

Aus der Abteilung Psychiatrie und Psychotherapie
Ärztlicher Direktor Prof. Dr. med. Andreas J. Fallgatter

**Emotion revealed through body motion:
gender impact**

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Krüger, Samuel Herbert

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Dekan: Professor Dr. rer. nat. Bernd Pichler

Betreuerin: Professor Dr. Marina Pavlova, PhD

1. Berichterstatter: Professor Dr. med. Annette Conzelmann
2. Berichterstatter: Professor Dr. rer. nat. Christoph Braun

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Meinem Bruder Jonathan

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List of abbreviations

ADHD	Attention Deficit Hyperactivity Disorder
ASD	Autism Spectrum Disorders
BM	Biological Motion
BOLD	Blood Oxygen Level Dependent
EBA	Extrastriate Body Area
EEG	Electroencephalography
FBA	Fusiform Body Area
FFA	Fusiform Face Area
FFG	Fusiform Face Gyrus
fMRI	functional Magnetic Resonance Imaging
fNIRS	functional Near Infrared Spectroscopy
IFG	Inferior Frontal Gyrus
IPC	Interpersonal predictive coding
MEG	Magnetoencephalography
MTC	Medial Temporal Cortex
O ₂ HB	Oxygenated Haemoglobin
OT	Oxytocin
pSTS	posterior Superior Temporal Sulcus
STS	Superior Temporal Sulcus
T	Tesla
TD	Typically Developing
tDCS	transcranial Direct Current Stimulation

1. BODY MOTION PROCESSING AND BODY LANGUAGE READING

1.1 GENERAL INTRODUCTION: WHAT IS BODY LANGUAGE READING AND WHY IT IS OF IMPORTANCE FOR OUR DAILY LIFE

Our daily life incorporates multiple interactions with other people. Most of these people are strangers: we see them just once sometimes even without being aware of it. Nevertheless we are capable to understand their body language in order to uncover possible threat or other emotions, their intentions and dispositions to be coped with. Accurate recognition and interpretation of other's emotions, mental state or even direction and speed of their motion is crucial for living in a social world.

In research on body language reading, it is important to eliminate other possible sources of information like outfit, age cues, and body shape. For proper studying body language reading, the point-light displays were created that had been first introduced by Swedish scholar Gunnar Johansson ([Johansson, 1973](#)). These displays represent a valuable tool for body motion studies: By presenting videos consisting only of dots placed on the main joints and head of an otherwise invisible human body, we provide observers with information revealed by body motion solely.

Human observers readily extract information from point-light videos. They identify not only a portrayed action and direction of movement, but also infer more subtle characteristics like gender of a point-light walker, emotional state, goal of displayed actions, or whether expressed intentions are true or false ones (e.g., [Runeson and Frykholm, 1983](#); [Pollick et al., 2001](#); [Elsner et al., 2012](#); for review, see [Pavlova, 2012](#)).

Point-light displays portraying human body motion can be modified in certain ways, for example by adding simultaneous noise ([Ikeda et al., 2005](#)) or placing the dots not on the ankles but in between. These modifications, however, do not make these displays unrecognizable for a human observer ([Bertenthal and Pinto, 1994](#)). What makes it harder for an observer to identify human body motion is to present a point-light walker upside down ([Sumi, 1984](#)). Even a priori information

about display inversion doesn't substantially affect the recognition (Pavlova and Sokolov, 2003).



Figure 1. Illustration of point-light biological motion. Left panel: A point-light walker represented only by a number of dots placed on the head and main body joints of the otherwise invisible figure on the Neckar Bridge in the medieval downtown of Tübingen. Right panel: A point-light walker facing right with canonical upright orientation (bottom), and rotated 180° in the image plane with display inversion (top). [The photo of Tübingen and image by Marina A. Pavlova. From Pavlova et al. (2017). “Wrong Way Up”: Temporal and Spatial Dynamics of the Networks for Body Motion Processing at 9.4 T. *Cerebral Cortex* 27: 5318–5330, doi:10.1093/cercor/bhx151. Copyright by the authors; reproduced with permission.]

In typically developing (TD) individuals, a conceivable link between basic ability to perceive biological motion (BM) and social abilities is confirmed by visual psychophysics: emotion recognition through BM is related to the visual sensitivity to body motion (Ikeda and Watanabe, 2009). Moreover, emotional valence of point-light body motion displays (such as happiness) can facilitate detection of BM within simultaneous masking elements (Lee and Kim, 2017). The capacity for extracting information from body motion appears to be intrinsically tied with social

cognitive abilities such as understanding of drives and emotions of others (Pavlova, 2012). For instance, inferring affect from point-light body motion and performance on the Reading Mind in the Eyes Test (RMET) are strongly tangled in adult females (Isernia et al., 2020).

Although mimic expressions are the most accessible part of a human being for reading emotional state, body-cues contribute importantly to conveying the emotional state of others. Body language is reported to be much more reliable due to higher awareness of a person to its facial expression and better control of it. Moreover, if observers are presented with conflict information from face and body motion, they rely upon bodily expressed emotion (Meeren et al., 2005).

TD individuals are proficient in inferring emotions and intentions of others represented by BM in point-light displays (e.g., Dittrich et al., 1996; Atkinson et al., 2004; Heberlein et al., 2004; Clarke et al., 2005; Manera et al., 2010; Alaerts et al., 2011; Actis-Grosso et al., 2015; Vaskinn et al., 2016). Perceivers can judge emotional content of dance represented by a few moving dots located on a dancer's body, with anger as the most reliably identified emotion (Dittrich et al., 1996). Revealing emotions from BM is fairly robust across cultures (Parkinson et al., 2017). Even economic decisions are influenced by other people through their whole bodily expressed states (Oullier and Basso, 2010).

Own experience of observers in action production promotes understanding of body language. The “mirror system” in the brain integrates the motion content with the motor repertoire resulting into a greater bilateral activation of premotor cortex, intraparietal sulcus, right superior parietal lobe and left posterior superior temporal sulcus visible in fMRI when observing familiar movements (Calvo-Merino et al., 2005). For that reason, it appears rational to use widely known movements for experimental settings for body language reading.

1.2 DEVELOPMENT OF BODY LANGUAGE READING

1.2.1 In children. The ability to detect BM and social characteristics of others unveiled by BM emerges early in life: already 2–3-day-old human newborns are tuned to displays depicting point-light human walkers (Bidet-Ildes et al., 2014) and

other vertebrates ([Simion et al., 2008; 2011](#)). Visual processing of BM and related social signals rapidly develops over early period of life (see [Pavlova, 2012](#) for comprehensive review of earlier developmental work).

