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Sexual dimorphism in hemispheric processing of faces in humans: A meta-analysis of 817 cases

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Abstract

A well-established neuroimaging literature predicts a right-sided asymmetry in the activation of face-devoted areas such as the fusiform gyrus (FG) and its resulting M/N170 response during face processing. However, the face-related response sometimes appears to be bihemispheric. A few studies have argued that bilaterality depended on the sex composition of the sample. To shed light on this matter, two meta-analyses were conducted starting from a large initial database of 250 ERP (Event-related potentials)/MEG (Magnetoencephalography) peer-reviewed scientific articles. Paper coverage was from 1985 to 2020. Thirty-four articles met the inclusion criteria of a sufficiently large and balanced sample size with strictly right-handed and healthy participants aged 18–35 years and N170 measurements in response to neutral front view faces at left and right occipito/temporal sites. The data of 817 male ($n = 414$) and female ($n = 403$) healthy adults were subjected to repeated-measures analyses of variance. The results of statistical analyses from the data of 17 independent studies (from Asia, Europe and America) seem to robustly indicate the presence of a sex difference in the way the two cerebral hemispheres process facial information in humans, with a marked right-sided asymmetry of the bioelectrical activity in males and a bilateral or left-sided activity in females.

Key words: sex differences; EEG/ERPs; face processing; FFA; N170; gender; social cognition

Introduction

The right hemispheric asymmetry and relative left visual field (LVF) advantage are generally considered face-specific properties (Rossion *et al.*, 2003a,b; Yovel, 2016; Jacques *et al.*, 2019). Functional magnetic resonance imaging (fMRI) and intracranial electrophysiological recording have suggested (since their discovery) that the fusiform face area (FFA) was activated bilaterally but more often in the right hemisphere, where a module in the human extrastriate cortex existed that was specialized for the perception of faces *vs.* objects (Kanwisher *et al.*, 1997; Haxby *et al.*, 2000). However, the role of the sex of viewers in determining the variability in hemispheric asymmetry has never been fully comprehended.

Particularly enlightening is the case of prosopagnosic patients, who, if they were female and manifested a left lateralized N170 to faces [reflecting the activity of the fusiform gyrus (FG); Koessler *et al.*, 2019], were sometimes considered anomalous and inexplicable cases. For example, a prosopagnosic patient (P.S.) showed an 'atypical' left N170 that was considered peculiar with respect to the 'normal' N170 component observed in healthy individuals and on right lateral-occipital electrodes (e.g. Prieto *et al.*, 2011). Again, in a further observation of prosopagnosic patients in which three male and two female

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patients were considered (Harris *et al.*, 2005), two out of the three male patients showed a right-sided M170 response that was not sensitive to faces (as opposed to houses), while the third patient showed a right-sided sensitivity to faces. For the two female patients, one showed a lack of sensitivity to faces at the M170 level, while the second showed left-sided sensitivity. For the control group, the sex composition was not specified, but the statistical analyses performed on N170 responses to faces *vs.* houses showed that the main effect of hemisphere approached significance, with measured M170 amplitudes somewhat larger in the left hemisphere. The latter piece of evidence was not fully comprehensible in light of the supposed right lateralization of M170. Again, Dobel *et al.* (2008) found early left-hemispheric dysfunction of face processing in congenital prosopagnosic patients (half of whom were female), but the authors were puzzled by these results interpreted in terms of compensation for impaired configural processing.

Proverbio *et al.* (2006) were among the first to raise the problem caused by not considering the sex of participants in determining the patterns of bilaterality or even left hemispheric asymmetry in FFA activation or N170 scalp distribution in ERP studies. In a review of the literature (Proverbio *et al.*, 2006), it was observed that face-specific N170 responses were bilateral, or even left-sided, in studies using experimental samples in which women were the majority (e.g. Harris *et al.*, 2005; Jemel *et al.*, 2005; Meeren *et al.*, 2005; Valkonen-Korhonen *et al.*, 2005; Righart and De Gelder, 2006).

In this regard, a potential source of bias might have certainly been the recruitment of only male participants for early PET (Positron Emission Tomography) investigations, linked to the invasiveness of this neuroradiological technique for fertile female individuals (as, for example, in a foundational study by Sergent *et al.*, 1992, or later studies such as Rossion *et al.*, 2003a). Interestingly, this allowed the current observation that in these early neurometabolic studies, the face areas were invariably more activated over the right hemispheres and not quite bilaterally as in fMRI studies (performed also in women) in which FG activation appeared bilaterally, for example, the fMRI study by Clark *et al.* (1996) including six women and three men or the more recent combined fMRI/ERP study by Lazar *et al.* (2014) including 20 men and 37 women, both reporting bilateral activation of the FG during face processing.

Although the right-sided activation of the FG and inferior occipital gyrus OFA (Occipital Face Area) is considered by some authors a standard and to-be-expected pattern of lateralization (e.g. Rossion *et al.*, 2003b; Pitcher *et al.*, 2014; Niina *et al.*, 2015; Jacques *et al.*, 2019), recently, clear evidence of sex differences in the hemispheric distribution of face-responsive areas has been provided. Liu *et al.* (2020), through a systematic comparison with functional neuroimaging meta-analyses, established a statistically significant concentration of human gray matter volume (GMV) sex differences within brain regions that subserve face processing. In particular, in the right visual field condition, only female participants showed significantly larger left-hemispheric than right-hemispheric N170 amplitudes, whereas male participants did not show such a modulation. The effect corresponded to a greater responsivity of left-hemispheric processes underlying the N170 component in female participants (Stasch *et al.*, 2018). Jacques *et al.* (2019) recorded intracranial electrodes implanted in 11 male and 13 female patients with intractable epilepsy and found that both the left and right FG were active during face processing (as also found by Allison *et al.*, 1999; Barbeau *et al.*, 2008).

