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► To cite this version:

Ornella Godard, Arnaud Leleu, Mohamed Rebaï, Nicole Fiori. Sex differences in interhemispheric communication during face identity encoding: Evidence from ERPs. *Neuroscience Research*, 2013, 76 (1-2), pp.58-66. 10.1016/j.neures.2013.03.005 . hal-01184513

HAL Id: hal-01184513

<https://hal.science/hal-01184513>

Submitted on 4 Apr 2024

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Sex differences in interhemispheric communication during face identity
encoding: Evidence from ERPs

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Abstract

Hemispheric lateralization and interhemispheric transmission times (IHTTs) depending on the sex of twenty-four participants were examined at the level of the first visual ERP components (P1 and N170) during face identity encoding in a divided visual-field paradigm. While no lateralization-related and sex-related differences were reflected in the P1 characteristics, these two factors modulated the N170. Indeed, N170 amplitudes indicated right hemisphere (RH) dominance in men and a more bilateral functioning in women. N170 latencies and the derived IHTTs confirmed the RH advantage in men but showed the reverse asymmetry in women. Altogether, the results of this study suggest a clear asymmetry in men and a more divided work between the hemispheres in women, with a tendency toward a left hemisphere (LH) advantage. Thus, by extending the pattern to the right-sided face processing, our results generalize previous findings from studies using other materials and indicating longer transfers from the specialized to the non-specialized hemisphere especially in the male brain. Because asymmetries started from the N170 component, the first electrophysiological index of high-level perceptual processing on face representations, they also suggest a functional account for hemispheric lateralization and sex-related differences rather than a structural one.

Key-words: hemispheric communication, hemispheric specialization, sex-related differences, face identity encoding, N170-IHTTs, divided-visual field paradigm.

Introduction

The human brain is composed of two hemispheres specialized in the processing of specific information. It is now well admitted that the left hemisphere is specialized in the processing of verbal information whereas the right hemisphere is specialized in the processing of visuo-spatial information (e.g. Hellige, 1990). This divided work between the hemispheres is called “hemispheric specialization” or “hemispheric lateralization”. Although hemispheres present specialization for specific functions, they work together and exchange continuously information via the largest white matter structure in the brain: the *corpus callosum* (CC). Surgical transections of this structure in humans have provided evidence that, in general, the CC communicates perceptual, cognitive, mnemonic and motor information between the two brain hemispheres (Bogen, Fisher, & Vogel, 1965; Hofer & Frahm, 2006).

In order to better understand how hemispheres share information, several studies focused on the interhemispheric transfer of information. At a behavioral level, interhemispheric transfer has been evaluated using the Crossed-Uncrossed reaction time Difference (CUD). The CUD studies have been reviewed by Marzi et al. (1991) and Braun (1992) via a meta-analysis of a large sample of studies using mainly simple reaction times tasks. Those two meta-analyses highlighted a general faster transfer from the right to the left hemisphere (R-to-L) than transfer in the reverse direction (L-to-R). While Marzi et al. (1991) interpreted this asymmetrical transfer in terms of greater number of neurons projecting from the right to the left hemisphere than the opposite, Braun (1992) suggested that the asymmetry in the transfer could be explained by a left visual field (LVF) advantage in this kind of tasks, due to a right hemisphere dominance in attentional control. Hence, the asymmetry observed in the transfers may also depend on the hemispheric specialization.

Nevertheless, although the CUD method was the first to provide assessment of interhemispheric transfers, it does not allow distinguishing all components integrated in the

behavioral measure (i.e., sensory, perceptual, decisional, or motor information; Milner & Lines, 1982). Electrophysiological method provides a better estimation of the interhemispheric transmission times (IHTTs) at several levels of processing (Saron & Davidson, 1989). Using the divided visual-field paradigm, studies of human event-related potentials (ERPs) classically showed that contralateral responses following unilateral stimulation are consistently faster than the ipsilateral responses (e.g., Andreassi, Okamura & Stern, 1975). Consequently, IHTTs are calculated with latency differences between ERP components recorded over the ipsilateral hemisphere to the stimulated visual field and those recorded over the contralateral hemisphere to it. For example, using a letters matching task, Brown and collaborators calculated the IHTTs from P1 and N1 latencies recorded over parietal sites, and found faster transfer from the R-to-L than the reverse direction for both P1 and N1 (Brown & Jeeves, 1993; Brown, Larson & Jeeves, 1994). Whereas these results seem to confirm the CUDs findings, the material and the task involved verbal information, for which the left hemisphere is specialized. As a consequence, it suggests that transfer is faster from the *non-specialized* hemisphere for the task (the RH) to the *specialized* one (the LH) than in the opposite direction during early processing in the visual system reflected by the first ERP components.

To directly investigate this question, Nowicka, Grabowska and Fersten (1996) used two kinds of information for which hemispheric specialization has been clearly shown: a letter matching task for which the LH is specialized and low spatial frequency gratings matching task for which the RH is specialized. For both tasks, results highlighted that the transfer was faster from the *non-specialized* hemisphere for the task to the *specialized* one than in the reverse direction. The authors suggest the existence of a mechanism allowing information being rapidly and efficiently processed by the specialized hemisphere. Larson & Brown (1997) used also two tasks for which the hemispheric lateralization differs: a verbal task (letter-matching) and a visuo-spatial task (pattern of circles matching). The P1 and N1 components were recorded on

parietal sites according to the visual field and the hemisphere. Findings replicated a significant visual field-by-hemisphere interaction for the verbal task, showing a faster N1-IHTT R-to-L hemisphere (from the non-specialized hemisphere to the specialized one) than the reverse direction. However, for the visuo-spatial task, no significant difference between the two directions was found. Thus, while using verbal tasks and materials for which the left hemisphere is specialized provided many evidences for a faster R-to-L transfer, findings using right-sided visuo-spatial information were found to be mixed.