Most developmental studies, however, focused on the ability to perceive BM, including the visual sensitivity to BM, visual preference for BM, and identification of BM direction. Little is known about the ability to infer social information such as social agency and other characteristics such as drives, emotions and intentions. It was suggested that BM processing can serve as a hallmark of social cognition and, therefore, social abilities and BM processing may be firmly linked ([Pavlova, 2012](#)). Furthermore, developmental paths in revealing social traits and characteristics through BM have been largely neglected, whereas the early development of other social abilities (such as affective facial processing) has attracted much attention.

TD preschoolers aged 3 and 5 years are able to spontaneously recognize not only point-light displays depicting a human walker, but also other vertebrates (such as dogs) and a bird, and 5-year old children exhibit the same performance level as adults ([Pavlova et al., 2001](#)). Similar findings are reported when 6-year-olds, 9-year-olds, and adults discriminate point-light BM depicting different human actions: all age groups of participants perform near the ceiling level without age differences in accuracy ([Freire et al., 2006](#)). By adding simultaneous noise (i.e., additional moving dots) to point-light displays the visual signal-to-noise ratio is reduced, making BM tasks deliberately more demanding and difficult to perform. The sensitivity to these masked BM linearly improves with age. 9-year-olds (but not 6-year-olds) distinguish BM from masking noise as well as adults do ([Freire et al., 2006; Annaz et al., 2010](#)).

Only a few studies investigated social aspects of BM perception in infancy. By comparing the ability to detect social signals between TD infants at 4 and 9 months, it was shown that infants aged 9 months with an increased interest in social stimuli excel on a developmental index compared to their peers without such interest ([Kutsuki et al., 2009](#)). When point-light displays and full-light (whole-body) movies showing an actor turned to look at a target either to the left or the

right side were presented to infants, both 9 and 12-month-old infants are tuned to the direction of attention of a full-light agent, whereas only 12-month-olds are able to follow the attentional shift of a point-light figure. This suggests early abilities for visual sharing of socially relevant information with a point-light agent. These findings account for a basic developmental step in the ability to integrate higher-level social information from point-light displays during this developmental period (Yoon and Johnson, 2009; Furuhata and Shirai, 2015).

The findings on development of body language reading in typical and atypical development are extremely sparse, and this topic requires further research efforts. Very little is known about children's ability to recognize affective BM, though from an evolutionary point of view, body language reading is even more important than face affect recognition or tuning to speech prosody: people are often seen at a distance, and one can perceive patterns of BM, posture and gait before some cues from facial expression become available (Van Meel et al., 1993). Two earlier studies with full-light BM displays investigating emotion recognition from solo dance have reported that by 8 years of age, children achieve adult performance level in emotion recognition from dancing movement. However, already performance of 4-year-olds is above chance level (Boone and Cunningham, 1998; Lagerlof and Djerf, 2009).

Yet one has to take into account that emotions represented by dance are often exaggerated and/or symbolic, and therefore, how these findings can be generalized to daily-life body language reading remains unclear. In a study with a relatively large number of children aged 4-17 years, participants had to indicate whether BM point-light displays portray happiness, sadness, fear or anger (Ross et al., 2012). Children as young as 4 years old perform above chance in decoding affect from body language: this holds true for all four portrayed emotions. However, children perform worse than adults. By connecting performance to age of each participant, a bilinear developmental trajectory with a steep increase during childhood followed by a much slower rate of improvement after 8.5 years of age could be drawn. In this study, no gender differences in performance were found (Ross et al., 2012). This outcome has important implications for understanding the maturation of social cognition. Most recently proposed two-

process model claims that the mechanism underlying BM detection comprises a fast-motion-detection ability and a slow global structure-from-form interpretation ability, which is shaped by experience (Hirai and Senju, 2020). Further research is required to obtain a more detailed insight into the developmental trajectories of body language reading.

1.2.2 In adults. As already mentioned above (p. 6), healthy TD adults are able to interpret information about intentions, emotions and dispositions expressed by point-light actors. Previous studies show that observers are able to reliably recognize emotions (such as fear, anger, grief, joy, surprise, and disgust) from point-light BM of trained dancers (Dittrich et al., 1996). Yet, the emotional content of the upright point-light clips was rated less accurate as compared to the full-scene videos. The neuropeptide oxytocin (OT) plays an important role for interpersonal bonding: After a single-dose of intranasal OT (24 IU), performance on the emotion-rating task becomes better (Bernaerts et al., 2016; Wynn et al., 2019). Emotional valence of BM affects the sensitivity to point-light gait (masked by an additional set of dots taken from the same point-light walker display) with highest sensitivity (but also with greatest response bias) to angry and lowest sensitivity to neutral walking (Chouchourelou et al., 2006). The sensitivity to slightly camouflaged BM is related to both anger and happiness (Ikeda and Watanabe, 2009). Superiority effect of happiness in body language reading is also reported: BM detection within noise is not only facilitated by actor's happiness, but happiness is easier to recognize than other emotions (Lee and Kim, 2017). The ability to reveal identity of point-light dancers and expression intensity correlates with self-reported empathy (Sevdalis and Keller, 2011). Alexithymia (i.e., inability to identify and describe emotions in the self) is correlated with confidence in rating of emotion valence through point-light body language (Lorey et al., 2012).

It is also possible to identify the emotional content of interpersonal communication of two actors through point-light displays. The recognition of the presented emotional content is impaired when either one of two portrayed actors is completely missing or is changed to a mirrored version of the other actor (Clarke et al., 2005). The original videos presented upside-down show a preserved ability

in the recognition of joy and love, whereas the recognition of anger, disgust, fear or romantic love is decreased. A database was created with several sets of different social actions presented by male and female couples (Manera et al., 2010). There are, for example, displays portraying an agent performing a communicative gesture which is followed by a responding action of a second agent. It could be shown that by changing the communicative action of the first agent to an independent action, the correct rating of the expected action of the second agent is reduced. Changing interval time between communicative gesture and responding action leads to impairments in prediction of the anticipated action (Manera et al., 2011, 2013).

