Cerebral Cortex October 2015;25:3468–3474
doi:10.1093/cercor/bhu175
Advance Access publication August 6, 2014

Sex Differences in the Neuromagnetic Cortical Response to Biological Motion

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Body motion is a rich source of information for social interaction, and visual biological motion processing may be considered as a hallmark of social cognition. It is unclear, however, whether the social brain is sex specific. Here we assess sex impact on the magnetoencephalographic (MEG) cortical response to point-light human locomotion. Sex differences in the cortical MEG response to biological motion occur mostly over the right brain hemisphere. At early latencies, females exhibit a greater activation than males over the right parietal, left temporal, and right temporal cortex, a core of the social brain. At later latencies, the boosts of activation are greater in males over the right frontal and occipital cortices. The findings deliver the first evidence for gender-dependent modes in the time course and topography of the neural circuitry underpinning visual processing of biological motion. The outcome represents a framework for studying sex differences in the social brain in psychiatric and neurodevelopmental disorders.

Keywords: biological motion, dynamic topography, gender, MEG, neural circuitry, point-light displays, sex differences, social brain, time course

Introduction

Visual sensitivity to human body motion may serve as a hallmark of daily-life social cognition, and a basis for nonverbal communication and social competence (Pavlova 2012). In experimental research, body motion is often represented by a point-light technique as a set of dots on the joints of an otherwise invisible body. This helps to isolate information revealed by body motion from other cues. Visual sensitivity to point-light body motion emerges early in life: already 2–3-day-old human newborns are tuned to displays depicting point-light walkers (Bidet-Ildei et al. 2014) and other vertebrates (Simion et al. 2008). A wealth of brain imaging and neuropsychological work in typically developing adults and children, lesional patients, and individuals with neurodevelopmental disorders suggest that visual processing of point-light biological motion involves the parieto-temporal junction and fusiform gyrus, portions of the parietal and frontal cortices, primarily in the right hemisphere, and subcortical structures such as the cerebellum and amygdala (e.g., Grossman et al. 2000; Vaina et al. 2001; Pavlova, Marconato, Sokolov, Braun, Birbaumer, Krägeloh-Mann 2006; Pavlova et al. 2007; Saygin 2007; Sokolov et al. 2010, 2012, 2014; Krakowski et al. 2011; Buzzell et al. 2013; Han et al. 2013; Kröger et al. 2013; White et al. 2014; for review, see Puce and Perrett 2003; Pavlova 2012). Recent voxel-based morphometry analysis indicates that gray matter volumes of the left posterior superior temporal sulcus (pSTS) and ventral premotor cortex (PMC) may be considered as predictors of individual differences in detection of camouflaged point-light biological motion (Gilaie-Dotan et al. 2013). Transcranial magnetic stimulation over the pSTS and PMC affects visual sensitivity to biological motion (Grossman et al. 2005; van Kamenade et al. 2012). It appears that processing of biological motion engages a specialized neural network with a hub in the right temporal cortex (e.g., Grossman and Blake 2002; Beauchamp et al. 2003; Gobbini et al. 2007; Pavlova et al. 2004; Kaiser et al. 2010; Herrington et al. 2011), where this network topographically overlaps and likely communicates with the social brain, namely, with the neural circuits underlying our ability for perception and understanding of emotions, intentions, drives, desires, dispositions of others, and body language reading.

It is unclear, however, whether the social brain is sex-specific, although growing evidence points to sexual dimorphism of the brain (e.g., Cahill 2006). There is a paucity of research examining sex differences at a neurobiological level. Yet behavioral data are also controversial. According to popular beliefs about female superiority on visual social cognition tasks there are some indications for gender influence on visual biological motion processing in common marmosets (*Callithrix jacchus*): females but not males exhibit curiosity to point-light biological motion (Brown et al. 2010). Newly hatched female chicks demonstrate a stronger preference for point-light biological motion of a walking hen (even over a walking cat) than their male peers (Miura and Matsushima 2012). Yet, alterations in point-light biological motion processing with age appears to be unaffected by observers' gender (Billino et al. 2009). Gender congruency between perceivers and actors enhances visual priming of camouflaged point-light human locomotion (Bidet-Ildei et al. 2010). Female and male observers respond differently when judging whether a point-light walker shown in a frontal view is facing toward (approaching) or backward (retreating): for females, the facing bias for male walkers is weaker (Schouten et al. 2010, 2013).