In addition, another factor that can account for differences in hemispheric specialization and interhemispheric transfer is the sex of the participants. Indeed, some studies reported sex differences during verbal and visuo-spatial information processing, with the male brain being more asymmetrically organized than the female brain (McGlone, 1980; Voyer, 1996; Kansaku, Yamaura, & Kitazawa, 2000; Gur, Alsop, Glahn, Petty, Swanson, Maldjian, et al., 2000). Men have also been found to have greater hemispheric asymmetry during facial information processing using behavioral (Rizzolatti & Buchtel, 1977; Allen, Richey, Chai, and Gorski, 1991; Bourne, 2005; Godard & Fiori, 2010) and electrophysiological methods (Fiori, Chaby, and George, 2001; Proverbio, Brignone, Matarazzo, Del Zotto, and Zani, 2006; Proverbio, Riva, Martin, and Zani, 2010; Proverbio, Riva, Zani, and Martin, 2011). In these studies, face coding was found to be bilateral, or left lateralized, in women and right-hemisphere-lateralized in men. Moreover, in a face identity matching task, interhemispheric cooperation was found to be asymmetrical in men and symmetrical in women (Godard & Fiori, 2012).

Considering IHTTs at the level of ERP components, Nowicka and Fersten (2001) used a letter-matching task with the divided-visual field technique in order to assess sex-related differences. They found earlier N170 over parietal than occipital sites and a sex by transfer directions interaction. Whereas no sex effect was observed for the R-to-L direction, men presented a longer L-to-R than women leading to an asymmetrical transfer in men (longer from

the L-to-R than from the R-to-L) and a symmetrical one in women. This study was the first to report sex differences in IHTTs of verbal information. More recently, Moes, Brown, and Minnema (2007) also highlighted sex differences in the IHTTs of verbal information. They used the same paradigm of Brown et al. (1994) with a “name” letter matching task (rather than a physical identity matching task) in which a pair of letters was presented during 60 ms in one visual-field. They first confirmed the asymmetry of IHTTs, with R-to-L being significantly shorter than L-to-R. They also found shorter L-to-R IHTTs in women than men, supporting more symmetrical IHTTs in women. Overall, Moes et al. (2007) and Nowicka & Fersten (2001) highlighted that the longer transfer from the *specialized* hemisphere to the *non-specialized* hemisphere is observed only in men, at least during the processing of verbal information.

In order to examine whether longer transfer from the specialized to the non-specialized hemisphere may be generalized, and whether this asymmetry in transfers depends on sex, assessing IHTTs with tasks and/or materials involving the right hemisphere is necessary. This issue has recently been challenged by Proverbio, Mazzara, Riva, and Manfredi (2012) using face information for which the right hemisphere dominance is well-known (e.g., Sergent, Ohta & MacDonald, 1992). Surprisingly, like in verbal tasks, results indicated a longer L-to-R transfer in men and symmetrical IHTTs in women. According to the authors, this discrepancy may be explained by the sex categorization task they used which depends more on local processing, mainly subtended by the left hemisphere. Therefore, the main purpose of the present study was to investigate sex differences in IHTTs during face identity encoding, which relies more on global processing implemented in the right hemisphere, especially at the level of the early N170 ERP component (Jacques & Rossion, 2009). Participants performed an identity matching task, in which the probe face was briefly presented either in the left or in the right visual-field, followed by a central target face. Thus, IHTTs were calculated from the P1 and N170 latencies in ERPs time-locked with the probe face onset (i.e., during identity encoding

rather than during the matching/discrimination process). With respect to an asymmetrical transfer in men - longer transfer from the *specialized* to the *non-specialized* hemisphere - and a symmetrical one in women, our main hypothesis suggests longer R-to-L than L-to-R IHTTs in men only. Considering that these transfer times are related to the hemispheric specialization, we also expected that men would have earlier and greater N170 over the RH, whereas women would have equivalent N170 over both hemispheres.

Material and Method

Participants

Twenty-four paid volunteers (twelve women) participated in the study after giving informed consent. They were undergraduate students at the University of Rouen, with the women ranging in age from 21 to 30 years (mean=25.2 \pm 2.3), and the men ranging in age from 22 to 32 years (mean=26.3 \pm 3.1). Handedness was evaluated with a questionnaire (Dorthe, Blumenthal, Jason, and Lantz, 1995) which measured handedness on a continuum from -1 (strongly left-handed) to +1 (strongly right-handed). All participants were predominantly right-handed. The mean handedness quotient was 0.74 (range from .36 to .95, SD= .13) for women and 0.73 (range from .50 to .98, SD= .16) for men. No Sex effect on the handedness quotient was found [$t(22) = .052$; $p = .82$]. All participants had normal or corrected-to-normal vision. Because sex hormones might play a role in modulating functional brain asymmetries and IHTTs (Hausmann & Güntürkün, 2000; Bayer, Kessler, Güntürkün, and Hausmann, 2008), and in order to avoid steroid hormones fluctuations and eventual biases in the results, all the women who participated in the study took usually a non progestative birth-control pill.

Material

The stimuli were 18 colored pictures of faces drawn from The NimStim database (Tottenham, Tanaka, Leon, McCarry, Nurse, Hare, et al., 2009). These pictures resulted of 6 different identities (3 males and 3 females) expressing 3 different emotions (neutral, fear and happy). They were used to present two different images of the same person in the matching procedure. Using the Adobe PhotoShop software package, faces were mounted on a grey background of mean luminance and scaled to an image size of 300 * 391 pixels. The images subtended a visual angle of $6^\circ \times 9^\circ$ in the horizontal and vertical dimensions, respectively. Stimuli were presented on a computer running E-prime 1.2 software (PST, Inc.). Screen resolution was 1024 by 768 pixels.

Procedure

The task was a face identity matching task. After the electrode-cap placement, subjects were seated on a chair in a light-attenuated room. The stimuli were displayed against a light grey background at viewing distance of 57 cm. The subject's head was held in place by a chin rest, and they were instructed and trained to fixate the central cross on the screen during the entire duration of each trial.