1.2.3 In elderly. Older people often show difficulties in the perception of motion such as direction detection, evaluation of speed of moving patterns (Ball and Sekuler, 1986; Norman et al., 2003) or in 3-Dimensional structure-from-motion perception (Andersen and Atchley, 1995; Norman et al., 2000). Previous studies have shown decreased detection of point-light BM camouflaged by a cloud of noise for older compared to younger adults (Billino et al., 2008; Pilz et al., 2010). However, it seems that older adults' performance on BM tasks substantially improves with increasing stimulus duration (Norman et al., 2004; Pilz et al., 2010; Spencer et al., 2016). This suggests that changes in BM perception might in part be related to increasing processing times. In addition, older adults seem to use different strategies when processing BM. In elderly, observers require more distance in virtual space between themselves and a point-light walker to integrate BM information than younger adults (Legault et al., 2012): Their performance decreases markedly at a distance as far as 4 m (a distance that is critical for collision avoidance), whereas performance in young adults remains constant up to 1 m. Perceptual-cognitive training of observers aged 64-73 years eliminates the difference in BM perception after only a few weeks (Legault and Faubert, 2012). Functional magnetic resonance imaging (fMRI) in 19 healthy older adults (age range 62-78 years) and in 19 younger adults (age range 20-30 years) shows increased temporal and frontal activation in the older group for low-level motion but no differences for BM. Time-course analyses in regions of interest known to be involved in both types of motion processing likewise did not reveal any age

differences for BM processing (Biehl et al., 2017). This outcome shows that while low-level motion processing in healthy aging requires recruitment of additional resources, BM processing appears to be relatively preserved.

Previous research suggests that the ability to perceive emotional stimuli decreases with age: older adults are impaired in recognizing emotional expressions from static faces (Lambrecht et al., 2012). Recent work shows that body language reading (such as emotion recognition through body motion) remains rather accurate over age: only recognition of sadness (but not angry and happy displays that are more exaggerated) at short durations is lower in elderly (Spencer et al., 2016). It is also reported, however, that older adults perform poorly on decoding actions and emotions from point-light displays (Insch et al., 2012).

The question arises: How does age, not just of an observer, but also of an actor affect BM processing. Age may influence the ability to recognize other people's body expressions by changes in one's own ability to perform certain action over the life-span (i.e., an own-age bias may occur, with best recognition for one's own age). To address this issue, point-light displays of children, young adults and older adults (>70 years) expressing six different emotions were presented to observers of the same three age-groups (Pollux et al., 2016). No evidence for the predicted own-age bias was found. Children better recognized older actors' expressions of 'active emotions,' such as anger and happiness. Taken together, these findings suggest that age-related changes in one's own action production affect body language reading in young children only (probably because they interact more frequently with older adults). Overall, it appears that both BM processing (as compared to other types of motion) and body language reading are relatively intact in elderly.

1.3 BRAIN NETWORKS ENGAGED IN BODY LANGUAGE READING

With the advent of sophisticated tools and techniques over the past decades, brain imaging has contributed to considerable progress in our understanding of the networks underlying BM processing and body language reading.

In TD individuals, BM processing relies on a large-scale network with foci in the parieto-temporal junction and fusiform gyrus (or fusiform face area, FFA), and in the parietal and frontal cortices, with right-hemispheric dominance ([Grossman et al., 2000](#); [Vaina et al., 2001](#); [Puce and Perrett, 2003](#); [Grossman and Blake, 2002](#); [Michels et al., 2005](#); [2009](#); [Gobbini et al., 2007](#); [Saygin, 2007](#); [Herrington et al., 2011](#); [Pavlova et al., 2017](#); see also meta-analyses [Grosbras et al., 2012](#); [Engell and McCarthy, 2013](#)). The hub of this circuitry lies in the right posterior superior temporal sulcus, pSTS ([Grossman and Blake, 2002](#); [Beauchamp et al., 2003](#); [Gobbini et al., 2007](#); [Kaiser et al., 2010](#); [Herrington et al., 2011](#); [Dasgupta et al., 2017](#)), where this network likely topographically overlaps and communicates with the social brain.

Brain imaging work (which is mostly based on functional magnetic resonance imaging, fMRI) had been primarily restricted to localization of brain areas involved in social cognition. For understanding proper functioning of neural circuits and especially its pathology, one has to consider dynamic changes in brain activation unfolding over time ([Pavlova, 2017b](#)). Magnetoencephalography (MEG) reveals temporal dynamics of the cortical response to BM in healthy adults ([Pavlova et al., 2004](#)), and in children who suffer congenital periventricular lesions to the white matter ([Pavlova et al., 2006](#)). Electroencephalography (EEG) in TD adults uncovers topographically similar responses to BM over the extrastriate occipital and right temporal cortices (e.g., [Hirai et al., 2003](#); [Jokisch et al., 2005](#); [Krakowski et al., 2011](#); [Han et al., 2013](#); [White et al., 2014](#)). BM processing requires intact communication within this distributed brain network.

Only recently, engagement of brain structures beyond the cerebral cortex, such as the cerebellum, has been identified ([Sokolov et al., 2012](#); [2014ab](#); [Jack et al., 2017](#)). Most recently, whole head ultra-high field 9.4T fMRI along with analysis of the blood oxygen level dependent (BOLD) response revealed distinct large-scale ensembles of regions playing in unison during different stages of BM processing ([Pavlova et al., 2017](#)). The only task-related fMRI functional connectivity study on BM processing suggests the right FFG, MTC and STS to be interconnected, and that the STS exclusively interacts with insula and IFG ([Dasgupta et al., 2017](#)). These findings speak to a “gatekeeper role” of the STS, receiving pre-processed

information from the FFG and MTC but being the only region communicating with higher-order areas. However, recent integrative analysis of structural and effective brain connectivity sheds light on architecture and functional principles of the BM circuitry which is organized in a parallel rather than hierarchical way (Sokolov et al., 2018).

