prete & Tommasi, 2014). Moreover, a further explanation for the right-hemispheric superiority in face recognition, and in particular for female faces, takes into account an additional factor, concerning the early interactions between infants and caregivers, mainly mothers, namely a leftward bias in maternal cradling, that could be attributable to the fact that in this way the infant's facial signals directly reach the mother's right hemisphere, preferentially devoted to face processing (i.e., Huggenberger et al., 2009; see also Marzoli, Prete & Tommasi, 2014) and to emotion recognition (Gainotti, 1972; Prete et al., 2015a; Prete et al., 2015b). In line with this idea, it could be hypothesized that female faces are better recognized than male faces when presented in the LVF (right hemisphere) and in inverted orientation ("Upright-Inverted" condition), because of the exposure to the upside-down perspective of a female face in the early childhood: in this period, in fact, infants are held by mothers (preferentially on their left side) and are more likely exposed to the mother's face from a variety of vantage points. Accordingly, a right-hemispheric bias for the recognition of female faces, using chimeric faces, was also found in both female and male observers by means of a gender recognition task carried out by *Parente & Tommasi* (2008), supporting the right-hemispheric dominance in female-face processing, independently of the observers' gender. Moreover, no difference in the accuracy between female and male observers were found in a divided visual field paradigm in which participants were required to discriminate faces from non-faces (Hirnstein, Hausmann & Güntürkün, 2008), or to recognize the identity of a face (Godard & Fiori, 2010).

To conclude, the present study confirms the right-hemispheric superiority in face processing and extends this ability also to stimuli transformed by multiple spatial manipulations (inverted and exploded faces). We speculate that this hemispheric superiority could possibly be linked to both right-handedness and the leftward bias in maternal cradling (Marzoli, Prete & Tommasi, 2014). This circumstance casts doubts on the possibility of a right-hemispheric superiority for all categories of stimuli with which we have expertise, because it is evident that exploded faces are unusual stimuli for observers (even more so if they are also inverted). The present findings should be intended as a further confirmation of the right-hemispheric dominance in face processing, showing the robustness of this neuropsychological fact even in cases of extreme spatial manipulations of the stimuli. These conclusions need further investigations. For instance, it has to be noticed that in the present study participants were asked to maintain their initial position during the whole task and to fixate the central cross, but neither eve movements nor head position were monitored, thus caution is needed in the interpretation of the present results, and possible further studies should investigate the strength of the present conclusions by adding direct measurements of both eye movements and head position during the lateralized presentation of the stimuli. Moreover, the hypothesis drawn in this study could be tested by using stimuli other than faces in order to directly compare performance and hemispheric abilities in the matching of different classes of stimuli, as well as by comparing the performance of female and male participants.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

The authors received no funding for this work.

Competing Interests

Luca Tommasi is an Academic Editor for PeerJ.

Author Contributions

- Giulia Prete conceived and designed the experiments, performed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables.
- Daniele Marzoli conceived and designed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables.
- Luca Tommasi conceived and designed the experiments, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.

Human Ethics

The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers):

The present study did not involve patients, children or animals, as well as drugs, genetic samples or invasive techniques, thus it was not subject to ethical review by the academic medical research board. Nevertheless, informed consent was obtained from all participants and the experiment was conducted in accordance with the ethical standards prescribed by the Declaration of Helsinki.

Data Availability

The following information was supplied regarding data availability:

The raw data can be found in Supplemental Information 1.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/ 10.7717/peerj.1456#supplemental-information.