Gender of observers affects body language reading in point-light biological motion movies depicting knocking at a door, but effects are modulated by emotional content of actions: males surpass in recognition accuracy of happy actions, whereas females tend to excel in recognition of angry knocking (Sokolov et al. 2011). A similar pattern of results was found for subtle emotions expressed by point-light human locomotion: males surpass females in recognition accuracy and readiness to respond to subtle happy walking portrayed by female actors, whereas females tend to be better in recognition of angry locomotion expressed by male actors (Krüger et al. 2013). Females are more accurate in recognition of point-light

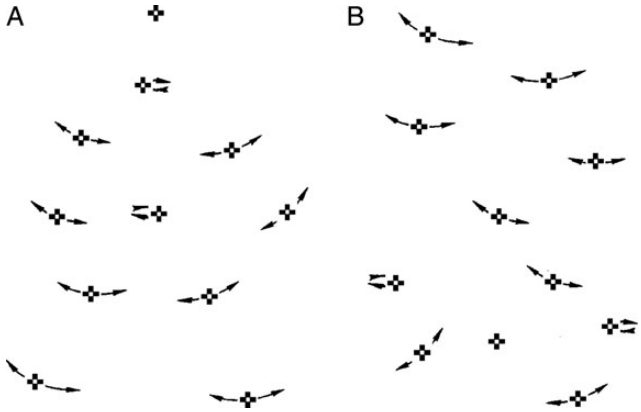

Figure 1. Static sample stimuli. Participants were presented with a randomized set of either (*A*) a canonical point-light human figure walking as if on a treadmill, or (*B*) its spatially scrambled version. Vectors illustrate motion of each dot. The displays are shown in reverse contrast: they were seen as a set of bright dots against a dark background. From Pavlova et al. (2004), copyright © 2004 Oxford University Press.

activities (such as walking, jumping on the spot, kicking a ball, and drinking from a bottle), and excel in some aspects of body language reading: they are faster in discrimination of emotional from neutral body motion (Alaerts et al. 2011). Most important, in agreement with the assumption that biological motion processing and social cognition are intimately linked (Pavlova 2012), in typically developing adults and individuals with autistic disorders, the ability to reveal emotions from point-light body motion is related to more basic capability for discrimination between canonical and scrambled biological motion (Alaerts et al. 2011; Nackaerts et al. 2012). In healthy adults, some aspects of social cognition (such as empathy) and performance on Reading the Mind in the Eyes Test are related to point-light biological motion processing (Miller and Saygin 2013).

In adult females, increased functional magnetic resonance imaging (fMRI) activation is found during passive viewing of point-light biological motion displays (waving, pat-a-cake, and peek-a-boo) compared with scrambled versions over the regions known to be involved in social cognition, in particular, the temporal pole, medial temporal gyrus, cerebellum, and amygdala (Anderson et al. 2013). Yet sex differences in brain activation are less pronounced in children and adolescents aged 4–16 years (Anderson et al. 2013).

The motivation of the present work was to uncover sex-specific alterations in the time course and dynamic topography of the entire cortical network underpinning visual processing of biological motion. To this end, we focused on analyses of the whole-head magnetoencephalographic (MEG) response to biological motion during performance of a one-back repetition task with canonical and spatially scrambled point-light displays (Fig. 1).

Materials and Methods

Participants

Fourteen paid right-handed young adults (7 females and 7 males) with normal or corrected-to-normal vision were enrolled in the study. Age of females was 25 ± 2.75 years (median ± 95% confidence interval) and age of males was 25 ± 2.43 years. No age-related differences were found between females and males (Mann–Whitney test; $U = 18$, n.s.). None had a history of neurological or psychiatric disorders, head injuries, or medication at a period of examination. They were naïve as to the purpose of the study. Informed written consent was obtained in accordance with the requirements of the local Ethical Committee at the University of Tübingen Medical School. Analysis of MEG oscillatory response to biological motion in these participants was reported earlier (Pavlova et al. 2004). Here, we examined sex-related differences in cortical activation to biological motion displays by uncovering alterations in the evoked root mean square (RMS) activity.