The sequence for a trial was as follows: a fixation cross was displayed (1000 ms) followed by a probe face (80 ms) in the left visual field (LVF) or the right visual field (RVF). Probe faces were presented with their inside edge 3.6° from the central fixation cross. After a presentation of a greyscale screen for 1100 ms, a target face appeared centrally (during 1000 ms) and the subject answered by pressing a key on the keyboard. Inter-trial interval varied randomly from 1500 ms to 2500 ms. In order to ensure that the subjects understood the task, sixteen practice trials were completed.

For each subject, an experimental session included 6 blocks of 24 trials (2, Visual field: LVF, RVF \times 2, Response: same, different \times 6 facial identities) which were each randomly

repeated 4 times (a total of 576 trials). A “same” / “different” matching procedure was used. Half of the subjects had to press “M” key with the right index (on AZERTY keyboard) when probe and target faces were the same person, and “Q” key with the left index when the faces were two different people, as quickly and accurately as possible. For the other half, this key and finger assignment was reversed. In half of trials, the identities of probe and target faces were the same, and in the other half, they were different.

EEG recording and analysis

EEG was continuously recorded from 32 Ag/AgCl electrodes mounted in an electrode cap (Waveguard, ANT) according to the 10-10 classification system with respect to a reference electrode placed in a frontocentral position (AFz), at a sampling rate of 256 Hz (band-pass filter: 0.1-100Hz). Electrode impedance was kept below 10 k Ω . The electrodes used were: O1, Oz, O2, POz, P7, P3, Pz, P4, P8, M1, M2, CP5, CP1, CP2, CP6, T7, C3, Cz, C4, T8, FC5, FC1, FC2, FC6, F7, F3, Fz, F4, F8, Fp1, Fpz, Fp2. Epochs were synchronized with the onset of the probe face. A 40 Hz low-pass filter was applied off-line, and trials contaminated with eye movements or other artifacts were rejected ($\geq \pm 75$ μ V). ERPs were averaged for 1200ms, including a 200ms baseline before stimulus onset and a 1 s interval after stimulus onset, and re-referenced to a common average reference. Only recordings from trials with correct responses were used. EEG data were analyzed using ASA 4.6 (ANT, Inc.).

Two components were analyzed: P1 and N170. They were defined as the maximal positivity and negativity in the range of 70-180 ms and 130-220 ms respectively, on occipito-temporal (P7 on the LH and P8 on the RH), parietal (P3 on the LH and P4 on the RH), and centro-parietal (CP5 on the LH and CP6 on the RH) electrodes. The minimum numbers of trials per conditions was 235 and the maximum numbers was 288 trials.

Statistical analyses

Repeated-measures ANOVAs were conducted on latencies (ms) and amplitudes (μV) of both components according to the *Sex* as between-subject factor, and *Visual field* (LVF, RVF), *Hemisphere* (RH, LH), and *Electrodes* (P7/8, P3/5, CP5/6) as within subject factors. IHTTs were calculated with latency differences between ERP components recorded over the ipsilateral hemisphere to the stimulated visual field and those recorded over the contralateral hemisphere, and analyzed according to *Sex* as between-subject factor, and *Direction* (L-to-R, R-to-L), and *Electrodes* (P7/8, P3/5 and CP5/6) as within subject factors. All effects with two or more degrees of freedom were adjusted for violations of sphericity according to the Greenhouse–Geisser correction. Post-hoc comparisons were done to determine the significance of pairwise contrasts, using Fisher’s one-factor LSD procedure ($\alpha = 0.05$).

Grand average ERPs depending on the visual field of presentation, the hemisphere and the electrodes are shown on Figure 1 for women and on Figure 2 for men. All the data relative to the P1 amplitudes and latencies are presented in Table 1 and the data relative to the N170 amplitudes and latencies are presented in Table 2, according to the *Sex*, the *Visual field* of presentation, the *Hemisphere* and the *Electrodes*.

“Insert Table 1 and Table 2”

“Insert Figure 1 and Figure 2”

Results

P1 Amplitude

Factor Electrode had a significant effect [$F(1.5,33.7)=38.56$; $\epsilon= .76$; $p<.00001$] indicating larger P1 amplitudes on P7/8 electrodes than on P3/4 and on CP5/6 ($p<.0001$) and no differences between P3/4 and CP5/6 ($p=.36$). While the Electrode by Hemisphere interaction was close to significance threshold [$F(1.5,32.5)=3.23$; $\epsilon= .74$; $p=.07$], the Hemisphere by Electrode by Visual field interaction was significant [$F(1.7,36.6)=12.66$; $\epsilon= .83$; $p<.0002$]. Hence, the Visual field by Hemisphere interaction has been examined for each Electrode sites. While on P7/8 and P3/4 electrodes, it tended to be statistically significant [$F(1,22)=3.50$; $p=.075$ and $F(1,22)=3.18$; $p=.088$ respectively], it was not the case on CP5/6 ($F<1$). Descriptively, on P7/8 and on P3/4 the P1 was larger over the directly stimulated hemisphere (e.g., RH after LVF presentation) than over the indirectly stimulated one. Main effects of Visual field and Hemisphere were not significant and there were no effects or interactions including the Sex factor (all $p>.12$).

In order to assess if one hemisphere evoked a larger P1 than the other one after a direct stimulation (in the contralateral visual field), amplitudes over the RH after a LVF stimulation and over the LH after a RVF stimulation were compared. No significant differences were found whatever the electrodes despite some trends (all $p>.053$).

P1 Peak-latency

While all main effects were not significant (all $p>.10$), Visual field by Hemisphere interaction was statistically significant [$F(1,22)=132.13$; $p<.00001$]. This one-way interaction indicated shorter P1 latency over the directly stimulated hemisphere than over the indirectly stimulated one. This interaction was modulated by the Electrode [$F(1.9,40.7)= 3.79$; $\epsilon= .93$;

$p=.03$] showing a strong Visual Field \times Hemisphere interaction on P7/8 [$F(1,22)=102.34$; $p<.0001$] and on CP5/6 [$F(1,22)=136.04$; $p<.0001$] and a weaker one on P3/4 [$F(1,22)=46.54$; $p<.0001$]. All other interactions were not significant (all $p>.14$).