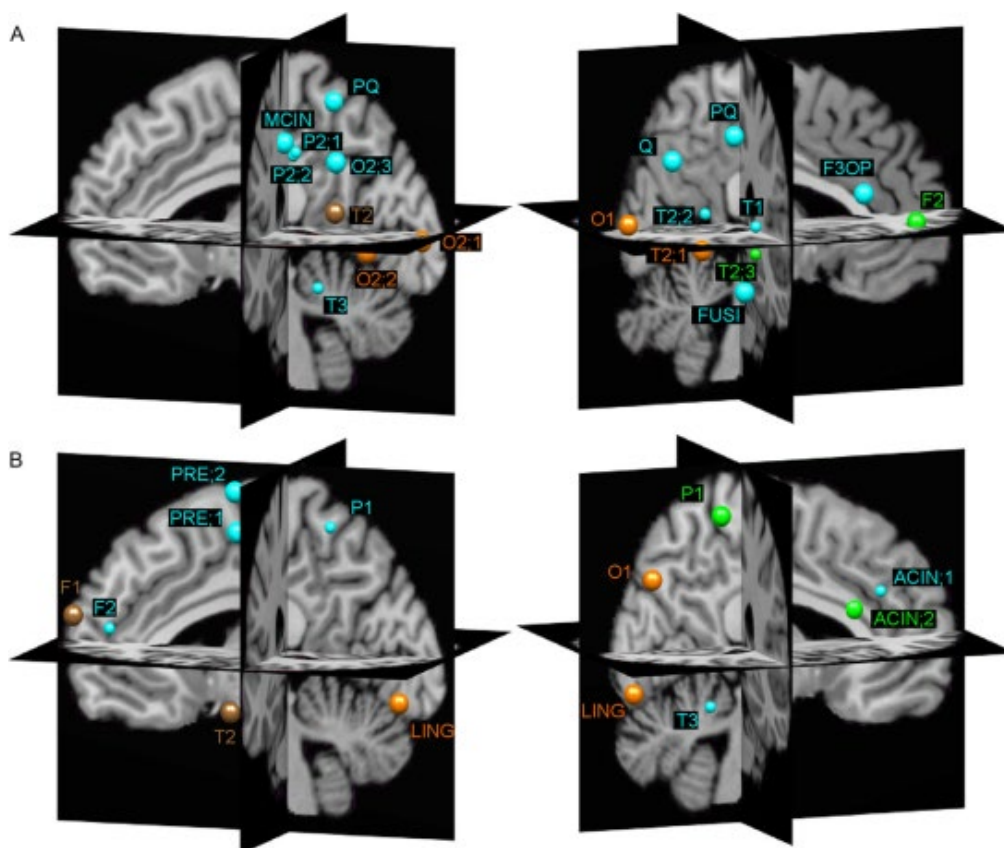


Figure 2. Overview of large-scale brain networks with different temporal dynamics. Brain regions exhibiting greater activation to (A) upright versus inverted BM in the left (left panel) and in the right (right panel) brain hemisphere; (B) inverted versus upright BM in the left (left panel), and in the right (right panel) hemisphere. Regions with similar temporal dynamics of the blood oxygen level dependent (BOLD) response are color coded. Large spheres represent regions that differentiate between upright and inverted BM at least in 1 out of 4 temporal intervals (time bins); small spheres represent regions where display-specific effects were not found in any single bin. From Pavlova et al. (2017). “Wrong Way Up”: Temporal and Spatial Dynamics of the Networks for Body Motion Processing at 9.4 T. *Cerebral Cortex* 27: 5318–5330, doi:10.1093/cercor/bhx151. Copyright by the authors; reproduced with permission.

Research on the brain networks dedicated to affective body language reading in normalcy and pathology is extremely sparse (Heberlein et al., 2004; Peelen and

Caramazza, 2010; Atkinson et al., 2012; Kim et al., 2015; Jastorf et al., 2015; Mazzoni et al., 2017). Preserved emotion recognition and impaired personality rating occurs in patients with damage to the right somatosensory cortices, whereas patients with damage to the left frontal opercular cortices have difficulties in emotion rating but fail to judge personality traits (Heberlein et al., 2004). The effect of transcranial direct current stimulation (tDCS) [either anodal (excitatory) or cathodal (inhibitory)] by electrodes mounted over the right pSTS (target) and orbito-frontal cortex (reference) on the performance on emotion recognition task from BM is modulated by the emotional valence of the stimuli. Recognition of emotions with a negative emotional valence (sadness and anger) was increased when receiving anodal stimulation compared to cathodal stimulation (Vonck et al., 2015). In foreseeing intentional actions of others, the ability of interpersonal predictive coding (IPC) is crucial for predicting communicative actions. In patients with schizophrenia, symptoms of social misbehavior could be caused by deficits in predictive coding. Patients and healthy controls had to perform a detection task of identifying communicative or non-communicative actions of a first actor, followed in 50% of trials by the presence of a second actor. As a result, the communicative gesture leads to the presumption of the presence of a second actor, compromising the rate of correct answers. Against expectations, patients with schizophrenia and TD individuals showed a similar impact on the correct response rate. This leads to conclusion that processing of BM based on reflexive recognition is not impaired to a further extent in schizophrenic compared to TD individuals (Okruszek et al., 2019).

The processing of emotional content of body language is thought to rely mostly on body kinematics. To identify brain areas for emotion recognition from gait, highly controlled dynamic body-movement stimuli based on real human motion-capture data were created and testified (Roether et al., 2009). Using fNIRS during the performance of an emotion recognition task and a speed control test, increases in cortical oxygenated haemoglobin (O₂HB) in response to visual stimulation during emotion discrimination were measured (Schneider et al., 2014). Negative emotions activated right occipito-temporal and left temporal and temporo-parietal areas whereas fearful and angry gait elicited higher activation

increases during the emotion recognition task compared to the speed task with the same stimuli. The activation pattern is different for the task on emotion recognition as compared to the task on speed recognition with the same set of visual stimuli. It is connected to emotion-coping processes, involving different brain-areas for visual association and for body/motion recognition ([Schneider et al., 2014](#)). Similar stimuli were used for another study, with differentiated 5 levels of emotional intensity for each emotion. Brain selectivity to emotional gait stimuli in the STS, amygdala, fusiform body area (FBA) and extrastriate body area (EBA) were revealed by fMRI during the rating task of emotional content and intensity. For visually identical stimuli, the amygdala showed a stronger response when the stimulus was perceived as emotional. Besides, the level of amygdala activity was linked positively to the emotional intensity ([Goldberg et al., 2015](#)).

Not only differentiating the emotional state of performers engaged in social interaction, but also inferring the absence of emotional content in body language reading is of vital importance for effective social interaction. Most recent analysis of fMRI data uncovers the brain circuits signaling the absence of emotion in body language reading indicating greater activation of the right amygdala and midline cerebellar vermis to non-emotional as opposed to emotional body language. Furthermore, the effective connectivity between the amygdala and insula predicts our ability to detect the absence of emotion in body language ([Sokolov et al., 2020](#)).

1.4 GENDER DIFFERENCES IN BODY LANGUAGE READING

Efficiency of body language reading is affected by a plenty of factors. One of them is since long ago present in prejudices according with women are better in social skills. Most of studies on gender differences in social cognition are based on emotion recognition from static facial expressions. Women perform generally better in processing of non-verbal cues: for example, men are more likely to misconceive friendliness in a woman as sexual interest and sexual interest as friendliness ([Farris et al., 2008](#)). Girls aged 3.5 years perform on emotion recognition tasks as well as boys aged 5 years ([Boyatzis et al., 1993](#)).