Stimuli, Task, and Experimental Design

The point-light stimuli and task are described in detail elsewhere (e.g., Pavlova et al. 2004). In brief, participants were presented with 2 types of displays: a canonical point-light walker consisting of 11 dots on the head and main joints of an invisible figure and a spatially scrambled configuration, for which the spatial positions of dots were randomly rearranged on the screen (Fig. 1) so that the display lacked an implicit coherent structure. All other display characteristics remained the same. The walking figure, facing right, was seen moving as if on a treadmill. A gait cycle was completed in 40 frames with frame duration of 31 ms that produced a walking speed of ~48 cycles per minute. The configurations were generated by Cutting's algorithm (Cutting 1978), and subtended a visual angle of 9° in height and 6° in width. Participants were presented with a randomized set of 200 stimuli of both types. The stimuli appeared for 650 ms on a blank screen with an inter-stimulus interval that varied randomly between 2.5 and 3.0 s. Participants fixated a gray cross in the middle of the screen that was seen during the whole run. They performed a one-back repetition task lifting a forefinger placed in a nonmagnetic light-beam response box following the offset of the second of 2 consecutive identical stimuli of each type. One-back repetition task obligates attention to all types of stimuli and, therefore, reduces possible attention effects on recorded MEG traces.

MEG Recording and Analysis

For recording cortical activity, the whole-head MEG system (CTF Systems, Inc.; Vancouver, Canada) was used. This system consisted of 151 hardware first-order magnetic gradiometers distributed with an average distance of 3 cm between sensors. A participant was seated in an electromagnetically shielded chamber (Vakuum-Schmelze, Hanau, Germany). The signals were sampled at a rate of 312.5 Hz. A baseline was recorded during 300 ms prestimulus. Participants were instructed to blink only during inter-trial intervals. Vertical eye movements were monitored by electroencephalography/electrooculography recording from the left eye (impedance was kept below 5 kΩm). Both at the beginning and at the end of each recording session, the participant's head position was determined with 3 localization coils fixed at the nasion and the periauricular sites. Sessions with head movements exceeding 0.5 cm were discarded. Each MEG recording session (during presentation of a set of 200 stimuli in a run) lasted 10–12 min. All epochs of MEG activity were first automatically and then manually inspected for artifacts. Epochs containing blinks or eye movements (greater than ±100 μV) were rejected. The only trials analyzed were those for which a motor response was not required. If a participant failed to respond to the second identical stimulus, all trials were discarded beginning from the last correct response. Per participant, a total of ~70 correct artifact-free trials were processed for each type of stimulus. For each participant, we computed difference in RMS amplitude in response to the canonical against control scrambled configuration. RMS analysis was performed in equivalent temporal windows of 50 ms from 0 to 500 ms separately for all sensors over the occipital, parietal, temporal, and frontal areas of each brain hemisphere. The sensors over the different cortical areas were defined in accord with the standard MEG sensor layout.

Results

Behavioral Data

Participants (both females and males) performed the task with great accuracy reaching ceiling level of performance (Pavlova et al. 2004). There were just a few errors. For each participant,

the miss rate was calculated as a ratio of the number of failures to respond to the second identical stimulus of each type to the total number of the required responses. For analysis of false alarm rate, the number of false alarms for each type of stimulus was divided by the total number of trials in which this type of error might occur. Analysis of gender impact on behavioral response indicates that in females the miss rate to the canonical point-light walker was 0.028 ± 0.041 (mean ± standard deviation) and to the scrambled display it was 0.016 ± 0.022. In males, the miss rate to the canonical walker was 0.008 ± 0.014, and to the scrambled walker it was 0.005 ± 0.013. No gender differences in the miss rate were found either in response to the canonical or to the scrambled walker (Mann–Whitney test; $U = 19$ and $U = 17$, n.s., respectively). Whereas in females, the false alarm rate to the canonical point-light walker was very low 0.004 ± 0.007, male participants did not make any false alarms. In response to the scrambled display, false alarm rate in females was 0.004 ± 0.011, and in males it was 0.009 ± 0.017. No difference between females and males in false alarm rate in response either to the canonical or scrambled walker was found ($U = 17.5$ and $U = 28$, n.s., respectively).