Again, in order to evaluate if one hemisphere responded faster than the other one after a direct stimulation (in the contralateral visual field), latency over the RH after a LVF stimulation and over the LH after a RVF stimulation were compared. No significant differences were found whatever the electrodes (all $p>.22$).

P1-IHTTs

Only the main effect of Electrode was significant [$F(1.9,40.7)= 3.79$; $\epsilon= .93$; $p=.03$]. Transfer was equivalent between P3/4 and P7/8 ($p=.19$) or CP5/6 ($p=.17$), however, it was significantly longer when calculated on CP5/6 than on P7/8 ($p=.008$). All main other effects or interactions were not significant (all $p>.10$).

N170 Amplitude

The main effect of Electrode was significant [$F(1.3,27.9)=23.2$; $\epsilon= .63$; $p<.00002$] showing larger N170 on the electrodes P7/8 than on P3/4 ($p<.00001$) and on the electrodes CP5/6 ($p<.00001$), but no difference between these two last sites ($p=.36$). Electrode effect tended to be modulated by the factor Hemisphere [$F(1.4,31.8)=3.38$; $\epsilon= .72$ $p=.061$] with greater amplitudes on the RH than on the LH on P7/8 ($p<.0001$) and on P3/4 ($p<.005$) but not on CP5/6 ($p=.07$). Hemisphere by Visual field interaction was significant [$F(1,22)=10.71$; $p<.005$] indicating a larger amplitude over the RH than over the LH after a LVF stimulation ($p=.0008$) but no difference between the hemispheres after a RVF stimulation ($p=.48$).

Again, amplitudes over the RH after a LVF stimulation and over the LH after a RVF stimulation were compared in order to evaluate if one hemisphere evoked a larger response than the other one after a direct stimulation. This difference was not statistically significant ($p=.16$).

As the Visual field by Hemisphere by Electrode by Sex interaction was significant [$F(1.7,38.1)=4.42$; $\epsilon=.87$; $p<.025$], two separated analyses were conducted: one analysis for the group of men and another one for the group of women. All other effects or interactions were not significant (all $p>.11$).

In men, again, we observed a significant effect of Electrode [$F(1.4,14.9)=18.6$; $\epsilon=.68$; $p<.0005$]. Interestingly, the N170 was larger over the RH than over the LH [$F(1,11)=9.07$; $p=.012$] and the Visual field by Hemisphere interaction was significant [$F(1,11)=7.35$; $p=.02$]. When faces were presented in the RVF, N170 was equivalent over the LH and the RH ($p=.20$) whereas, when faces were presented in the LVF, N170 was larger over the RH than over the LH ($p=.0003$). Other effects or interactions were not significant (all $p>.08$). When comparing amplitudes over the directly stimulated hemispheres, the N170 was larger over the RH than over the LH after a direct stimulation (in the LVF and the RVF respectively; $p=.0004$).

In women, we observed the same main effect of Electrode [$F(1.2,13.4)=8.53$; $\epsilon=.61$; $p=.009$]. The Visual field by Hemisphere interaction was significant [$F(1,11)=5.59$; $p=.037$] and qualified by a significant two-way interaction between Visual field, Hemisphere and Electrode [$F(1.8,20.1)=7.54$; $\epsilon=.92$; $p<.005$]: Visual field and Hemisphere factors interacted significantly on P7/8 electrodes [$F(1,22)=9.34$; $p=.01$] and on CP5/6 [$F(1,22)=13.24$; $p=.005$] but not on P3/4 [$F(1,22)=3.66$; $p=.069$]. On P7/8 and CP5/6 electrodes, greater amplitudes were observed on the RH after a LVF stimulation and also on the LH after a RVF stimulation. When comparing amplitudes over the RH, after a LVF stimulation, and over the LH, after a RVF stimulation, for electrodes P7/8 and CP5/6 no significant difference appeared ($p>.17$).

N170 peak-latency

The main effect of Electrode tended to be significant [$F(1.6,34.5)=3.22$; $\epsilon=.78$; $p=.063$] showing that the N170 was earlier on P7/8 than on P3/4 ($p=.015$) but not on CP5/6 ($p=.24$). Visual field by Hemisphere interaction was significant [$F(1,22)=31.35$; $p<.00005$] reflecting an earlier N170 over the directly stimulated hemisphere than over the indirectly stimulated one. The significant Sex by Hemisphere interaction indicated an earlier N170 over the RH than over the LH in men and the reverse pattern in women [$F(1,22)=12.52$; $p<.005$]. All other main effects or interactions were not significant ($p>.14$).

Again, in order to check if one hemisphere responded faster than the other one after a direct stimulation (in the contralateral visual field), latency over the RH after a LVF stimulation and over the LH after a RVF stimulation were compared. No significant difference was found ($p=.92$).

N170-IHTTs

According to our main hypothesis, the Sex \times Transfer Direction interaction was statistically significant [$F(1,22)=12.52$; $p<.005$] highlighting that in men the transfer was faster from the L-to-R direction than from the R-to-L ($p=.02$). Interestingly, the reverse pattern was observed in women with faster transfer from the R-to-L than from the L-to-R direction ($p=.021$). As a consequence, transfer from the L-to-R was shorter in men than in women ($p=.003$) but there was no significant sex differences for the R-to-L transfer despite a trend ($p=.08$). All other main effects or interactions were not significant ($p>.33$). Figure 3 shows the N170-IHTTs according to the direction in men and in women.