Despite the fact that females are widely believed to be more proficient in body language reading, the experimental data in both healthy individuals and patients with deficient social abilities is not only sparse but also beyond simple interpretation (Pavlova, 2017b). Females are more accurate in recognition of point-light activities (such as walking, jumping on the spot, kicking a ball, drinking from a bottle) and excel in some aspects of body-language reading: they are faster in discrimination of emotional from neutral BM (Alaerts et al., 2011). Females are more accurate in body language reading (affective dynamic whole-body expressions of happiness, sadness, anger, and neutral) than males; however, males with schizophrenia perform better than females with schizophrenia (Strauss et al., 2015).

Most recently it was shown that BM processing and the extraction of emotional content from BM are gender specifically linked. Forty participants (20 males and 20 females) were presented with the same point light BM displays performing two different tasks: emotion recognition or gender identification. They also had to identify either actor gender or emotional state from a set of static photographs from the Reading the Mind in the Eyes Test. Although no gender effects on the performance of the BM tasks were documented, in males the accuracy in recognition of emotions was linked to the accuracy in gender recognition. For females, the performance on the Reading the Mind in the Eyes Test was associated to the accuracy and response time in body language reading (Isernia et al., 2020). These findings point to gender-specific modes in visual social cognition and trigger investigation of body language reading in neuropsychiatric disorders, most of which are gender-specific.

1.5 GOALS

Gender effects in body language reading are largely unknown, and a few previous findings are controversial. Investigation of gender impact on body language reading is of substantial value for clarification of the nature of neurodevelopmental and psychiatric disorders (such as autistic spectrum disorders (ASD), schizophrenia, attention deficit hyperactivity disorder (ADHD),

eating and anxiety 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.

The motivation of the present work was to clarify whether, and, if so, how gender affects body language reading (recognition of emotions in point-light displays of knocking motion and human locomotion) in TD adult individuals. The present work intends to make an initial step in filling the gap, and to clarify whether, and, if so, how perceiver's gender affects recognition of emotional expressions conveyed by actions of others. More specifically, we asked (i) whether gender affects recognition of emotions represented by body motion, or, in other words, whether females excel in recognition of emotional actions; and (ii) whether gender effects depend on emotional content of actions.

In the first study, we addressed these issues by administering participants a three alternative-forced choice task: participants had to indicate whether a display portrayed happy, neutral or angry knocking on a door.

In the second study, in addition to the issues (i) and (ii) listed above, we asked (iii) whether gender effects in body language reading are impacted by actor gender. We also did use the other repertoire of expressive actions: human locomotion versus knocking motion in the first study. We implemented a point-light methodology that helps to isolate information revealed by motion from other cues (shape, color, etc.). Perceivers saw only a few bright dots placed on the main joints of an invisible actor, so that all other clues except for motion characteristics were eliminated.

2. Gender affects body language reading

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Gender affects body language reading

Arseny A. Sokolov^{1,2}, Samuel Krüger¹, Paul Enck³, Ingeborg Krägeloh-Mann¹ and Marina A. Pavlova^{1,4*}

¹ Department of Pediatric Neurology and Child Development, Children's Hospital, Medical School, Eberhard Karls University of Tübingen, Tübingen, Germany

² Department of Neurosurgery, Medical School, Eberhard Karls University of Tübingen, Tübingen, Germany

³ Department of Psychosomatic Medicine and Psychotherapy, Medical School, Eberhard Karls University of Tübingen, Tübingen, Germany

⁴ Institute of Medical Psychology and Behavioral Neurobiology, MEG Centre, Medical School, Eberhard Karls University of Tübingen, Tübingen, Germany

Edited by:

Marco Tamietto, Tilburg University, Netherlands

Reviewed by:

Ute Habel, RWTH Aachen University, Germany

Marco Del Giudice, University of Turin, Italy

*Correspondence:

Marina A. Pavlova, Developmental Cognitive and Social Neuroscience Unit, Department of Paediatric Neurology and Child Development, Children's Hospital, Medical School, Eberhard Karls University of Tübingen, Tübingen, Germany.
e-mail: marina.pavlova@uni-tuebingen.de

Body motion is a rich source of information for social cognition. However, gender effects in body language reading are largely unknown. Here we investigated whether, and, if so, how recognition of emotional expressions revealed by body motion is gender dependent. To this end, females and males were presented with point-light displays portraying knocking at a door performed with different emotional expressions. The findings show that gender affects accuracy rather than speed of body language reading. This effect, however, is modulated by emotional content of actions: males surpass in recognition accuracy of happy actions, whereas females tend to excel in recognition of hostile angry knocking. Advantage of women in recognition accuracy of neutral actions suggests that females are better tuned to the lack of emotional content in body actions. The study provides novel insights into understanding of gender effects in body language reading, and helps to shed light on gender vulnerability to neuropsychiatric and neurodevelopmental impairments in visual social cognition.

Keywords: visual perception, biological motion, social cognition, gender

INTRODUCTION

Body language reading is of immense importance for adaptive social behavior and non-verbal communication. This ability constitutes a central component of social competence. Healthy perceivers are able to infer emotions and dispositions of others represented by point-light body movements that minimize availability of other cues (Pollick et al., 2001; Atkinson et al., 2004; Heberlein et al., 2004; Clarke et al., 2005; Ikeda and Watanabe, 2009; Rose and Clarke, 2009). Perceivers can reliably judge emotional content of dance represented by a few moving dots placed on the dancer's body (Dittrich et al., 1996). Visual sensitivity to camouflaged point-light human locomotion is modulated by the emotional content of gait with the highest sensitivity to angry walking (Chouchourelou et al., 2006). Observers can discriminate between deceptive and true intentions conveyed by body motion, and true information is precisely detected despite misleading endeavors (Runeson and Frykholm, 1983; Grèzes et al., 2004a,b).

But how do we know whom to trust or who is attracted to us? Such judgments are vital to social interaction, and men and women appear to show profound differences in cues attended to. Yet research on sex differences in visual social cognition has been mainly limited to static face images, in particular, still photographs. In accordance with widespread beliefs, females exhibit higher sensitivity to non-verbal cues: they better discriminate friendliness from sexual interest (Farris et al., 2008) and are more proficient in recognition of facial emotions (Montagne et al., 2005). Females without and with Asperger syndrome are better at recognizing emotions from dynamic faces than males (Golan et al., 2006). Moreover, females tend to better recognize emotions from faces than from voices, whereas males exhibit the opposite tendency. As a rule, however, facial expressions and static body postures can only signal emotional states and affect, but do not provide information

about how to deal with it. Dynamic body expressions, gestures, and actions of others are a richer and more ecologically valid source of information for social interaction (De Gelder, 2006, 2009; Pavlova, 2009). The other important advantage of bodily expressions is that whereas face expressions (similarly to a verbal information flow) are believed to be easily kept under control, body movements reveal our true feelings. When emotions expressed by faces and bodies are incongruent, recognition of facial expressions is affected by emotions revealed by body (Meeren et al., 2005). Brain imaging indicates that emotions expressed by dynamic bodies as compared to faces elicit greater activation in a number of brain areas including the superior temporal sulcus (STS), a cornerstone of the social brain (Kret et al., 2010). Experimental evidence obtained primarily in patients with lesions and cortical blindness favors the assumption that emotional body language can be processed automatically, without visual awareness and attention (for review, see Tamietto and de Gelder, 2010).