Following each run, participants briefly indicated any stimulus interpretations they might have had. All female and male participants spontaneously reported seeing the canonical walker, and their impression was vivid resulting in high ratings of the display's vividness on a 5-point unipolar scale. No gender differences in the ratings were found ($U = 25.5$, n.s.; mean, 4.29 ± 0.49 and 4.29 ± 0.76, for females and males, respectively). For the scrambled walker, the ratings were low in the absence of any gender differences ($U = 26$, n.s.; 1.43 ± 0.54 and 1.71 ± 1.11, for females and males, respectively).

Sex Differences in MEG Activity

Individual data were submitted to a 4-way ($2 \times 10 \times 4 \times 2$) repeated-measures analysis of variance, ANOVA, with a between-subject factor Gender of observers (female and male) and within-subject factors Time window, Cortical region

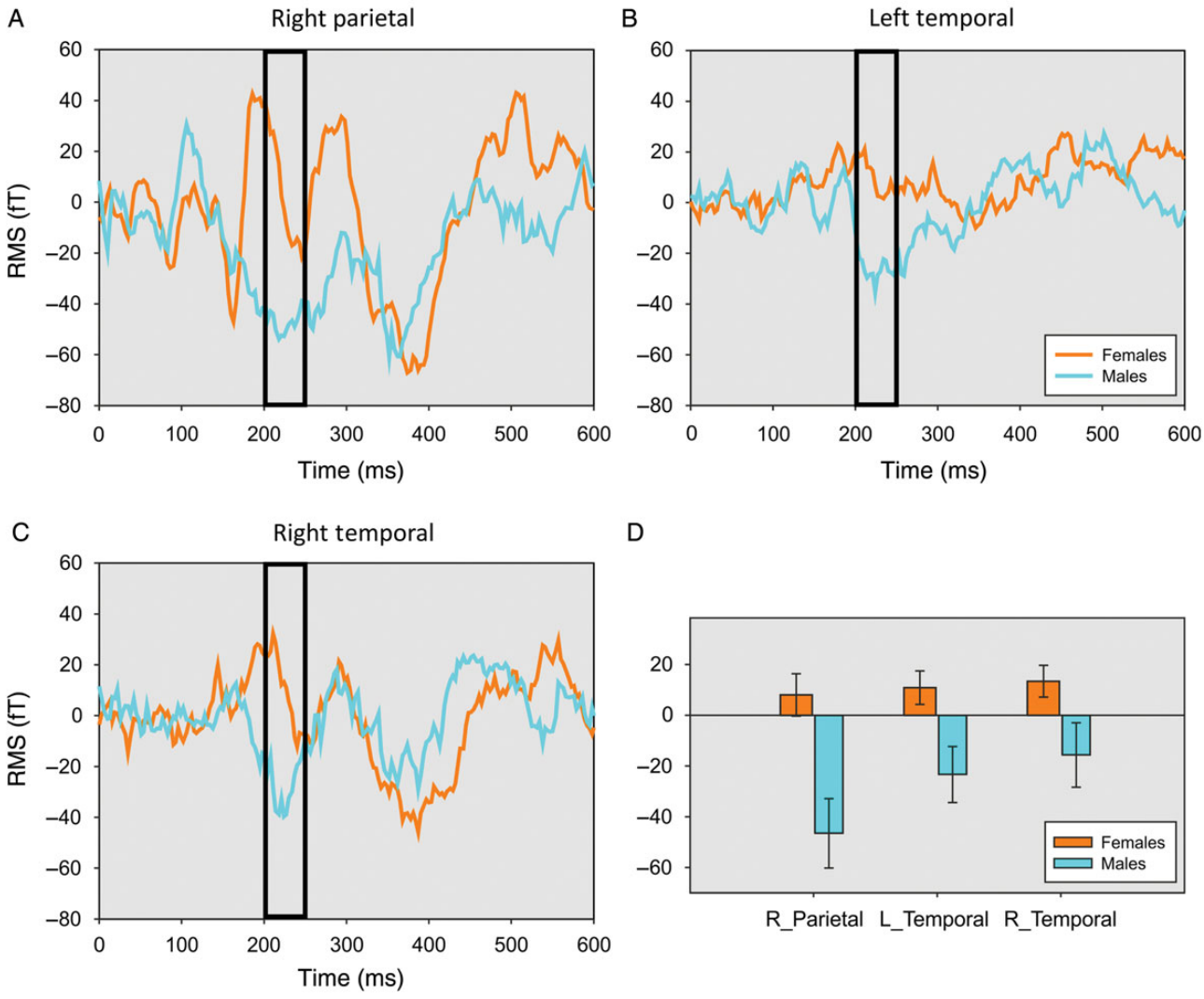

Figure 2. Sex effects in early MEG response to biological motion. The RMS neuromagnetic response to a point-light canonical walker as compared with a scrambled display over (*A*) the right parietal, (*B*) left temporal, and (*C*) right temporal cortices. At a latency of 200–250 ms from the stimulus onset, the RMS response is significantly greater in females. (*D*) The cortical RMS responses are plotted separately for females and males. R_Parietal, L_Temporal, and R_Temporal stand for the right parietal, left temporal, and right temporal cortex, respectively. Vertical bars represent ±SEM.