“Insert Figure 3”

Discussion

The present study was designed to assess sex differences in IHTTs of face information by using the divided-visual field technique during identity encoding. In this task, participants saw briefly a probe face either in the LVF or in the RVF followed by a central target face. They had to decide if both faces belonged to the same person or not. This task ensured that participants focused their attention on the probe face and encoded identity while their EEG was recorded. Two early ERP components have been analyzed over three sites (P7/8, P3/4 and CP5/6): the P1 and the N170. It was hypothesized that men would present asymmetrical transfer with longer R-to-L than L-to-R and women a symmetrical one. According to the asymmetrical transfer, it was also expected that men would present a right-hemispheric dominance in amplitudes and latencies and women a more bilateral functioning. Whereas findings on the N170 amplitudes confirmed this last prediction, N170 latencies and IHTTs also confirmed the right hemisphere dominance in men but indicated a reversed asymmetrical transfer in women, suggesting a LH advantage. As discussed below, this may have several explanations, such as task difficulty, analytic processing, or verbal influences during perception. Nonetheless, by using a right-sided task, the present study generalized that asymmetry in IHTTs depends on hemispheric specialization, with longer transfer from the specialized to the non-specialized hemisphere, and further indicated that asymmetries in hemispheric dominance and transfers depend on the sex of the participants.

The P1 was the first ERP component observed during identity encoding of the probe face, peaking at around 120 ms after stimulus-onset over posterior electrodes, maximal at occipito-temporal sites (i.e., P7/8 electrodes). Results showed strong trends for greater amplitudes in the contralateral hemisphere to the visual field of presentation (i.e., the directly stimulated hemisphere; e.g., the RH with a LVF presentation) over parietal and occipito-temporal electrodes. Furthermore, the P1 was significantly earlier over this contralateral

hemisphere than over the ipsilateral one for all sites, but with an advantage for occipito-temporal and centro-parietal electrodes. This last finding allows validating our divided-visual field paradigm: the probe face information presented in one visual-field is first received by the contralateral hemisphere and then, is transferred to the other one. It also confirms previous ERPs studies in human which classically showed that when using the divided visual-field paradigm, contralateral responses following unilateral stimulation are consistently faster than the ipsilateral responses (e.g., Andreassi, Okamura & Stern, 1975). The P1-IHTTs derived from these differences in latencies were found to be shorter when calculated on electrodes P7/8 than on CP5/6. However, they did not reveal an asymmetrical transfer in general or depending on sex which is consistent with the findings of Proverbio et al. (2012). Altogether, results on the P1 characteristics suggest that no hemispheric specialization and/or sex-related differences occur 120 ms after stimulus-onset, at least during face identity encoding. This can be explained by the fact that the P1 is too early to be related to face processing. Indeed, according to Rossion and Caharel (2011), this component is sensitive to low-level visual cues and does not reflect high-level face perception (i.e., the activation of a face representation in the visual system) which is rather indexed by the N170 component, starting about 60 ms later.

The N170 peaked approximately 180 ms after stimulus-onset, especially over occipito-temporal electrodes, which is consistent with previous observations (for a review on the N170, see Rossion and Jacques, 2008). Like P1 latencies, N170 latencies confirmed earlier responses in the directly stimulated hemisphere with no hemisphere-related advantage. However for amplitudes, the interaction between Electrode and Hemisphere, albeit non-significant, showed a strong trend for a greater amplitude over the RH than over the LH on occipito-temporal and centro-parietal sites, suggesting a right-sided dominance for the face identity encoding task. Supporting this view, the significant hemisphere by visual field interaction indicated that the N170 was larger over the RH than over the LH after a LVF presentation but not after a RVF

stimulation for which the amplitudes were equivalent over both hemispheres. This finding confirmed that the face identity task used in the present study led to a right-hemispheric dominance at the early encoding stage of face processing indexed by the N170, which is in accordance with previous studies (e.g. Jacques and Rossion, 2009; Caharel, d'Arripe, Ramon, Jacques, Rossion, 2009).

Most interestingly, sex differences appeared at this early “face sensitive” stage. Indeed, while the N170 component was found to be larger and earlier over the RH in men, this wave was in similar magnitude in women over both hemispheres, and even earlier over the LH. This pattern of hemispheric asymmetry for face processing fits well with previous behavioral and electrophysiological studies highlighting a strong right-hemispherical dominance in men and a more bilateral functioning or a tendency toward a left asymmetry in women (Rizzolatti & Buchtel, 1977; Allen et al., 1991; Bourne, 2005; Fiori et al., 2001; Godard & Fiori, 2010, 2012; Proverbio et al., 2006, 2010, 2011, 2012). It also widely supports findings indicating a more asymmetric organization of the male brain for other kind of processing (McGlone, 1980; Voyer, 1996; Kansaku et al., 2000; Gur et al., 2000). Furthermore, the hemisphere by visual field interaction in amplitudes for each sex indicated that the N170 was larger over the RH in men only after LVF presentation while no difference were observed with RVF presentation. Conversely in women, the N170 was always larger over the directly stimulated hemisphere (i.e., larger in the RH ~~with~~ after LVF presentation and larger in the LH after RVF presentation). The comparison of amplitudes recorded over both hemispheres after *direct* stimulation highlighted a greater N170 over the RH only in men. These results further support the advantage of the RH during identity encoding in men, and a more divided work between the hemispheres in women.

Importantly and according to our main goal, the N170-IHTTs were found to be different in men and in women. The R-to-L transfer was found to be longer than the L-to-R transfer in men whereas the reverse pattern was observed in women. In men, considering the RH advantage

found in amplitudes and latencies, this result showed that transfer is longer from the *specialized* hemisphere to the *non-specialized* one which is consistent with the findings of Nowicka and Fersten (2001) and Moes et al. (2007) obtained with verbal material. In other words, it generalizes for different information and task that IHTTs depend on hemispheric lateralization, at least in men. Note that these asymmetries in transfers may more depend on task than information because longer L-to-R transfers with faces (i.e., same information) were recently observed by Proverbio and collaborators (2012), but during sex categorization (i.e., different task). Future studies must be designed to help clarify this outstanding issue.