Unfortunately, in the majority of early paradigmatic studies such as Bentin *et al.* (1996), subjects' sex was not mentioned or considered as a factor and the majority of state-of-the-art ERP studies published before 2010 (see Supplementary Appendix 1) included experimental samples with less than 10 men and 10 women as subjects, thus making it impossible to evaluate the role of participants' sex in N170 hemispheric asymmetry. Later studies [such as Lazar *et al.* (2014) or Proverbio *et al.* (2010), testing a larger sample of female and male participants] have reported a bilateral N170 response to faces in women as opposed to a right-sided N170 response in men.

Over time, inconsistencies in the literature have been explained in various ways by taking into consideration (i) subjects' handedness, with studies reporting a right lateralization of FFA in right handers but not in left handers (Willems *et al.*, 2010), (ii) sexual preference (Dobrin and Steeves, 2011), with evidence that homosexual participants showed more accurate face recognition than heterosexual participants in the RVF (Right Visual Field) (left hemisphere) (Brewster *et al.*, 2011) and (iii) face familiarity, with studies reporting that left FFA was involved in unfamiliar face coding, while right FFA was involved in familiar face recognition (Avidan and Behrmann, 2005). To shed light on this matter, Proverbio *et al.* (2010) measured ERP responses in strictly right-handed and heterosexual male and female viewers in response to unfamiliar faces and found a bilateral pattern of N170 distribution in women and a right-sided N170 distribution in men. Therefore, the sex of the participants was able to explain the different patterns of lateralization in this study regardless of other possible intervening factors. In fact, there might be a similar, reduced lateralization of certain functions in females and in left handers. In this regard, Pletzer and Harris (2018) found a correlation between sex and testosterone levels in inducing stronger lateralization (and lesser brain connectivity) in subjects engaged in local/global analysis, with males showing stronger hemispheric asymmetries than natural cycling women.

Electrophysiological investigations involving source reconstruction can be very enlightening about the role of the two hemispheres in face processing. For example, in the combined fMRI/ERP study by Lazar *et al.* (2014) performed with a sample of 24 right-handed subjects, it was found a sex difference in hemispheric asymmetry for face processing (Table 1 for study details). They found that the supra-threshold voxels (reflecting the magnitude of activation) for N170 sources to neutral faces were much higher in the left FG in women and in the right FG in men. Similarly, source reconstruction data obtained by Proverbio *et al.* (2010) in a sample of 50 subjects, in which ERPs were recorded to faces of various ages, showed a bilateral activation of FG in women and a right-lateralized focus of activity in men. Again, the MEG study by Tiedt *et al.* (2013) performed on a sample of 26 subjects showed a sex difference in FG activation with stronger M170 dipoles in the right FG in men, and no hemispheric asymmetry in women (Table 1 for details).

The aim of the present study was to provide a comprehensive analysis of the largest possible electromagnetic literature on face processing, including ERP, MEG and VEP studies, to determine whether the biological sex of viewers affected the way the left and right face areas were engaged in face perception, as reflected by the amplitude of N170/M170 responses. Repeated-measures analyses of variance (ANOVAs) were performed on the mean N170 amplitude values recorded to neutral faces in a large set of studies (covering 817 individual cases), while a further ANOVA was applied to individual data recorded covering 360 individual cases (170 F, 190 M).

Table 1. Description of some electrical neuroimaging studies showing a sex difference in FG activation across hemispheres, in the N170 latency range

Paper	Journal	Stimulus type	Task	Measured signals
1. Lazar *et al.* (2014)	*Behav Brain Research*	Faces, houses	Same/different	fMRI supra-threshold voxels corresponding to N170
2. Proverbio *et al.* (2010)	*PLoS One*	Faces, objects	Target detection	SwLORETA N170 dipoles (135–185 ms)
3. Tiedt *et al.* (2013)	*PLoS One*	Familiar faces	Passive viewing	M170 strength (146–186 ms)

	Male		Female		Ss M	Ss F	RHand	Age
	lFG	rFG	lFG	rFG				
1	49.1	53	49.1	30.2	12	12	Yes	18.9
2	13.5	15	19.2	18.9	25	25	Yes	22.36
3	17.3	35.5	34.9	35.6	13	13	Yes	25.46

Notes: lFG = left fusiform gyrus; rFG = right fusiform gyrus; Ss M = number of male subjects; Ss F = number of female subjects; RHand = right-handedness; age = subjects' age in years.

Therefore, in this study, two meta-analyses were performed on the available data. Meta-analysis #1 (applied to the mean values of N170 recorded at left and right sites, as found in 17 independent ERP/MEG studies) and Meta-analysis #2 (applied to the individual values of N170 recorded in single subjects, as reported in seven independent ERP studies).

Materials and methods

Inclusion and exclusion criteria

The corpus of literature included any ERP and MEG investigation published in peer-reviewed biomedical journals found in PubMed (or via PubMed) from 1985 to 10 December 2020. Two hundred fifty published scientific papers (listed in Supplementary Appendix 1) were found and analyzed according to the criteria described below.

The inclusion criteria were as follows: experimental samples should include at least 10 males and 10 females. All participants should be humans, healthy (controls were checked in clinical studies), strictly right handed and aged between 18 and 35 years. It is known that handedness is capable of affecting N170 lateralization (Schrammen *et al.*, 2020). The sex of the participants and the hemisphere of recording were reported in the printed papers, a factor in statistical analyses or provided by the authors of the study. N170/M170 amplitude values had to be recorded at left and right occipito/temporal sites. Stimuli had to be front-view neutral faces, and if mixed with other stimulus material (such as objects, houses, angry faces, etc.), the ERP data considered should only pertain to responses to neutral faces. Since it is known that the emotional content of facial expressions may engage the two cerebral hemispheres differently (Adolphs *et al.*, 2001), faces should be neutral or slightly smiling with no other emotional manipulation. The task might include different stimulus categories or tasks but should include a passive viewing or attentive task resulting in visual perception of neutral faces.