To a great surprise, however, gender impact on body language reading is largely unknown. A few studies conducted at the beginning of the 80s based on the profile of non-verbal sensitivity (PONS) test, which includes body motion (neck to knees) video clips, point to the superiority of females in body language reading (e.g., Blank et al., 1981). However, this test has some serious methodological limitations; for example, it is based on body motion video clips of only one female actor. Although sex differences represent a rather delicate topic, underestimation, or exaggeration of possible effects can retard progress in the field.

The present work intends to make an initial step in filling the gap, and to clarify whether, and, if so, how perceiver's gender affects recognition of emotional expressions conveyed by actions of others. More specifically, we ask (i) whether gender affects recognition of emotions represented by body motion, or, in other words, whether

females excel in recognition of emotional actions; and (ii) whether gender effects depend on emotional content of actions. To this end, healthy young females and males were presented with point-light displays portraying knocking at a door with different emotional expressions (happy, neutral, and angry). We took advantage of a point-light technique that helps to isolate information revealed by motion from other cues (shape, color, etc.). Perceivers saw only a few bright dots placed on the main joints of an otherwise invisible arm (**Figure 1**) so that all other clues except for motion characteristics were abandoned.

MATERIALS AND METHODS

PARTICIPANTS

Thirty four healthy adults, students of the University of Tübingen Medical School (aged 20–36), were enrolled in the study. Mean age of females (20 participants) was 23.8 ± 3.7 years, and mean age of males (14 participants) was 22.9 ± 2.0 years. There was no age difference between female and male participants ($t_{32} = 0.95$, $p = 0.35$, ns). The groups were also comparable in terms of educational and socio-economic status. All participants had normal or corrected-to-normal vision and heterosexual orientation. None had a history of neurological or psychiatric disorders including autistic spectrum disorders (ASD), schizophrenia, head injuries, or medication for anxiety or depression. None had previous experience with such displays or tasks. Participants were run individually. Informed written consent was obtained in accordance with the requirements of the local Ethical Committee at the University of Tübingen Medical School.

STIMULI AND PROCEDURE

We used point-light displays portraying knocking arm motion (Pollick et al., 2001, 2002). Point-light displays were recorded during performance of knocking with different emotional content (happy, neutral, and angry). We chose to use animations with happy and angry motions, because happiness and anger are reported to be quite similar on the activation dimension, and these animations tended to have fast and jerky movements (Pollick et al., 2001). Display creation is described in detail elsewhere (Pollick et al., 2001). In brief, recording was performed using a 3D position measurement system at a rate of 60 Hz (Optotrak, Northern Digital Inc., Waterloo, ON, Canada). Each display consisted of six point-light dots placed on the head, shoulder, elbow, wrist, and the first and fourth metacarpal joints of an otherwise invisible

right hand (**Figure 1**). Point-light actors were seen facing right, in a sagittal view, and struck the surface directly in front of them. The size of all point-light knocking stimuli was standardized in such a way that in the first frame, the distance from the head to the first metacarpal joint was identical for all actors. For each emotion, six different displays with equal number of knocking performed by female and male actors were created. By using the Presentation software (Neurobehavioral Systems Inc., Albany, CA, USA), each video was displayed five times per experimental session resulting in 30 trials per emotion. The whole experimental session consisted of a set of 90 displays representing three emotions in a random order, and took about 15–20 min per participant. Each display was shown for 1 s. We used a three alternative-forced choice paradigm. On each trial, participants indicated (by pressing with their dominant hand one of three respective keys on a computer keyboard) whether a display portrayed happy, neutral, or angry knocking. Positions of the keys were counterbalanced between participants. Participants were told that they have to perform the task as accurately as possible. No immediate feedback was given regarding performance.

RESULTS

Percentage correct in recognition of emotions conveyed by knocking is represented in **Figure 2A**. In both females and males, recognition of all emotional expressions was above chance level ($p < 0.001$). However, recognition of happy knocking was less accurate than of neutral and angry actions. This is consistent with the outcome of previous studies on emotion recognition through point-light human locomotion (Chouhourelou et al., 2006; Ikeda and Watanabe, 2009) and dance (Dittrich et al., 1996) that show better recognition of angry over happy motion.

Individual number of correct responses was submitted to a 2×3 repeated-measures ANOVA (as assessed by the Shapiro–Wilk test, the data were normally distributed) with factors Gender (female/male) and Emotional expression of knocking (happy/neutral/angry). This analysis revealed the lack of a main effect of gender ($F_{(1,32)} = 0.21$, $p = 0.648$, ns). However, a main effect of emotional expression ($F_{(2,32)} = 82.94$, $p < 0.0001$) and interaction between the factors Gender \times Emotional expression ($F_{(2,32)} = 6.23$, $p < 0.003$) were highly significant. *Planned* pair-wise comparisons indicated that males outperformed in recognition of happy knocking ($t_{32} = 2.58$, $p < 0.015$, one-tailed, here and below Bonferroni corrected for multiple comparisons; $d = 0.84$), whereas females tended

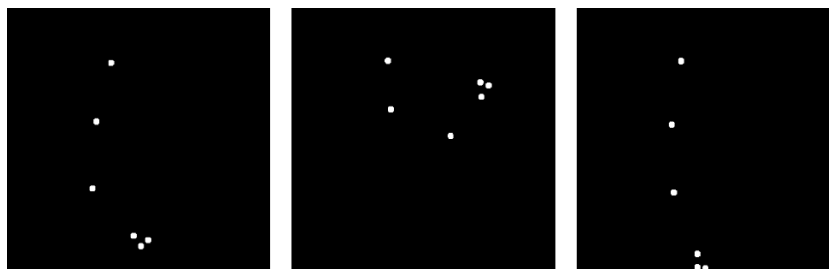


FIGURE 1 | Three static frames taken from the dynamic sequence representing knocking motion by a set of dots placed on the arm joints, shoulder, and head of an otherwise invisible actor. Actors were seen facing right, in a sagittal view, and struck the surface directly in front of them.