In women, the longer L-to-R transfer suggests that the LH may be the *specialized* hemisphere to encode face identity. However, as discussed above, findings on amplitudes rather indicate a symmetrical functioning. Moreover, whereas the L-to-R transfer was found to be longer in women than in men, there were no significant sex differences in IHTTs for the R-to-L direction despite a trend. Overall, the results obtained in women at the level of the N170 therefore corroborate a divided work between the hemispheres (especially in amplitudes), besides a left-hemispherical tendency when considering latencies and their derived IHTTs. This slight LH advantage in time overlapped with a bilateral functioning in amplitudes may appear for several reasons. For example, task difficulty may have contributed to a greater engagement of the LH, in line with a better across-hemisphere performance related to task difficulty during face processing (e.g., Compton, 2002). Identity encoding might be facilitated by interhemispheric cooperation in women when presentation of faces in only one visual field with short durations leads to an increased difficulty. Otherwise, with respect to analytic processing of faces implemented in the LH, compared to the holistic processing subtended by the RH (Sergent, 1982; Hillger & Koenig, 1991), it might be that women use more local information than men when they must encode identity. Another explanation could be that women perform the task with an added semantic or verbal strategy requiring the LH during face processing (e.g.,

Rhodes 1985), as compared to a “pure” perceptual-based analysis at work in men. Further investigations should help disentangle the contribution of each interpretation to the results observed in the present study.

It should be pointed out that in our opinion the term “interhemispheric transmission time” could be misunderstood when investigating ERP components such as the P1 or the N170. Indeed, the first transfer of information from the directly stimulated hemisphere to the other one may arise earlier in the visual system, namely as soon as the primary visual cortices are recruited (i.e., approximately 40 ms after stimulus-onset; see Bullier, 2001) through the most posterior fibers in the corpus callosum (e.g., Hofer & Frahm, 2006). As a consequence, IHTTs measured during the P1 and the N170 time-ranges seem more related to further communication between the hemispheres, rather reflecting a subsequent level of synchrony between them than the first one-way transfer.

Before concluding, we would also like to note that asymmetrical IHTTs may be related to structural factors such as the size of the occipital cortex in each hemisphere (Saron & Davidson, 1989), or the asymmetrical numbers of callosal fibers in each direction (Marzi et al., 1991), but they may also be attributed to functional factors such as a visual field advantage for the task (Braun, 1992), or a mechanism allowing information being rapidly processed by the specialized hemisphere (Nowicka et al., 1996). Because our findings indicate that asymmetries in IHTTs only appear during the “face sensitive” stage indexed by the N170, they mainly support a functional interpretation of IHTTs. In details, sex-related differences in transfers, and more generally hemispheric specialization-related differences in other ERP characteristics, are not observed when the visual system processes low-level physical properties (i.e., at the level of the P1 component; Rossion & Caharel, 2011), but only when high-level perceptual processes are engaged to encode faces. Thus, asymmetrical transfers only appear when a functionally operant representation of the face is activated in the brain. Furthermore in men, they appear

because the RH is early activated when it is the first stimulated, indicated by the significant difference between the hemispheres for the direct stimulation conditions (RH/LVF *vs.* LH/RVF). Hence, the later activation of the non-specialized LH during RVF presentation fits well with a recent finding indicating that this hemisphere can process face identity when it is first stimulated, but only with the support of the RH (Verosky & Turk-Browne, 2012). In addition, the present study indicates that such a mechanism is only present in the male brain, with a more efficient LH and a more overlapping processing between the hemispheres in women, such as discussed above.

In sum, this study showed that during face identity encoding, no hemispheric asymmetries and/or sex-related differences in amplitudes and time transfers between the hemispheres appear at the level of the P1 component, probably due to its time-range which is too early to account for face processing. Conversely, at the level of the face-sensitive N170, hemispheric lateralization was found and depended on sex. Whereas similar N170 amplitudes were observed over both hemispheres in women with shorter latencies over the LH than over the RH, a larger and shorter N170 was recorded over the RH than over the LH in men. When considering the visual field where faces were presented, amplitudes were always enhanced over the directly stimulated hemisphere in women, while in men this was true only for the RH. According to our main goal, N170-IHTTs asymmetry depended on the sex of the participants with longer L-to-R transfer than the R-to-L in women and the reverse pattern in men. Finally, this study shed some light on the relation between hemispheric lateralization, transfer asymmetry and sex of the participants, highlighting that the more asymmetrical organization of the male brain, reflected in electrophysiological interhemispheric transfers and found in previous studies using verbal material, can be generalized to right-sided tasks. It also suggests a functional account of asymmetries in IHTTs, because they are only observed when high-level perceptual processes are engaged by the visual system.

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Figure Captions

Table 1. P1 latency and amplitude according to the Visual field of presentation (RVF, LVF), Hemisphere (LH, RH) and Electrode (P7/8, P3/4 and CP5/6) for women and for men.

Table 2. N170 latency and amplitude according to the Visual field of presentation (RVF, LVF), Hemisphere (LH, RH) and Electrode (P7/8, P3/4 and CP5/6) for women and for men.

Figure 1. Grand-average ERP waveforms recorded at P7/8, P3/4 and CP5/6 in response to LVF/RH (bold) and RVF/LH (thin) in women. P1 and N170 components are indicated by an arrow on P8.

Figure 2. Grand-average ERP waveforms recorded at P7/8, P3/4 and CP5/6 in response to LVF/RH (bold) and RVF/LH (thin) in men. P1 and N170 components are indicated by an arrow on P8.

Figure 3. N170-IHTTs from the LH to the RH (L-to-R; black) and from the RH to the LH (R-to-L; grey) for men and for women. Error bars represent standard-error of the mean. In men, R-to-L transfer was significantly longer than the L-to-R ($*p<.05$) whereas it was the reverse pattern in women ($*p<.05$). The L-to-R transfer is significantly longer in women than in men ($p<.001$). No significant sex difference was found for the R-to-L transfer ($p=.08$).

Table 1. P100 latency and amplitude according to the Visual field of presentation (RVF, LVF), Hemisphere (LH, RH) and Electrode (P7/8, P3/4 and CP5/6) for women and for men.