Criteria for exclusion were having measured N170 responses only at midline (e.g. OZ), not having measured ERP/MEG signals to front-view faces (but, for example, to full bodies, inverted faces, profile faces, cartoon faces, etc.). For the experimental sample, exclusion criteria were the inclusion in the sample of left-handed people, elderly people or people younger than 18 years or children or infants, mostly or uniquely male or female participants, or unhealthy individuals (e.g. clinical patients). In addition, since some studies in which the authors detailed subjects' sexual preferences found that homosexual preference might be associated with better performance of the left hemisphere in face recognition tasks (Brewster *et al.*, 2011), data from non-heterosexual participants were discarded for homogeneity. Papers not meeting the above criteria (namely 216 out of 250 papers) were preliminarily discarded. The specific reasons are detailed below and are depicted in Figure 1.

To retrieve papers, searches were conducted through the PubMed National Library of Medicine site (https://pubmed.ncbi.nlm.nih.gov/) comprising more than 30 million citations for the biomedical literature from MEDLINE, life science journals and online books. Searches were performed using keywords such as 'Faces ERP N170' or 'Face perception VEP ERP', 'Face perception MEG M170 male female' and 'N170 faces women men'.

After the application of the above criteria, 34 papers were identified that met the inclusion criteria (see Figure 1). Unfortunately, for half of the papers, data were not available due to COVID restrictions or other factors. As shown in Figure 1, which displays the publication date for each paper, data from unavailable datasets were probably too old to be traced or retrieved by the authors. Only two papers from the available sample were published earlier than 2010.

The literature (250 articles) was retrieved mostly from the PubMed database or the references section of reviews found in PubMed. The initial data set included four doctoral theses (referring to published papers), 220 papers retrieved through keyword searches and 26 papers quoted by reviews or other papers on the same subject found in PubMed. For several papers that met the inclusion criteria, N170 mean values or, preferably, individual data were requested directly from the authors via an e-mail message sent to the corresponding author because the data were not disclosed within the paper. The requests were sent because it appeared that N170 amplitude values from left and right occipito/temporal sites were recorded from a sufficient number of female and male participants to neutral faces. At the time of the request, the pattern of N170 hemispheric lateralization in males and females in the specific findings was unknown to the authors of the present study (blind procedure). Furthermore, the detailed purpose of this meta-analysis was not immediately revealed to avoid introducing bias into the recruitment process. The object of the investigation was summarized as 'a meta-analysis on face-related N1 properties'. However, in some of these cases (17 non-available cases in Figure 1), the data were not made available or were not accessible because of COVID restrictions

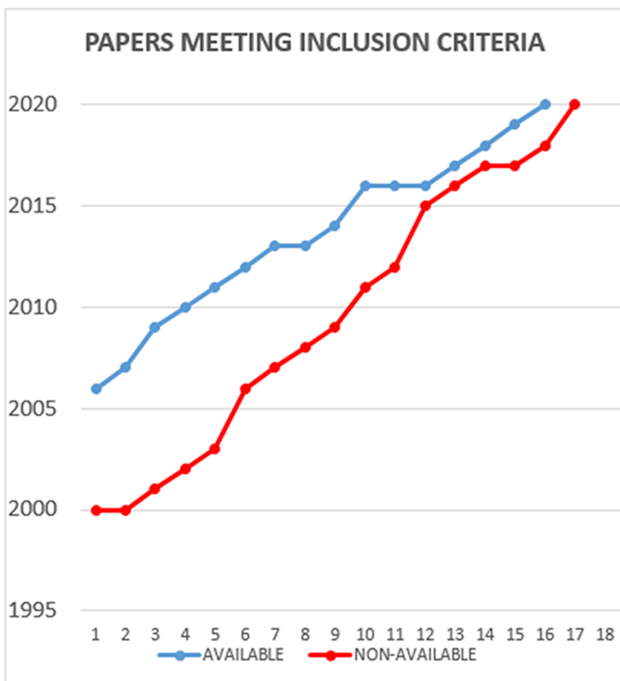

Fig. 1. Publication dates for the 35 papers meeting the inclusion criteria as a function of their availability.

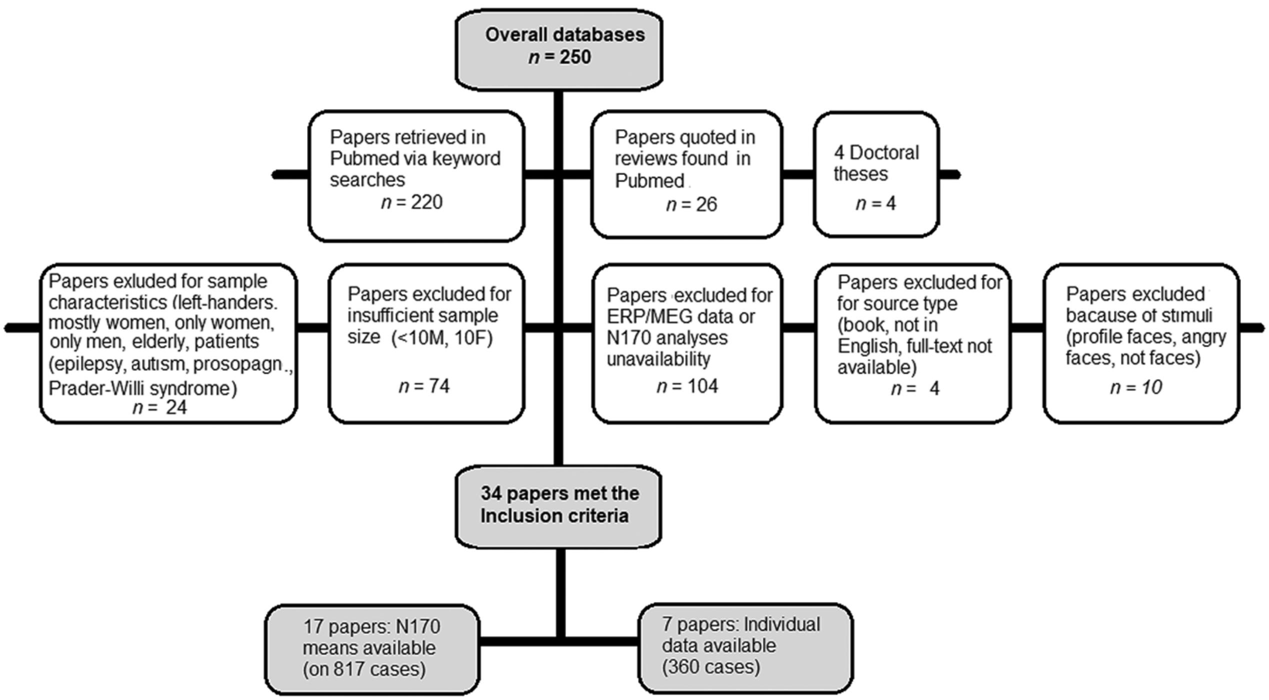

Fig. 2. Flow diagram of the present meta-analysis showing articles that were included and excluded.