REFERENCES

- Barton JJ, Press DZ, Keenan JP, O'Connor M. 2002. Lesions of the fusiform face area impair perception of facial configuration in prosopagnosia. *Neurology* 58(1):71–78 DOI 10.1212/WNL.58.1.71.
- **Bourne VJ, Hole GJ. 2006.** Lateralized repetition priming for familiar faces: evidence for asymmetric interhemispheric cooperation. *The Quarterly Journal of Experimental Psychology* **59(6)**:1117–1133 DOI 10.1080/02724980543000150.
- Bruce C, Desimone R, Gross CG. 1981. Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. *Journal of Neurophysiology* **46**(2):369–384.
- Cattaneo Z, Renzi C, Bona S, Merabet LB, Carbon CC, Vecchi T. 2014. Hemispheric asymmetry in discriminating faces differing for featural or configural (second-order relations) aspects. *Psychonomic Bulletin & Review* 21(2):363–369 DOI 10.3758/s13423-013-0484-2.
- Cooper TJ, Harvey M, Lavidor M, Schweinberger SR. 2007. Hemispheric asymmetries in image-specific and abstractive priming of famous faces: evidence from reaction times and event-related brain potentials. *Neuropsychologia* 45(13):2910–2921 DOI 10.1016/j.neuropsychologia.2007.06.005.
- Dahl CD, Rasch MJ, Tomonaga M, Adachi I. 2013. The face inversion effect in non-human primates revisited-an investigation in chimpanzees (Pan troglodytes). *Science Reports* 3:2504 DOI 10.1038/srep02504.
- Diamond R, Carey S. 1986. Why faces are and are not special: an effect of expertise. *Journal of Experimental Psychology: General* 115(2):107–117 DOI 10.1037/0096-3445.115.2.107.
- Gainotti G. 1972. Emotional behavior and hemispheric side of the lesion. *Cortex* 8(1):41–55 DOI 10.1016/S0010-9452(72)80026-1.
- Gauthier I, Tarr MJ. 1997. Becoming a 'Greeble' expert: exploring mechanisms for face recognition. *Vision Research* 37(12):1673–1682 DOI 10.1016/S0042-6989(96)00286-6.
- Godard O, Fiori N. 2010. Sex differences in face processing: are women less lateralized and faster than men? *Brain and Cognition* 73(3):167–175 DOI 10.1016/j.bandc.2010.04.008.
- **Gronenberg W, Ash LE, Tibbetts EA. 2007.** Correlation between facial pattern recognition and brain composition in paper wasps. *Brain Behavior and Evolution* **71(1)**:1–14 DOI 10.1159/000108607.
- Gross CG, Rocha-Miranda CE, Bender DB. 1972. Visual properties of neurons in inferotemporal cortex of the Macaque. *Journal of Neurophysiology* 35(1):96–111.
- Hirnstein M, Hausmann M, Güntürkün O. 2008. The evolutionary origins of functional cerebral asymmetries in humans: does lateralization enhance parallel processing? *Behavioural Brain Research* 187(2):297–303 DOI 10.1016/j.bbr.2007.09.023.

- Hole GJ, George PA, Eaves K, Rasek A. 2002. Effects of geometric distortions on face-recognition performance. *Perception* **31(10)**:1221–1240 DOI 10.1068/p3252.
- Huggenberger HJ, Suter SE, Reijnen E, Schachinger H. 2009. Cradling side preference is associated with lateralized processing of baby facial expressions in females. *Brain and Cognition* **70**(1):67–72 DOI 10.1016/j.bandc.2008.12.010.
- Johnson MH. 2005. Subcortical face processing. *Nature Reviews Neuroscience* 6(10):766–774 DOI 10.1038/nrn1766.
- Johnson MH, Dziurawiec S, Ellis H, Morton J. 1991. Newborns' preferential tracking of face-like stimuli and its subsequent decline. *Cognition* 40(1):1–19 DOI 10.1016/0010-0277(91)90045-6.
- Kanwisher N, McDermott J, Chun MM. 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience* 17(11):4302–4311.
- Kanwisher N, Tong F, Nakayama K. 1998. The effect of face inversion on the human fusiform face area. *Cognition* 68(1):B1–B11 DOI 10.1016/S0010-0277(98)00035-3.
- Kanwisher N, Yovel G. 2006. The fusiform face area: a cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society B* 361(1476):2109–2128 DOI 10.1098/rstb.2006.1934.
- Karim AR, Kojima H. 2010. The what and why of perceptual asymmetries in the visual domain. *Advances in Cognitive Psychology* 6:103 DOI 10.2478/v10053-008-0080-6.
- Leder H, Candrian G, Huber O, Bruce V. 2001. Configural features in the context of upright and inverted faces. *Perception* **30**(1):73–84 DOI 10.1068/p2911.
- Lundqvist D, Flykt A, Öhman A. 1998. *The Karolinska Directed Emotional Faces (KDEF)*. Stockholm: Department of Neurosciences Karolinska Hospital.
- Marzoli D, Prete G, Tommasi L. 2014. Perceptual asymmetries and handedness: a neglected link? *Frontiers in Psychology* 5:1–9 DOI 10.3389/fpsyg.2014.00163.
- McCarthy G, Puce A, Gore JC, Allison T. 1997. Face-specific processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience* 9:605–610 DOI 10.1162/jocn.1997.9.5.605.
- Moscovitch M, Moscovitch DA. 2000. Super face-inversion effects for isolated internal or external features, and for fractured faces. *Cognitive Neuropsychology* 17(1–3):201–219 DOI 10.1080/026432900380571.
- Moscovitch M, Winocur G, Behrmann M. 1997. What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. *Journal of Cognitive Neuroscience* 9(5):555–604 DOI 10.1162/jocn.1997.9.5.555.
- Parente R, Tommasi L. 2008. A bias for the female face in the right hemisphere. *Laterality* 13(4):374–386 DOI 10.1080/13576500802103495.
- Parr LA. 2011. The evolution of face processing in primates. *Philosophical Transactions of the Royal Society B* 366(1571):1764–1777 DOI 10.1098/rstb.2010.0358.
- Pichler P, Dosani M, Oruç I, Barton JJ. 2012. The nature of upright and inverted face representations: an adaptation-transfer study of configuration. *Cortex* **48(6)**:725–736 DOI 10.1016/j.cortex.2011.02.005.
- Prete G, D'Ascenzo S, Laeng B, Fabri M, Foschi N, Tommasi L. 2015a. Conscious and unconscious processing of facial expressions: evidence from two split-brain patients. *Journal of Neuropsychology* 9(1):45–63 DOI 10.1111/jnp.12034.
- Prete G, Laeng B, Fabri M, Foschi N, Tommasi L. 2015b. Right hemisphere or valence hypothesis, or both? The processing of hybrid faces in the intact and callosotomized brain. *Neuropsychologia* 68:94–106 DOI 10.1016/j.neuropsychologia.2015.01.002.