Sex	Visual field	Hemisphere	Electrode	P100 Latency (ms)		P100 Amplitude (μ V)	
				Mean	Standard-error	Mean	Standard-error
WOMEN	RVF	LH	P7	98,41	5,33	4,66	0,66
			P3	103,95	7,97	1,44	0,44
			CP5	98,08	7,97	1,89	0,24
		RH	P8	131,28	5,86	4,79	0,72
			P4	147,54	3,16	2,01	0,63
			CP6	152,10	3,99	1,65	0,44
	LVF	LH	P7	130,96	5,06	3,69	0,75
			P3	137,13	5,46	1,78	0,49
			CP5	138,76	6,16	1,61	0,31
		RH	P8	100,03	5,21	5,29	0,88
			P4	100,03	6,15	1,97	0,59
			CP6	100,03	5,33	2,14	0,34
MEN	RVF	LH	P7	113,53	5,95	4,66	0,66
			P3	105,35	6,21	1,44	0,44
			CP5	110,58	5,85	1,89	0,24
		RH	P8	138,88	6,15	4,79	0,72
			P4	143,44	7,01	2,01	0,63
			CP6	143,43	6,54	1,65	0,44
	LVF	LH	P7	141,19	6,79	3,69	0,75
			P3	140,54	6,23	1,78	0,49
			CP5	144,45	8,55	1,61	0,31
		RH	P8	114,55	5,32	5,29	0,88
			P4	120,13	9,19	1,97	0,59
			CP6	106,40	5,86	2,14	0,34

Table 2. N170 latency and amplitude according to the Visual field of presentation (RVF, LVF), Hemisphere (LH, RH) and Electrode (P7/8, P3/4 and CP5/6) for women and for men.

Sex	Visual field	Hemisphere	Electrode	N170 Latency (ms)		N170 Amplitude (μ V)	
				Mean	Standard-error	Mean	Standard-error
WOMEN	RVF	LH	P7	171,63	6,95	-6,48	1,64
			P3	168,38	6,82	-3,55	1,02
			CP5	165,44	7,39	-4,14	0,89
		RH	P8	189,86	6,62	-5,16	0,67
			P4	195,72	2,97	-2,98	0,57
			CP6	196,37	3,51	-2,17	0,47
	LVF	LH	P7	189,21	5,62	-4,34	1,20
			P3	185,96	6,10	-2,50	0,49
			CP5	188,23	5,63	-1,97	0,60
		RH	P8	182,05	7,24	-6,48	1,09
			P4	176,53	5,44	-3,84	0,49
			CP6	180,43	5,61	-3,77	0,53
MEN	RVF	LH	P7	190,59	8,61	-4,17	0,69
			P3	180,51	8,70	-2,47	0,40
			CP5	187,34	7,98	-2,18	0,35
		RH	P8	194,83	7,14	-5,66	1,17
			P4	183,12	7,93	-2,59	0,51
			CP6	190,60	7,22	-2,26	0,42
	LVF	LH	P7	199,38	5,67	-3,59	0,75
			P3	190,93	4,64	-1,82	0,41
			CP5	195,14	6,00	-1,48	0,39
		RH	P8	177,92	7,00	-6,26	0,84
			P4	172,39	5,45	-3,82	0,45
			CP6	172,38	6,65	-3,23	0,25

Figure 1. Grand-average ERP waveforms recorded at P7/8, P3/4 and CP5/6 in response to LVF/RH (bold) and RVF/LH (thin) in women. P1 and N170 components are indicated by an arrow on P8.