or the authors did not respond to the e-mail. The data related to 17 other papers (17 available cases in Figure 1) were available or made available upon request by the authors recruited with the same blind procedure. In one other case, the source was a book, and in two other cases, the language was foreign (not English). In six papers, N170 was elicited by emotional facial expressions.

Of the articles excluded because of their inclusion criteria (illustrated in Figure 2), for 74 papers that fulfilled the other inclusion criteria, the sample was insufficient because it included less than 10 men and/or 10 women. In three studies, some participants were left handed, while in three other studies, the participants were mostly women. In three studies, the participants were only men, and in four other studies, the participants were only women. In one case, the participants included elderly people. In 10 papers, the participants were clinical patients and therefore not healthy people (one study involved autism, three studies involved epilepsy, five studies involved prosopagnosia and one study involved Prader–Willi syndrome). In three studies, the stimuli were not faces; in another study, the stimuli were profile faces. We were not able to access one full-text paper (whose access was restricted), while 16 other papers were reviews of N170 to faces but lacked empirical data. In 38 cases, the data involved face responses and the sex of subjects and hemispheres, but ERP or MEG signals were not recorded. In 28 cases, ERP/MEG signals were recorded to faces in men and women, but N170 was not recorded. In six cases, hemisphere was not a factor or N170 was recorded from a midline electrode. In 15 cases, the sex of the participants was not a factor or information about the gender of the participants was not disclosed. In one case, N170 mean values were not available.

Meta-analysis # 1

Participants. Participants in meta-analysis #1 were 817 subjects recruited by 17 ERP- or MEG-independent investigations (Proverbio *et al.*, 2006, 2010, 2011, 2012; Blau *et al.*, 2007; Steindl, 2009; Godard *et al.*, 2013; Tiedt *et al.*, 2013; Lazar *et al.*, 2014; Ji *et al.*, 2016; Proverbio and Galli, 2016; Recio *et al.*, 2017; Zhu *et al.*, 2017; Stasch *et al.*, 2018; Gao *et al.*, 2019; Nowparast Rostami *et al.*, 2020; Rodríguez-Gómez *et al.*, 2020). The subjects were all strictly right handed and healthy, as certified by the authors of the above studies, with a mean age of 24.5 years (Table 2 for details). The subjects were 414 male and 403 female university students, and their ethnicity was Caucasian or Asian but may have included other ethnicities. The investigations were conducted on the American, Asian and European continents, namely, China = 2, USA = 3, Germany = 4, Italy = 5, France = 1, Austria = 1 and Spain = 1. No subject was affected by psychiatric or neurological disease. The subjects' right-handedness was assessed before EEG/ERP recording. Experiments were conducted with the understanding and written consent of each participant according to the Declaration of Helsinki (BMJ 1991; 302: 1194), with approval from the local Ethical Committees.

Stimuli, procedure and analysis. Faces were all presented at the center of the visual field (foveal presentation) except in Godard *et al.* (2013) study, where faces were presented in the two visual fields. Faces were neutral and upright; Table 2 for details about the task and procedure of each of the studies. Mean amplitude values of N170 (peaking on average at 171 ms) were measured at left and right occipito/temporal sites (Table 2 for a precise indication of recording sites).

A two-way repeated-measures ANOVA was performed on amplitude values of N170 recorded over the left and right occipito/temporal areas from the 14 studies. The factors were one between groups (sex: males and females) and one within groups (hemisphere: left and right). Tukey post hoc comparisons were conducted to assess differences among conditions.

Meta-analysis #2

Participants. Participants in meta-analysis #2 were 360 subjects recruited by seven independent investigations (Nowparast Rostami *et al.*, 2020, 37 females, 43 males; Proverbio and Galli, 2016, 13 females, 13 males; Godard *et al.*, 2013, 24 females, 24 males; Proverbio *et al.*, 2011, 10 females, 10 males, 2010, 20 females, 20 males; Recio *et al.*, 2017, 46 females, 68 males; Gao *et al.*, 2019, 20 females, 12 males). They were all strictly right-handed and healthy. In two cases, participants in the above studies were left-handed, ambidextrous, homosexual or bisexual. Their anonymous data were specifically indicated to us by the authors of the studies so that they could be excluded from our meta-analysis.

Overall, the sample comprised 360 healthy participants whose mean age was 24.5 years (Table 2 for details). No subject was affected by psychiatric or neurological disease. The subjects' right-handedness was assessed before EEG/ERP recording.

Stimuli, procedure and analysis. Faces were presented at the center of the visual field, except in Godard *et al.* (2013) study, where faces were presented in the two visual fields. Faces were all neutral and upright; the task consisted of detecting filler targets (animals and landscapes) or deciding about face orientation, learning faces, passive viewing or the same/different decision in the various studies. Mean amplitude values of N170 (peaking on average at 171 ms) were measured at left and right occipito/temporal sites (Table 2 for a precise indication of recording sites).

Two-way repeated-measures ANOVAs were performed on 360 pairs of N170 amplitude values relative to individual data from the seven studies. The factors were one between groups (sex: males and females) and one within groups (hemisphere: left and right). Tukey post hoc comparisons were conducted to assess differences among conditions. Scatterplot distributions were computed across the various factors and compared across sexes through the Statistica 10 application.

