It is currently believed that face processing predominantly activates the right hemisphere in humans, but available literature is very inconsistent. In this study, ERPs were recorded in 50 right-handed women and men in response to faces of different age and sex and technological objects. Results showed no sex difference in the amplitude of N170 to objects; a much larger face-specific response over the right hemisphere in men, and a bilateral response in women; a lack of face-age coding effect over the left hemisphere in men, with no differences in N170 to faces as a function of age; a significant bilateral face-age coding effect in women. LORETA reconstruction showed a significant left and right asymmetry in the activation of the fusiform gyrus (BA19), in women and men, respectively. The present data reveal a lesser degree of lateralization of brain functions related to face coding in women than men. In this light, they may provide an explanation of the inconsistencies in the available literature concerning the asymmetric activity of left and right occipito-temporal cortices devoted to face perception during processing of face identity, structure, familiarity or affective content.

Introduction

Rizzolatti and Buchtel (1977) originally found a sex difference in hemispheric lateralization for face processing, showing that in males RTs to faces were faster when stimuli were presented to the LVF/RH than RVF/LH, while they were symmetrical in females. More recently Godard (2010), based on the recording of P1, N170, and N250 ERP components, provided robust evidence that IHTT is more asymmetrical in the male than female brain during face processing, possibly explaining some sex differences in hemispheric lateralization. Notwithstanding that, is certainly not a shared knowledge in cognitive neuroscience that face processing is bilateral in the female brain and right-sided in the male brain, and such an assumption is not made anywhere in cognitive neuroscience manuals or clinical essays on prosopagnosia. Electromagnetic recordings have identified a posterior negative response peaking at about 170 ms (N170) that is larger to faces than other visual objects over the right hemisphere and thought to reflect processes involved in the structural encoding of faces. The combination of electromagnetic and neuroimaging data (Haxby et al., 2000) identified the N1 generator in the ventral occipito-temporal cortex (Henson et al., 2003), suggesting that N1 might be the manifestation of Face Fusiform Area (FFA) activity. A closer examination of the literature shows that face-specific N170 topographic distribution is often but not always right-sided in right-handed individuals. It is of great interest that N170 response was found to be bilateral or even left-sided in studies involving populations in which women were the majority (see the review by Proverbio et al., 2006a). The aim of the present study was to investigate whether there are sex-related hemispheric asymmetries for face processing. Face-sensitive N1 responses were measured over the occipital/temporal cortices in 50 right-handed observers. In two previous studies (Proverbio et al., 2006a; 2006b) it was found a bilateral activation of occipito/temporal cortex in women and right–lateralized activation in men during infant face processing as indexed by sensory ERP responses. Since in those studies all stimuli were infant faces, it lacked a control condition with non-face objects. We devised a paradigm in which face processing of persons of various age was contrasted with that of technological objects.
Methods

Fifty healthy right-handed Italian University students (25 males and 25 females) were recruited as volunteers for this experiment. Their handedness was assessed by the Italian version of the Edinburgh Handedness Inventory, a laterality preference questionnaire reporting right-handedness (0.80) and right ocular dominance for all participants. An ANOVA on laterality quotients proved no sex difference in the degree of lateral preference between men (0.81, SE = 0.03) and women (0.79, SE = 0.03). Almost half of the women practiced contraceptive control (N = 11). About half women were in the pre-ovulatory phase (N = 12), the others in the post-ovulatory phase (N = 11) at the time of EEG recording. 2 women did not provide data. Experiments were conducted with the understanding and the written consent of each participant. The experimental protocol was approved by the ethical committee of the University of Milano-Bicocca. Data from all participants were included in data analysis. Stimulus set comprised 520 colour pictures depicting nice-looking male and female faces of various ages (130 adults, 130 children, 130 toddlers) and 130 technologic/electronic complex objects of similar size and spatial distribution. Faces and objects were presented randomly mixed with 44 equiluminant infrequent targets depicting common natural or urban landscapes without visible persons (for further detail see Proverbio et al., 2010). An ANOVA showed no difference in stimulus luminance as a function of stimulus type (faces: adults = 16.4; children = 15.6; toddlers = 16.7; objects = 16 cd/cm²). Each slide was presented for 800 ms at the centre of a PC screen with an ISI ranging from 1300 to 1500 ms. The outer background was dark grey. In order to keep subject's attention toward visual stimulation, the task consisted of responding as accurately and quickly as possible to photos displaying landscapes (urban or natural scenarios without visible persons) by pressing a response key with the index finger of the left or right hand while ignoring all other pictures. The EEG was continuously recorded from 128 scalp sites at a sampling rate of 512 Hz. Horizontal and vertical eye movements were also recorded. Linked ears served as the reference lead. The EEG and electro-oculogram (EOG) were amplified with a half-amplitude band pass of 0.016–100 Hz. Electrode impedance was kept below 5 kΩ. EEG epochs were synchronized with the onset of stimuli presentation. The peak amplitude of occipito/temporal N170 component was measured at P9 and P10 in the time window 140–195 ms. ERP data were subjected to multifactorial repeated-measures ANOVA with one factor between (sex: males, females) and 2 factors within groups. Low Resolution Electromagnetic Tomography (LORETA) was performed on ERP waveforms at N170 time latency. LORETA was performed on group data and it identified statistical significant electromagnetic dipoles (p<0.05), the larger the magnitude, the more significant the activation. A realistic boundary element model (BEM) was derived from a T1 weighted 3D MRI data set by segmentation of the brain tissue. The BEM model consisted of one homogenic compartment made up of 3446 vertices and 6888 triangles. The head model was used for intra-cranial localization of surface potentials.