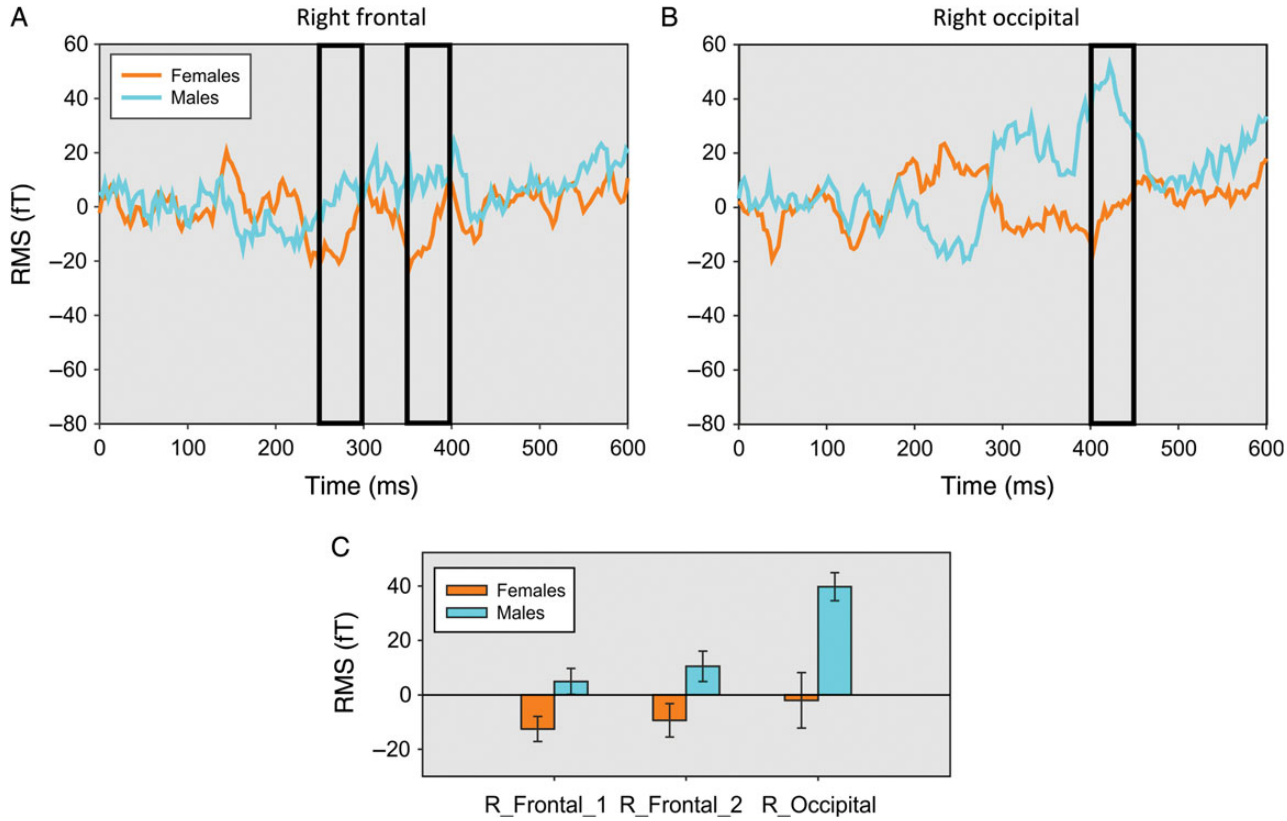

Figure 3. Sex effects in later MEG response to biological motion. The RMS neuromagnetic response to a point-light canonical walker as compared with a scrambled display. In males, the RMS response is significantly greater (*A*) over the right frontal lobe at latencies of 250–300 ms and 350–400 ms, and (*B*) over the right occipital cortex at a latency of 400–450 ms from the stimulus onset. (*C*) The cortical RMS responses are plotted separately for females and males. R_Frontal_1, R_Frontal_2, and R_Occipital stand for the first and second time window over the right frontal, and for the right occipital cortex, respectively. Vertical bars represent ±SEM.

(occipital, parietal, temporal, and frontal), and Hemisphere (right and left). The outcome reveals a main effect of Cortical region ($F_{3,36} = 3.4$, $P < 0.029$), Cortical region by Time window interaction ($F_{27,324} = 1.84$, $P < 0.008$), and Time window by Gender of observers interaction ($F_{9,108} = 2.67$, $P < 0.008$). Post hoc analysis of gender-related simple effects shows that irrespective of a cortical region and hemisphere, females exhibit greater RMS amplitude in the early time window of 200–250 