Results

Results of meta-analysis #1

ANOVA yielded the statistical significance of the hemisphere factor ($F_{1, 32} = 4.17$, $P < 0.05$), with N170 larger overall over the right (−5.6 μV, SE = 0.23) than the left hemisphere (−4.66 μV, SE (Standard Error) = 0.19). However, the further significance of sex x hemisphere ($F_{1, 32} = 7.3$, $P < 0.01$) showed a sex difference in the hemispheric distribution of N170. N170 was larger over the right hemisphere (RH: −5.51 μV, SE = 1.04) than the left hemisphere (LH: −4.28 μV, SE = 0.88) in men ($P < 0.01$) but bilateral in women (LH: −4.57 μV, SE = 0.88; RH: −4.44 μV, SE = 1.04. $P = 0.97$), as shown by post hoc comparisons among means and presented in Figure 3.

Results of meta-analysis #2

ANOVA yielded the statistical significance of the hemisphere factor ($F_{1, 358} = 32.8$, $P < 0.001$), with N170 larger overall over the right hemisphere (−5.6 μV, SE = 0.23) than the left hemisphere (−4.66 μV, SE = 0.19). Figure 4 shows a scatterplot distribution of individual values of N170. However, the further significance of sex x hemisphere ($F_{1, 358} = 7.3$, $P < 0.007$) showed a sex difference in hemispheric distribution of N170. N170 was larger over the right hemisphere (−5.51 μV, SE = 0.52) than the left hemisphere (−4.09 μV, SE = 0.49) in men ($P < 0.000001$) but bilateral in women (LH: −4.62 μV, SE = 0.5; RH: −5.16 μV, SE = 0.54. $P = 0.11$.), as shown by post hoc comparisons among means. As shown in Figure 5, N170 was always larger over the right recording sites (except in two subjects) in 190 male right-handed students,

Table 2. List of 17 papers that met the inclusion criteria and for which individual or mean N170 amplitude values were available/made available

Authors	Journal	Stimuli	Task	Cond.	Rhand	Age	Lat.	Elec.	Note
Stasch *et al.* (2018)	Biol Psychol	Famous, unknown faces	Respond to target	Lat RVF	yes	26.6	179	P7/8, PO7/8, PO9/10	
Lazar *et al.* (2014)	Behav Brain Res	Faces, houses	Passive viewing	Center	yes	18.9	166	P7/P8	
Proverbio and Galli (2016)	Soc Cogn Aff Neurosci	Faces, FIT, objects	Respond to animals	Center	yes	23.5	166	P9/P10	
Godard *et al.* (2013)	Neurosci Res	Unknown faces	Same/diff.	Lateral	yes	25.7	187	P7/P8	
Proverbio *et al.* (2012)	Neuropsycholog.	Unknown faces	Sex identification	Lateral	yes	24	172	P9/P10	
Ji *et al.* (2016)	Neurosci letter	Unknown faces	Respond to target	Center	yes	21.6	167	O1/2, T5/6	
Proverbio *et al.* (2011)	J Cogn Neurosci	Child, adult faces	Respond to landscape	Center	yes	22	170	P9/10, PPO9h/10 h, TPP9h/10 h	1
Proverbio *et al.* (2006)	BMC Neurosci	Infant faces	Respond to distress	Center	yes	33.7	159	OL, OR	2
Proverbio *et al.* (2010)	Plose One	Faces, objects	Landscape detection	Center	yes	22.36	170	P9, P10	3
Blau *et al.* (2007)	Behav Brain funct	Unknown faces	Ignore faces (lang. task)	Center	yes	27	170	PO9, PO10	4
Tiedt *et al.* (2013)	Plos One	Familiar faces	Passive viewing	Center	yes	25.46	170	Occ/Temp	5
Zhu *et al.* (2017)	Front Hum Neurosci	Faces, houses, characters	Respond to target	Center	yes	23.4	170	O1/2, T5/6	6
Rodríguez-Gómez *et al.* (2020)	Soc Cogn Aff Neurosci	Neutral faces	P viewing (reading)	Center	yes	20.5	170	P7, P8	7
Recio *et al.* (2017)	Soc Cogn Aff Neurosci	Neutral (video)	P viewing (chewing)	Center	yes	25.9	170	P9, P10	8
Nowparast Rostami *et al.* (2020)	Soc Cogn Aff Neurosci	Neutral faces	Learning/recognition	Center	yes	27	174	P9, P10	9
Steindl (2009)	Doct.thesis	Neutral faces	Sex identification	Center	yes	25.98	170	PO9, PO10	
Gao *et al.* (2019)	Psychophysiol.	Adult faces	Orientation detection	Center	yes	23.4	178	PO7/PO8	10
Means						24.5	171		

(Continued)

Table 2. (Continued)

Authors	Sex x Hem (*p* value)	Male LH	Male RH	RH > LH (P-value)	Female LH	Female RH	RH > LH (*P*-value)	# M	# F	Tot Ss
Stasch *et al.* (2018)	0.023	−4.87	−3.85	n.s.	−4.96	−3.28	LH > RH 0.006	27	27	54
Lazar *et al.* (2014)	0.001	−0.60	−3.71	NA	−4.32	−1.94	NA	20	27	47
Proverbio and Galli (2016)	n.s.	−0.77	−1.91	0.01	−0.08	−1.01	0.01	13	13	26
Godard *et al.* (2013)	0.025	−7.53	−9.18	0.012	−9.38	−9.89	n.s.	12	12	24
Proverbio *et al.* (2012)	0.009	−2.10	−1.70	n.s.	−3.38	−2.55	LH > RH 0.01	16	17	33
Ji *et al.* (2016)	n.s.	−7.22	−8.49	0.002	−6.20	−5.93	n.s.	42	42	84
Proverbio *et al.* (2011)	0.005	−1.09	−2.14	0.05	−1.51	−0.55	n.s.	10	10	20
Proverbio *et al.* (2006)	0.03	−2.41	−3.29	0.05	−1.50	−0.20	n.s.	20	20	40
Proverbio *et al.* (2010)	0.08	−3.23	−1.98	0.04	−3.23	−2.45	n.s.	25	25	50
Blau *et al.* (2007)	n.s.	−4.52	−4.14	n.s.	−3.22	−3.52	n.s.	15	19	34
Tiedt *et al.* (2013)	0.003	−1413	−2098	0.003	−1491	−1427	n.s.	13	13	26
Zhu *et al.* (2017)	0.053	−7.73	−8.59	0.032	−6.44	−6.07	n.s.	34	34	68
Rodríguez-Gómez *et al.* (2020)	NA	0.28	−0.71	NA	1.85	−0.40	NA	20	20	40
Recio *et al.* (2017)	n.s.	−5.81	−7.38	0.001	−5.44	−6.83	n.s.	68	46	114
Nowparast Rostami *et al.* (2020)	n.s.	−4.90	−6.00	0.003	−6.50	−7.60	n.s.	43	37	80
Steindl (2009)	NA	−1.81	−3.81	0.04	No asymmetry		n.s.	24	21	45
Gao *et al.* (2019)	n.s.	−4.25	−5.84	0.07	−3.94	−4.62	n.s.	12	20	32
Means		−4.28	−5.51		−4.57	−4.45		414	403	817