Results

The ANOVA performed on the peak amplitude values of N170 revealed a significant effect of stimulus content (F3,144 = 90.4; p<0.000001), showing a larger response to childish (toddler = −3.95 µV, SE = 0.37; child = −3.44 µV) than adult faces (−2.7 µV, SE = 0.33), as proved by post-hoc comparisons (p<0.01). Furthermore, N170 to faces was much larger (p<0.01) than to objects (−0.32 µV, SE 0.26). The further significance of hemisphere x sex (F1,48 = 7.57; p<0.008) showed the presence of a sex difference in N170 lateralization, with larger N170 over the right (−2.92 µV, SE = 0.55) than the left hemisphere in men (−1.95 µV, SE = 0.42), as indicated by post-hoc tests (p<0.01), and no significant asymmetry in women (RH = −2.35 µV, SE = 0.55, LH = −3.21 µV, SE = 0.42). ANOVA yielded the significance of stimulus content x hemisphere x sex (F 3,144 = 3.51, p<0.018). Post-hoc tests revealed no sex difference in the amplitude of N170 to objects. Furthermore, they showed a much larger face-specific response over the right than left hemisphere.
(Tod-obj = 5.4 µV at P10 and 2.41 at P9) in men (p<0.01), and a bilateral face specific response in women (Tod-obj = 3.79 µV at P10 and 3.0 µV at P9). It was also found a lack of face coding effect over the left hemisphere in men, with no difference in N170 to faces as a function of person's age. Conversely, a significant age-coding effect of over both hemispheres was found in women, with a larger N170 to toddler than adult faces (p<0.01) at both P9 and P10 sites and no hemispheric difference in the amplitude of N170 to faces. On the other hand, results showed larger right than left hemispheric responses to faces in men (adults, p<0.04; toddlers and children, p<0.00001).

In order to locate the possible neural circuits subtending face coding in the two sexes, two different swLORETA source reconstructions were performed, separately for men and women, on 170 amplitude measured in the time window 135–185 ms, which are displayed in Fig. 1. The inverse solution showed that the processing of adult faces in women was associated with a significant activity in the left fusiform gyrus (possibly corresponding to FFA), left MOG, right cuneus (BA18), left posterior cingulate cortex, and anterior brain regions (BA10/11). In men processing of adult faces was associated with activation in the right fusiform gyrus, the left MOG, right posterior cingulate cortex and anterior brain areas (BA10/11).

![SwLORETA inverse solution performed on brain activity recorded during the 135–175 ms. It is visible the different left/right lateralization of FFA activity.](image)

**Discussion**

Overall, electrophysiological and source localization data support previous literature about the existence of specific neural populations in the fusiform area and the middle occipital area devoted to face processing, as reflected by the amplitude of occipito/temporal N170 component of ERPs. Moreover, they seem to suggest a less marked lateralization in the activity of face-devoted brain regions in women than men. This finding, supported by the presence of a stronger left FG generator in women and right FG generator in men, results in a asymmetrical N170 surface amplitude in men, and a bilateral distribution in women (tending toward the left asymmetry). Moreover, over the left
hemisphere N170 amplitude did not vary as a function of face age in men but only in women. Our findings agree with Glocker et al. (2009) evidence of a clear left FFA activation in women during processing of infant faces. On the other hand, they do not directly agree with a recent investigation (Willems et al., 2010) suggesting a relation between handedness and FFA lateralization, since our female participants, showing a bilateral response of face responsive areas, were definitely right-handed.

Overall, the present data reveal a lesser degree of lateralization of brain functions related to face coding in women than men, both in terms of face-related N170 amplitude, and N170 object-face and adult/toddler discriminative response. In this light, our data may also provide an explanation of the inconsistencies in the available literature concerning the asymmetric activity of left and right occipito-temporal cortices devoted to face perception during processing of face identity, structure, familiarity or affective content.

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