WOMEN

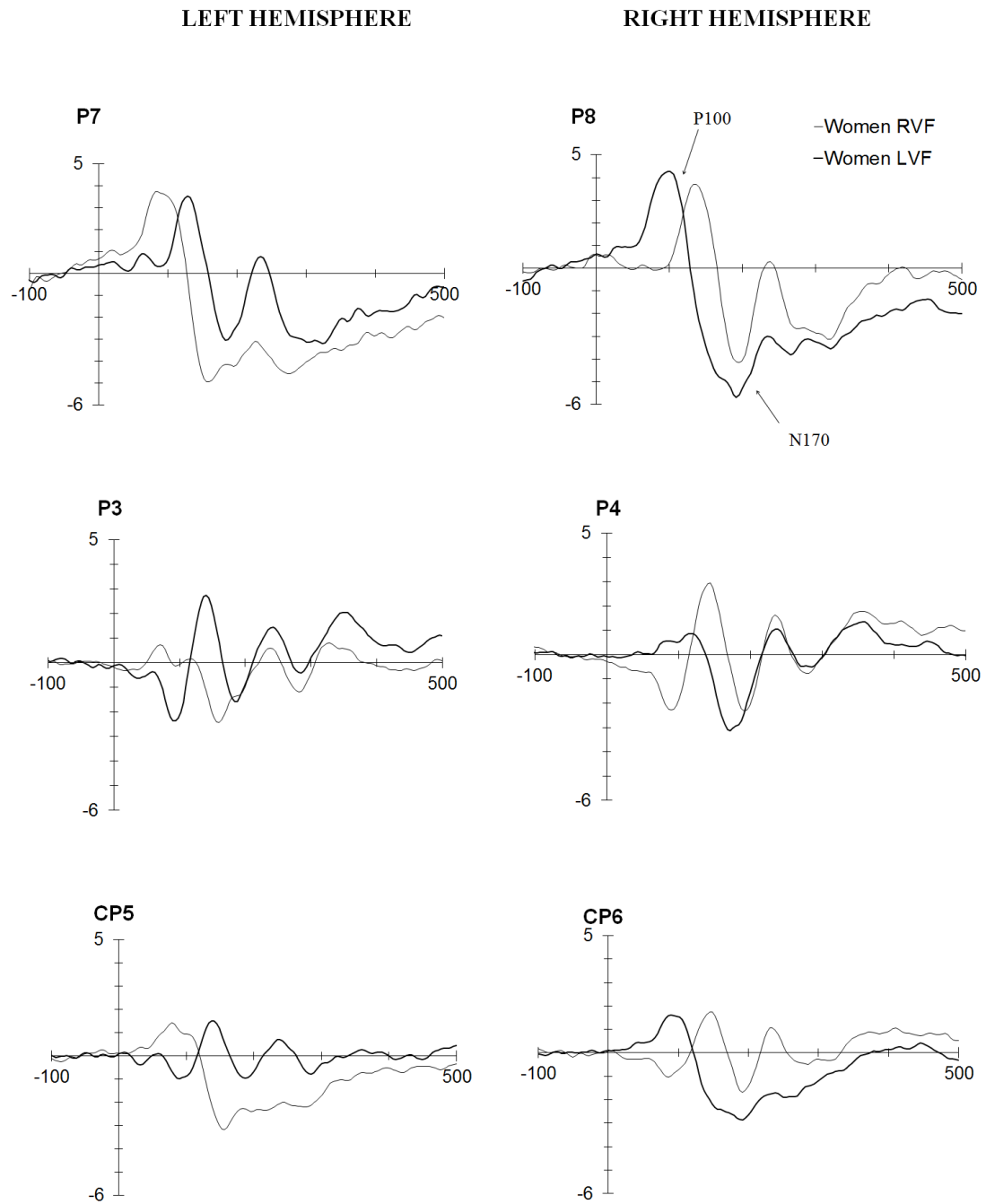


Figure 2. Grand-average ERP waveforms recorded at P7/8, P3/4 and CP5/6 in response to LVF/RH (bold) and RVF/LH (thin) in men. P1 and N170 components are indicated by an arrow on P8.

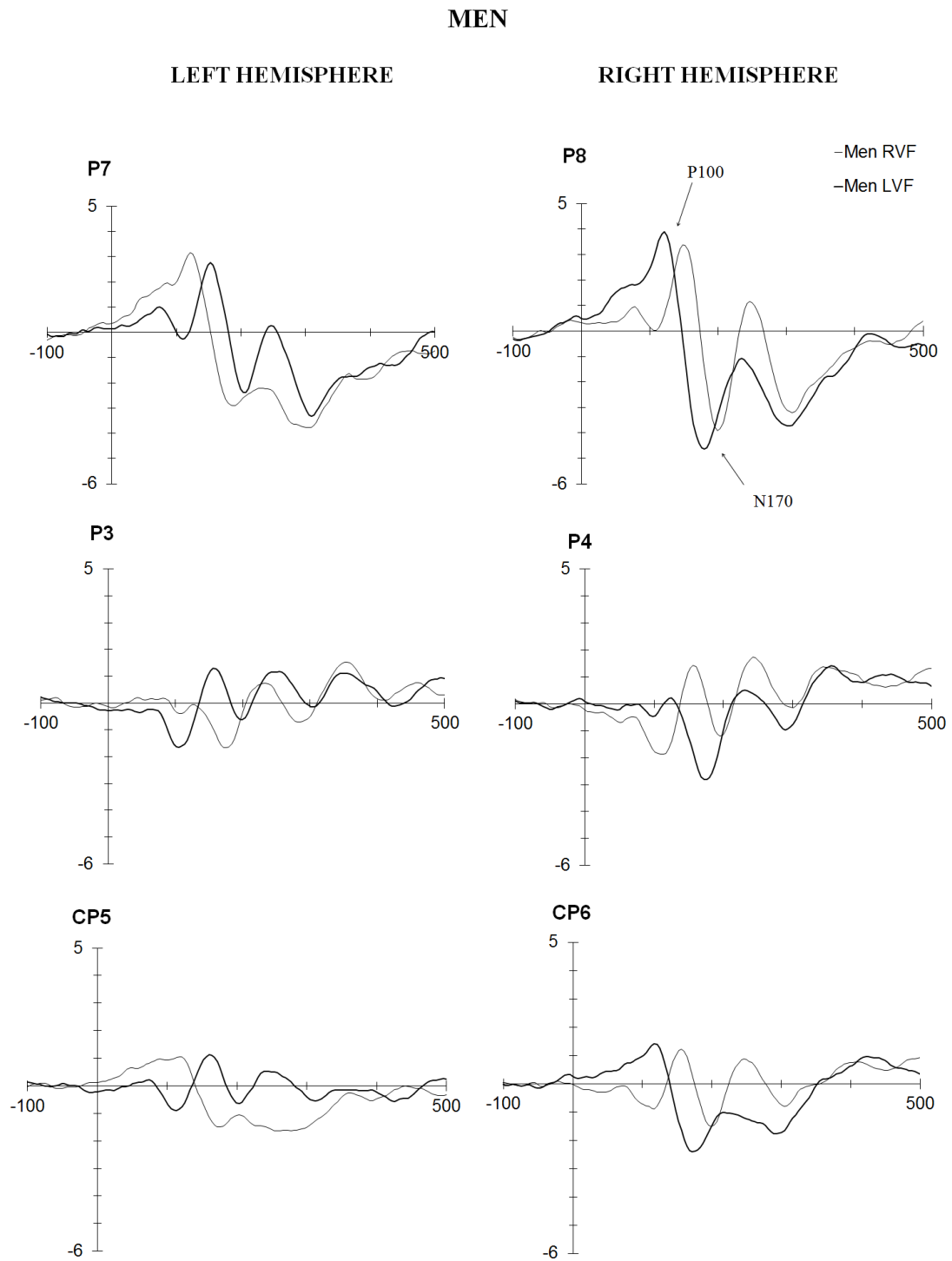


Figure 3. N170-IHTTs from the LH to the RH (L-to-R; black) and from the RH to the LH (R-to-L; grey) for men and for women. Error bars represent standard-error of the mean. In men, R-to-L transfer was significantly longer than the L-to-R ($*p<.05$) whereas it was the reverse pattern in women ($*p<.05$). The L-to-R transfer is significantly longer in women than in men ($p<.001$). No significant sex difference was found for the R-to-L transfer ($p=.08$).