Notes: The table provides information about the authors, the journal and year of publication, the stimulus type and tasks involved, the presentation conditions (foveal or peripheral), the existence of a significant interaction between sex and hemisphere in the amplitude of N170 (if any). Also provided are the mean values of N170 as recorded at left and right occipito/temporal sites (in µV), post-hoc comparisons significances (if any), the sample composition (number of males, women and total number) the mean age of participants, the mean N170 latency (in ms), the electrode sites of recording for N170. In the last row it can be found: the overall N170 mean amplitude values, the N170 mean latency value, the Ss' mean age. Notes 1: Data relative to adult faces; 2: Data relative to neutral faces; 3: Data relative to adult faces; 4: Data relative to neutral faces; 5: unit measure = fL-1; 6; data relative to adapters; 7: Data relative to prejudice-free condition: 8: Data relative to neutral faces; 9: Study 1; 10: Data relative to upright faces. Cond. = viewing condition; Lat = N170 peak latency in ms; RHand = right-handedness of participants; Elec. = electrodes of recording; Age = mean age in years.

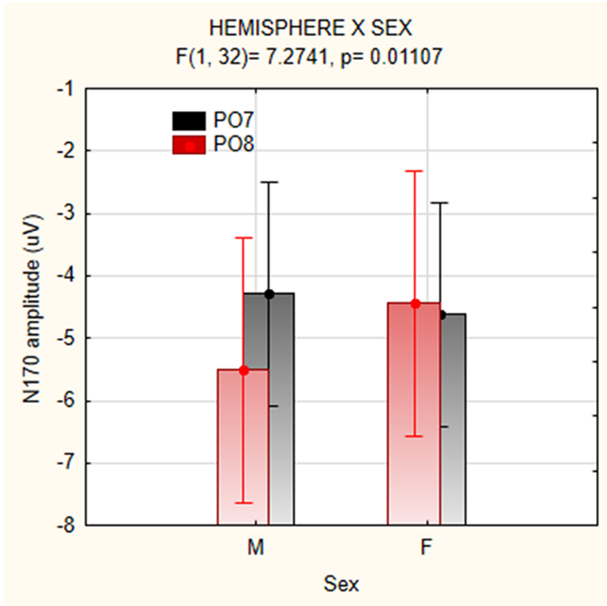

Fig. 3. Mean amplitude of occipito/temporal N170 components as recorded in women and men as a function of hemisphere of recording. Data related to meta-analysis #1 involving 817 healthy subjects.

while it appeared bilateral or even left sided in many of the 170 female students.

Discussion

The results of meta-analysis #1 (applied to the mean values of N170 recorded at left and right sites, as found in 17 independent ERP/MEG studies) and meta-analysis #2 (applied to the individual values of N170, as reported in 7 independent ERP studies) showed quite similar patterns, with a strictly right-sided distribution of N170 face responses in male students living on 3 different continents (Asia, USA and Europe) and a lack of significantly different hemispheric lateralization in females. As shown in Table 2, among 817 subjects, in only 1 case out of 17 articles was right hemispheric lateralization of N170 in response to faces (ironically, by Proverbio and Galli, 2016), while in two cases, left hemispheric lateralization for N170 was even reported (Proverbio *et al.*, 2012; Stasch *et al.*, 2018). On the other hand, for males, in no case was N170 left lateralization reported, while in the large majority of cases, statistically significant right hemispheric asymmetry was found. The results hint at a robust sex difference in hemispheric lateralization for face processing, which fits with previous MEG studies (e.g. Tiedt *et al.*, 2013) and, in principle, should be based on genetic or biological factors.

Quite recently, Liu *et al.* (2020) reached these conclusions by performing structural, functional and transcriptomic analyses of sex-biased brain areas. They found that relative GMV showed asymmetry in males in ventral occipitotemporal and distributed subcortical regions. Furthermore, through systematic comparison with functional neuroimaging meta-analyses, the authors found a statistically significant concentration of sex differences in GMV in brain regions that subserved face perception, including the FG, and more generally in brain circuits devoted to social cognition. Similarly, Lotze *et al.* (2019) found more GMV in the right FG, right occipital gyrus (OG) and right middle temporal gyrus (rMTG) in males than in females. These anatomical asymmetries might explain the different patterns of scalp distribution of bioelectrical responses found in the present meta-analyses in men and women.