ms ($P < 0.004$), whereas males tend to exhibit a greater response at later latencies ($P < 0.07$). At early latencies (200–250 ms, Fig. 2), the RMS response is greater in females as compared with males over the right parietal cortex (mean ± standard error, 8.02 ± 8.3 fT [femtotesla] in females and −46.5 ± 13.698 fT in males; $t_{(12)} = 3.4$, $P < 0.005$), left temporal cortex (10.87 ± 6.58 fT in females and −23.36 ± 11.04 fT in males, $t_{(12)} = 2.66$, $P < 0.02$), and over the right temporal cortex (13.4 ± 6.23 fT in females and −15.64 ± 12.69 fT in males; $t_{(12)} = 2.44$, $P < 0.03$). At later latencies (Fig. 3), the RMS response is greater in males as compared with females over the right frontal lobe at a latency of 250–300 ms (4.89 ± 4.77 fT in males and −12.6 ± 4.6 fT in females; $t_{(12)} = 2.64$, $P < 0.02$), and at a latency of 350–400 ms (10.46 ± 5.56 fT in males and −9.36 ± 6.11 fT in females, $t_{(12)} = 2.4$, $P < 0.03$). Over the right occipital cortex, males exhibit the greater RMS response at a latency of 400–450 ms (39.74 ± 5.13 fT in males and −1.99 ± 10.2 fT in females; $t_{(12)} = 3.65$, $P < 0.003$). Overall, sex differences occur primarily over the right brain hemisphere.