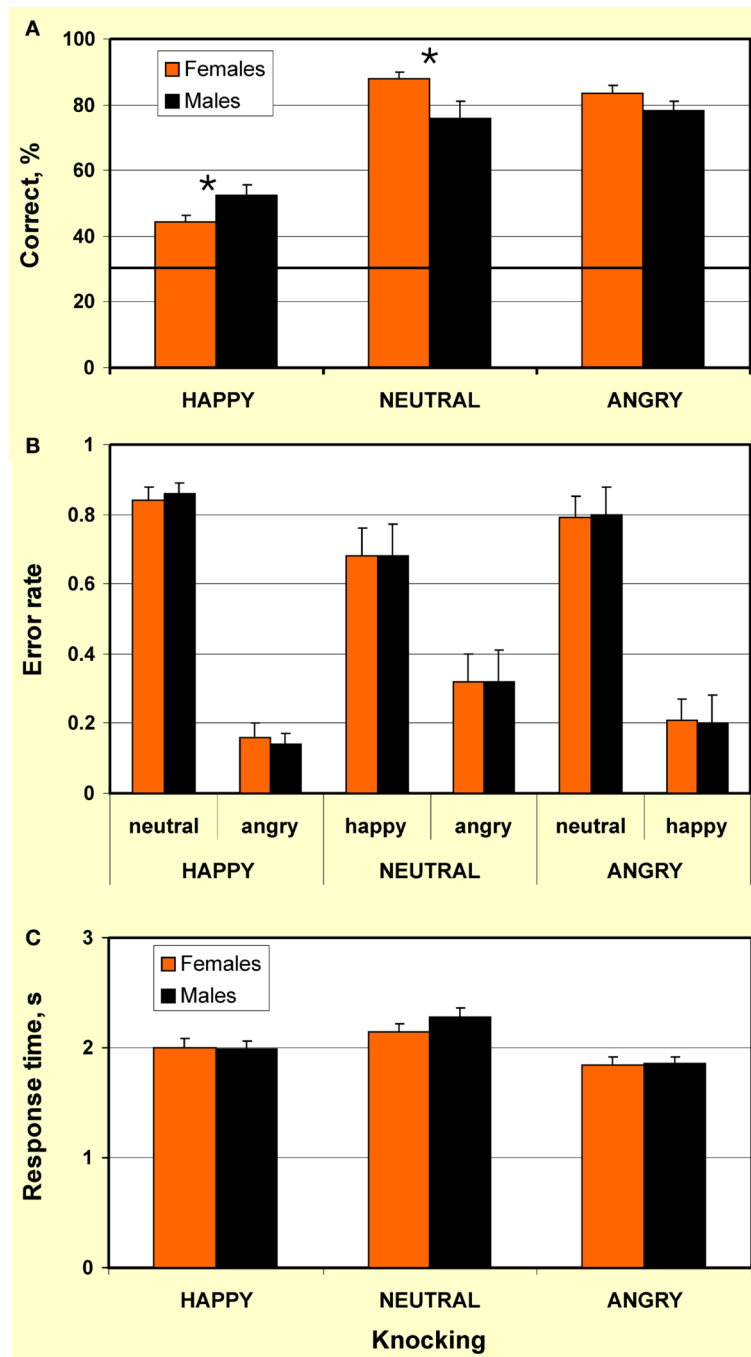


FIGURE 2 | Recognition of happy, neutral, and angry point-light knocking by females and males. (A) Percentage correct: Males outperformed in recognition of happy knocking ($p < 0.015$), whereas females excelled in recognition of neutral knocking ($p < 0.016$) and tended to over-perform in recognition of angry knocking ($p < 0.07$). Bold horizontal line indicates chance level. Significant differences are indicated by an asterisk; **(B)** Error rate: The lack of gender differences in error rate demonstrates that gender differences in recognition accuracy of emotional content of knocking were not caused by

gender-related bias for mistaking one emotion for another. Each bar represents an average ratio of the number of errors of particular type to the overall number of errors made for a display type (e.g., leftmost bar represents an average ratio of number of trials when happy knocking was mistaken for neutral knocking to the number of trials when happy knocking was mistaken for both neutral and angry knocking); **(C)** Response time to happy, neutral, and angry point-light knocking by females and males. Females and males do not differ in response time. Vertical bars represent \pm SE.

to over-perform in recognition of angry knocking ($t_{32} = 1.87$, $p < 0.07$, one-tailed) and excelled in recognition of neutral knocking ($t_{32} = 2.54$, $p < 0.016$, one-tailed, $d = 0.88$). The data, therefore,

reveals the lack of advantage of females in recognition accuracy. Instead, the findings indicate that sex effects in recognition accuracy are modulated by emotional contents of actions.

Error analysis (**Figure 2B**) indicated that by both females and males, happy knocking was mistaken for neutral knocking in more than 80% of wrong responses (error rate 0.84 and 0.86 for females and males, respectively; gender difference: $t_{32} = 0.42$, $p = 0.68$, two-tailed, ns). Error rate was calculated as an average ratio of the number of errors of particular type to the overall number of errors made for a display type). In turn, with a lack of gender differences, neutral knocking was misperceived as happy actions in about 70% of error responses (error rate 0.68 and 0.67 for females and males, respectively; gender differences: $t_{32} = 0.02$, $p = 0.99$, two-tailed, ns). In about 80% of error trials in response to angry knocking, both females and males mistook angry knocking for neutral knocking (error rate 0.79 and 0.8 for females and males, respectively; gender difference: $t_{32} = 0.14$, $p = 0.88$, two-tailed, ns). The lack of gender differences in error rate suggests that gender effects in recognition accuracy of emotional content of knocking observed in the present study are not caused by gender-related bias for mistaking one emotion for another.

For response time analyses, a 2×3 repeated-measures ANOVA was performed on individual values (as assessed by the Shapiro–Wilk test, the data were normally distributed) with factors Gender (female/male) and Emotional expression (happy/neutral/angry). This analysis did not reveal any effect of gender ($F_{(1,32)} = 1.56$, $p = 0.22$, ns) as well as any interaction of factors Gender \times Emotional expression on response time ($F_{(2,32)} = 1.42$, $p = 0.25$, ns; **Figure 2C**). However, a main effect of emotional expression was significant ($F_{(2,32)} = 35.16$, $p < 0.0001$), with the fastest response to angry knocking, and the slowest response to neutral knocking (**Figure 2B**). This shows that recognition of neutral knocking was more difficult than that of angry and happy knocking. *Post hoc* pair-wise comparisons showed no gender difference in response time to happy ($t_{32} = 0.09$, $p = 0.93$, two-tailed, ns, average 2.00 ± 0.39 and 1.99 ± 0.28 s from the stimulus onset, for females and males, respectively), neutral ($t_{32} = 1.21$, $p = 0.24$, two-tailed, ns; average 2.15 ± 0.33 and 2.28 ± 0.3 s, for females and males, respectively), and angry knocking ($t_{32} = 0.14$, $p = 0.89$, two-tailed, ns; average 1.84 ± 0.32 and 1.85 ± 0.28 , for females and males, respectively). Taken together, the findings suggest that gender does not affect speed of body language reading. For both females and males, however, the swiftness of response to body language depends on the emotional content of actions. Since it is difficult to interpret negative findings within a relatively small sample size that might be considered a limitation of the study, the lack of sex differences in error rate and response time has to be further explored.