The bilateral representation of face-responsive areas in women might be associated with greater female accuracy in tasks involving face recognition and decoding of facial expressions. Consistent with this hypothesis, many studies have demonstrated a greater ability to categorize emotional states through facial expressions in women than men (Hall *et al.*, 2010; Herlitz and Lovén, 2013; Thompson and Voyer, 2014). Finally, a large investigation involving the testing of 100 257 persons (Olderbak *et al.*, 2019) found a consistent advantage of females in perceiving facial emotion. Other studies found sex differences in face pareidolia, with a greater inclination of females to perceive faces in objects or shapes and anthropomorphize inanimate things (Pavlova *et al.*, 2014, 2015; Proverbio and Galli, 2016). This evidence is paralleled by many ERP studies showing sex differences in face processing (e.g. Proverbio *et al.*, 2006a, 2010, 2011; Stahl *et al.*, 2008; Sun *et al.*, 2010, 2017; Dzhelyova *et al.*, 2010; Godard *et al.*, 2013; Tiedt *et al.*, 2013; Ji *et al.*, 2016; Zhang *et al.*, 2016; Colasante *et al.*, 2017; Zhu *et al.*, 2017; Carrier-Toutant *et al.*, 2018; Stasch *et al.*, 2018; Nowparast Rostami *et al.*, 2020). More generally, this gender bias has been interpreted in light of a sex difference in social cognition (Proverbio and Galli, 2016; Li *et al.*, 2020; Kiesow *et al.*, 2020).

On the other hand, the sex difference in hemispheric recruitment of face-related areas might also be linked to a difference in the efficiency or rapidity with which visual crossed ipsilateral information is transferred to the other hemisphere via the corpus callosum. Indeed, a certain sex dimorphism in callosal anatomy and functionality is known to exist. A more rapid and symmetric interhemispheric transfer time (IHTT) in women than men has been shown for words (Nowicka and Fersten, 2001) and faces (Rizzolatti and Buchtel, 1977). Proverbio *et al.* (2012) investigated IHTT and hemispheric lateralization during face processing in the two sexes. ERPs were recorded in strictly right-handed individuals (16 men and 17 women) engaged in a face-sex categorization task. Occipital P1 and occipito/temporal

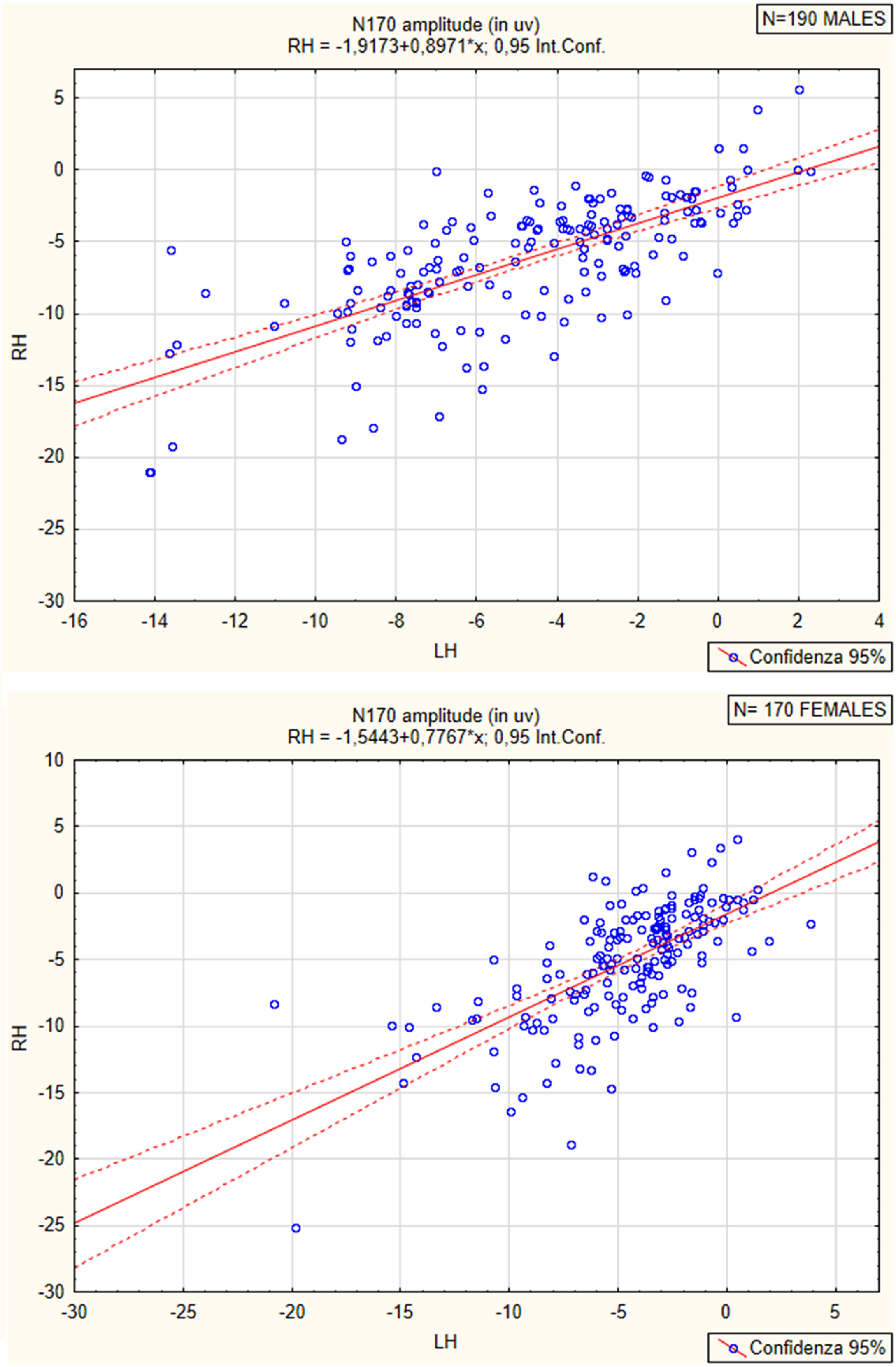

Fig. 4. N170 amplitudes recorded at right *vs.* left occipito/temporal sites in men (top) and women (bottom). The scatterplot distribution concerns the data contributing to meta-analysis #2 involving the individual data of 170 females and 190 males.