Discussion

The present work was aimed at uncovering sex-specific alterations in the time course and dynamic topography of the entire cortical network underpinning visual processing of biological motion. For this purpose, we analyzed the whole-head MEG response to biological motion during performance of a one-back repetition task with unmasked canonical and spatially scrambled point-light displays. The outcome indicates that in the absence of behavioral differences, gender of observers affects the cortical evoked neuromagnetic RMS activation in response to human locomotion: (1) Sex differences in the cortical MEG response to biological motion occur mostly over the right brain hemisphere; (2) In females, early cortical response to biological motion is greater over the right parietal, left temporal and right temporal cortex; and (3) In males, later cortical response is greater over the right frontal and occipital cortices.

In the present study, sex differences in the cortical neuromagnetic response to biological motion were found over the regions that are known to be profoundly engaged in visual processing of social signals, in particular, in the right brain hemisphere (e.g., Grossman et al. 2004, 2005; Gobbini et al. 2007; Pavlova et al. 2010; Kaiser et al. 2010; Herrington et al. 2011; Han et al. 2013). Already in 8-month-old infants, the averaged negative amplitude of the event-related potentials (ERPs) in the right hemisphere is greater in response to canonical than to scrambled point-light biological motion (Hirai and Hiraki 2005). While viewing upright as compared with inverted point-

light biological motion displays of the whole body, infants of this age exhibit larger positive ERP amplitude over the right parietal cortex at a latency of 200–300 ms (Reid et al. 2006). In healthy adults, electroencephalographic findings on biological motion processing identify early and late ERP components with peaks varying in different studies from 120 to 300 ms for the first and from 190 to 500 ms for the second component (Hirai et al. 2003, 2005; Hirai and Hiraki 2005; Krakowski et al. 2011; Jokisch et al. 2005; White et al. 2014). It appears that, in particular, early stages in visual processing of biological motion are associated with the right hemisphere (Hirai et al. 2003; Krakowski et al. 2011; Kröger et al. 2013). Some studies also report a late (beyond 300 ms) medial posterior positivity/ventral lateral negativity (MPP/VAN) ERP component (Hirai and Hiraki 2005; Krakowski et al. 2011; White et al. 2014), which likely reflects involvement of higher-order top-down and task-relevant cognitive processes.

Our MEG findings show that earlier stages in visual processing of biological motion are associated with greater cortical activation in females. Keeping in mind that from the evolutionary and socio-cultural points of view, female roles are often associated with offspring care providing and detecting a potential danger, it appears that the female brain may be more visually tuned to human locomotion. In accordance with this, recent behavioral data suggest that in contrast to men, body motion stimuli automatically capture women's attention even if these displays are irrelevant for the task and serve as distractors (Bidet-Ildei and Bouquet 2014). In males, late boosts of cortical activation over the right frontal and occipital cortices may point to a stronger higher-order cognitive involvement in biological motion processing. The greater activation over the right frontal cortex likely reflects engagement of decision processes, whereas late boosts over the right occipital cortex may be driven by feedback from the cortical regions involved in higher-order cognitive processing. However, this assumption requires further experimental proof.

Most remarkable outcome of this work is that females exhibit greater activity over the right temporal cortex, a hub of the social brain, where the network specialized for biological motion processing topographically overlaps and communicates with the neural circuitry underpinning visual social cognition (perception and understanding of social properties of others such as intentions, emotions, and expectations). Brain activation during visual processing of point-light biological motion overlaps topographically, especially, in the right temporal cortex, with the network engaged in visual perception of agency and social attribution in Heider-and-Simmel-like movies representing motion of geometric shapes (e.g., Gobbini et al. 2007; Pavlova et al. 2010). Yet sex differences are not evident in the neural circuitry underpinning visual processing of social interaction in Heider-and-Simmel-like animations. Instead, sex differences are observed only in the regions engaged in perceptual decision making: in males, the MEG oscillatory induced gamma response boosts later over the left prefrontal cortex (Pavlova et al. 2010). It appears that females anticipate social interaction predicting others' actions ahead of their occurrence, whereas males require accumulation of more sensory evidence for proper decisions.