- Ramon M. 2015. Perception of global facial geometry is modulated through experience. *PeerJ* 3:e850 DOI 10.7717/peerj.850.
- Ramon M, Rossion B. 2012. Hemisphere-dependent holistic processing of familiar faces. *Brain and Cognition* 78(1):7–13 DOI 10.1016/j.bandc.2011.10.009.
- Rizzolatti G, Umiltà C, Berlucchi G. 1971. Opposite superiorities of the right and left cerbral hemispheres in discriminative reaction time to physiognomical and alphabetical material. *Brain* 94(3):431–442 DOI 10.1093/brain/94.3.431.
- Rosa Salva O, Farroni T, Regolin L, Vallortigara G, Johnson MH. 2011. The evolution of social orienting: evidence from chicks (Gallus gallus) and human newborns. *PLoS ONE* 6(4):e18802 DOI 10.1371/journal.pone.0018802.
- Rosa Salva O, Mayer U, Vallortigara G. 2015. Roots of a social brain: developmental models of emerging animacy-detection mechanisms. *Neuroscience & Biobehavioral Reviews* 50:150–168 DOI 10.1016/j.neubiorev.2014.12.015.
- **Rosa Salva O, Regolin L, Vallortigara G. 2010.** Faces are special for newly hatched chicks: evidence for inborn domain-specific mechanisms underlying spontaneous preferences for face-like stimuli. *Developmental Science* **13(4)**:565–577 DOI 10.1111/j.1467-7687.2009.00914.x.
- Rossion B, Dricot L, Devolder A, Bodart JM, Crommelinck M, De Gelder B, Zoontjes R. 2000. Hemispheric asymmetries for whole-based and part-based face processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience* **12(5)**:793–802 DOI 10.1162/089892900562606.
- Schulz C, Kaufmann JM, Walther L, Schweinberger SR. 2012. Effects of anticaricaturing vs. caricaturing and their neural correlates elucidate a role of shape for face learning. *Neuropsychologia* 50(10):2426–2434 DOI 10.1016/j.neuropsychologia.2012.06.013.
- Somppi S, Törnqvist H, Hänninen L, Krause CM, Vainio O. 2014. How dogs scan familiar and inverted faces: an eye movement study. *Animal Cognition* 17(3):793–803 DOI 10.1007/s10071-013-0713-0.
- Sugita Y. 2008. Face perception in monkeys reared with no exposure to faces. *Proceedings of the National Academy of Sciences* 105(1):394–398 DOI 10.1073/pnas.0706079105.
- Trottier L, Pratt J. 2005. Visual processing of targets can reduce saccadic latencies. *Vision Research* 45(11):1349–1354 DOI 10.1016/j.visres.2004.12.007.
- Vallortigara G. 2012. Core knowledge of object, number, and geometry: a comparative and neural approach. *Cognitive Neuropsychology* 29(1–2):213–236 DOI 10.1080/02643294.2012.654772.
- Verosky SC, Turk-Browne NB. 2012. Representations of facial identity in the left hemisphere require right hemisphere processing. *Journal of Cognitive Neuroscience* 24(4):1006–1017 DOI 10.1162/jocn_a_00196.
- Wiese H, Kaufmann JM, Schweinberger SR. 2014. The neural signature of the own-race bias: Evidence from event-related potentials. *Cerebral Cortex* 24(3):826–835 DOI 10.1093/cercor/bhs369.
- Wright DB, Sladden B. 2003. An own gender bias and the importance of hair in face recognition. *Acta Psychologica* 114(1):101–114 DOI 10.1016/S0001-6918(03)00052-0.
- Yin RK. 1969. Looking at upside-down faces. *Journal of Experimental Psychology* 81(1):141 DOI 10.1037/h0027474.
- Yovel G. 2015. An integrative review of neural and cognitive face-selective measures. *Neuropsychologia* In Press DOI 10.1016/j.neuropsychologia.2015.09.026.