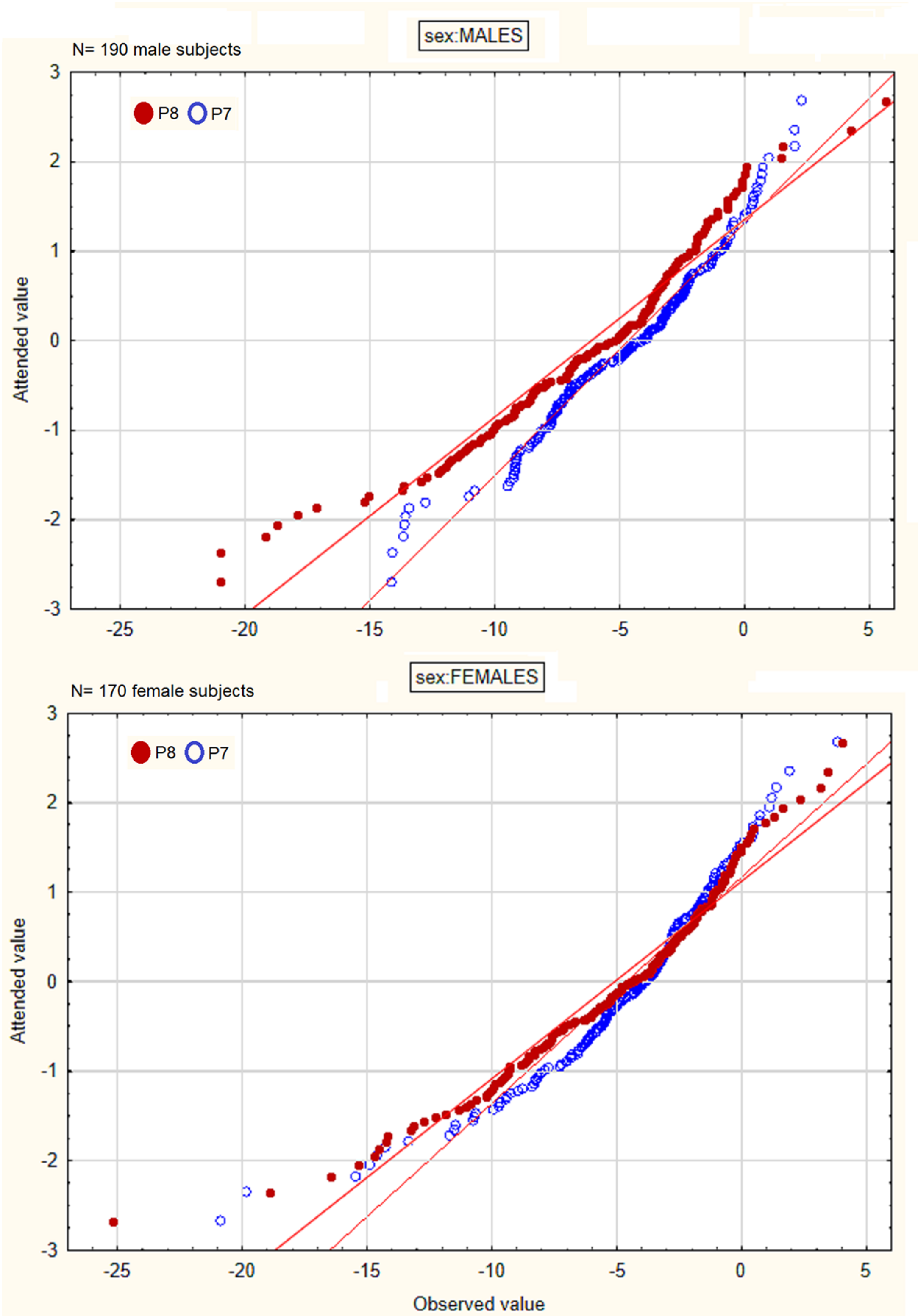

Fig. 5. Linear distribution of N170 amplitudes recorded in men (top) and women (bottom) as a function of electrode of recording (P8 *vs.* P7) meta-analysis #2. Right hemispheric asymmetry for N170 was observed in 188 out of 190 males, while N170 was bilateral (or even left-sided) in many of the 170 female subjects.

N170 were left lateralized in women and bilateral in men. N170 to contralateral stimuli was greater over the right in men and the left in women. The IHTT was ~4 ms at the P1 latency level and ~8 ms at the N170 level. It was asymmetric in men, with faster latencies in the LVF/RH→LH (170 ms) direction than in the right visual field/LH→RH (185 ms) direction, while it was symmetric in women. This evidence suggests that this asymmetry in callosal transfer times might be caused by faster transmission times of face-related information via fibers departing from the more efficient to the less efficient hemisphere. In this view, the more efficient face area in men would be the right face circuit. The faster (visual) callosal transmission times in female humans have been explained by the presence of a thicker splenium (Davatzikos and Resnick, 1998; Dubb *et al.*, 2003). In addition, diffusion tensor imaging studies (e.g. Ingalhalikar *et al.*, 2014) have measured structural and functional brain connectivity in men and women and found that male brains were structured to facilitate within-lobe and within-hemisphere connectivity, whereas female brains showed greater interhemispheric connectivity and greater cross-hemispheric participation. This finding fits with the evidence of an increased bilaterality in the neural system devoted to face processing in females.

Overall, the results of statistical analyses seem to robustly indicate the presence of a sex difference in the way the left and right hemispheres process facial information (see also Pavlova, 2017), with a marked right-sided asymmetry of the bioelectrical activity in males and a bilateral distribution in females. This activity especially reflects the activation of the face fusiform area, thought to be the main intracranial source of the M170/N170 potentials evoked by faces (e.g. Pizzagalli *et al.*, 2002; Kume *et al.*, 2016). The results of this study should encourage researchers to consider the gender of participants and not assume that a prevalence of males gives a representative picture of all humankind (Cahill, 2006; Woitowich and Woodruff, 2019). This is crucial for neuroscientific, neurological and genetic and neuropharmacological studies (Galea *et al.*, 2020; Shansky and Woolley, 2016; Woitowich.

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Conflict of interest

None declared.

Supplementary data

Supplementary data are available at *SCAN* online.

Data availability statement

The authors confirm that the data supporting the findings of this study are available within the article and its supplementary materials. Any other detail is available upon request to the corresponding author.

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