More generally, gender-related brain differences do not always parallel behavior. Instead, several types of interrelations between behavior and brain mechanisms in respect to sex differences potentially occur: (1) gender-related differences both in overt behavioral and brain responses to visual social stimuli; (2) gender-related differences detectable either at the behavioral level or (3) solely in brain activation; and (4) a lack of gender-related differences both at the overt behavioral level and brain activation. The present findings deliver the first evidence for gender-dependent modes in the time course and topography of the neural circuitry underpinning visual processing of biological motion. In light of the absence of differences in behavioral responses, it is conceivable that gender-related dimorphism in the cortical response may prevent behavioral differences if they are maladaptive, and in such a way promote adaptive behavioral response.

Further investigation of sex differences in visual processing of biological motion and body language reading would encourage clarification of the nature of neurodevelopmental and psychiatric disorders characterized by impairments in social cognition. Many of these disorders are gender specific: females and males are differently affected in terms of clinical picture, prevalence, and severity. Females are more often affected by anxiety disorders with a ratio of 2:1 or even 3:1, and gender differences increase with age (Craske 2003; Beesdo-Baum and Knappe 2012). Depression is approximately twice as common in females as in males (Diflorio and Jones 2010). By contrast, males have a higher risk for developing autistic spectrum disorders than females, with a sex ratio of ~4:1 (Newschaffer et al. 2007) or even higher, but females are more severily affected. Neuroanatomy of autism differs between females and males (Lai et al. 2013). Schizophrenia occurs 1.4 times more frequently in males than females, and the onset of disease is earlier in men (Picchioni and Murray 2007). Males are at a 14–20% higher risk for premature birth and of its complications in the brain development and cognition (Pavlova and Krägeloh-Mann 2013). Males are more often affected by attention deficit hyperactivity disorder, ADHD (Bloom et al. 2012). Some aspects of biological motion processing are reported to be impaired in these and other gender-specific diseases: in schizophrenia (Kim et al. 2005, 2011, 2013; Hastings et al. 2013; Spencer et al. 2013), in autism (e.g., Klin et al. 2009; Kröger et al. 2013; Nackaerts et al. 2012), in obsessive compulsive disorders (OCD; Kim et al. 2008), in ADHD (Kröger et al. 2014), and in individuals who were born preterm (e.g., Pavlova, Marconato, Sokolov, Braun, Birbaumer, Krägeloh-Mann 2006; Pavlova, Sokolov, Birbaumer, Krägeloh-Mann 2006; Taylor et al. 2009; see Pavlova 2012). Yet gender impact on impairments in biological motion processing and body language reading is poorly understood. Clarification of sex impact on neural circuits underpinning biological motion processing would provide novel insights into understanding of gender vulnerability to psychiatric and neurodevelopmental deficits in social cognition (Pavlova 2012).

Conclusions

By analysis of cortical neuromagnetic activity, the present work delivers the first evidence for gender dependent modes in time course and topography of the neural circuitry underpinning visual processing of biological motion. The findings show that in the absence of behavioral differences, gender of observers affects the cortical evoked RMS response to human locomotion: (a) sex differences in the cortical MEG response to biological motion occur mostly over the right brain hemisphere; and (b) females exhibit greater early cortical response

over the right parietal and bilateral temporal cortex, whereas males exhibit greater later cortical response to biological motion over the right frontal and occipital cortex. Gender-related differences in the time course and topography of cortical neuromagnetic response found in this study may prevent behavioral differences if they are maladaptive. The outcome represents a framework for studying sex differences in the social brain in psychiatric and neurodevelopmental disorders.

Funding

This work was supported by the Else Kröner Fresenius Foundation (grant 2013_A127), the Reinhold Beitlich Foundation, and the Heidehof Foundation (grant 59073.01.1/3.13) to M.A.P. C.B.-I. was supported by the grant of the National Center for Scientific Research (CNRS), France.

Notes

We greatly appreciate Krunoslav Stingl and Christoph Braun at the MEG-Center of the University of Tübingen Medical School for assistance with MEG data analysis, and Jürgen Dax and Gabriele Walker-Dietrich for technical assistance with MEG recording. *Conflict of Interest*: None declared.

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