DISCUSSION

The outcome of the study indicates that gender affects accuracy rather than speed of body language reading. To the best of our knowledge, the present work delivers the first evidence for sex effects in body language reading. The gender effect, however, is modulated by the emotional content of actions. Females tend to excel in recognition accuracy of angry knocking, whereas males over-perform in recognition of happy actions. Furthermore, females clearly surpass males in recognition of emotionally neutral knocking. The lack of gender differences in error rate suggests that gender effects in recognition accuracy are not caused by gender-related bias.

Based on popular wisdom, one can expect that while women possess soft skills in social perception including high sensitivity to positive emotional signals and subtle details, men might outperform in recognition of negative menacing expressions. This assumption is based on the different evolutionary and socio-cultural roles of both genders (e.g., Biele and Grabowska, 2006; Proverbio et al., 2008). High sensitivity of women to positive emotions has been related to their role as primary offspring care providers. Social cognition in men is presumably connected with active interactions and immediate reactions, and, therefore, emotion perception is likely associated with motor programs. Anger detection is usually associated with a need to act, for example, escape from a person or prepare to confront a person. However, the data available are controversial. In the present study, males over-perform in recognition of emotionally positive happy actions. These data agree with findings showing that men appear to exhibit stronger brain activation in response to positive pictures (depicting landscapes, sport activities, families, and erotic scenes) than women (Wrase et al., 2003; Sabatini et al., 2004; Gasbarri et al., 2007). Moreover, males are equally responsive to happiness conveyed through static and dynamic happy faces (males rate the intensity of dynamic and static expressions of happiness equally high), whereas females are less responsive to happiness in static faces (Biele and Grabowska, 2006). Presumably, this indicates that males are better tuned to subtle expressions of happiness in faces and actions. This might hold true, at least, for a population of young men with a high social status and educational level as those participated in the present study. The prominent outcome of the study is that females had a clear advantage in recognition of neutral knocking. This suggests that women are better tuned to the lack of emotional content in body actions. Future research should clarify whether gender effects in body language reading occur with other repertoires of actions, and with other arrays of emotions.

What is the nature of gender effects in body language reading? One possibility is that gender differences have neurobiological sources (Cahill, 2006; Jazin and Cahill, 2010), and brain mechanisms underpinning body language reading are sex-specific. The social cognition network, commonly referred to as the *social brain*, primarily involves the parieto-temporal junction, temporal cortices including the fusiform face area and the STS, orbitofrontal cortices, the amygdala (Adolphs, 2003), and the left lateral cerebellum (Sokolov et al., 2010). The right STS is a cornerstone for processing of meaningful body motion (Grossman and Blake, 2002; Pavlova et al., 2004; Pelphrey et al., 2004). Is the social brain sex-specific? This is an open question.

To date, studies of sex effects on the social brain have been limited to investigation of face expressions or body actions represented in still photographs. Brain activation in females is reported to be more bilaterally distributed, presumably providing greater contribution of both hemispheres to identification of facial affect (Bourne, 2005; Proverbio et al., 2010). Females show stronger event-related potential (ERP) response to emotional faces (Orozco and Ehlers, 1998). However, the findings are controversial. Sex effects are found in the blood oxygen level dependent (BOLD) response of the amygdala to happy, but not to fearful faces (Killgore and Yurgelun-Todd, 2001). On the other hand, a significant correlation between functional magnetic resonance imaging (fMRI) activity of the amygdala and behavioral response to fearful faces is observed

in males only (Derntl et al., 2009a). Both behavioral and amygdala responses to threat-related face expressions are correlated with testosterone level (Derntl et al., 2009b).

In accordance with widespread belief, it is reported that the female brain is more responsive to social stimuli represented in still images (Proverbio et al., 2009). Recent ERP findings indicate that in females, processing of actions' goals occurs earlier (Proverbio et al., 2010). Neuroimaging reveals that gender effects are not evident in the neural circuitry underpinning visual processing of social interaction, but rather in the regions engaged in perceptual decision making: the neuromagnetic gamma response over the left prefrontal cortex peaks earlier in females (Pavlova et al., 2010a).

Gender effects at behavioral level do not necessarily imply that there is sex-related difference in brain activation subserving body language reading. Moreover, gender differences in performance on social cognition tasks can be impacted by socio-cultural stereotypes (Pavlova et al., 2010b). Several types of interrelations between behavioral measures and brain mechanisms engaged in social perception should be taken into account: (i) sex differences both in behavioral and brain responses; (ii) sex differences detectable either at behavioral level or only in brain activation; and (iii) absence of sex differences both at behavioral and brain levels (Pavlova, 2009). Noteworthy, gender-related dimorphism in the brain may not only elicit but also prevent behavioral differences if they are maladaptive (De Vries, 2004).

Future research should be directed at uncovering sex differences in brain activity during body language reading. Such investigation would also shed light on sex differences in neuropsychiatric conditions characterized by impairments in social cognition such as ASD, depression, and schizophrenia. It is known that males are

more commonly affected by ASD than females, with a ratio of about 4:1 (Newschaffer et al., 2007). Females, however, are affected much more severely, and, therefore, in high functioning autistic individuals this ratio is even much higher. Although there is some behavioral evidence that individuals with ASD have difficulties in revealing information about emotions from point-light body movements (Moore et al., 1997; Hubert et al., 2007; Parron et al., 2008), it is unclear whether females and males with ASD differ in body language reading. The lack of studies in females with ASD calls for a thorough investigation of their profile. The other important issue for future research is sex differences in visual social cognition in survivors of premature birth. Males are at a 14–20% higher risk of premature birth (Melamed et al., 2010) and of its complications in the brain and cognition. Adolescents who were born prematurely are likely to exhibit difficulties in visual social cognition (Pavlova et al., 2008), but gender effects are largely unknown. Clarification of gender impact on body language reading and underlying brain networks would provide novel insights into understanding of gender vulnerability to neuropsychiatric and neurodevelopmental impairments in visual social cognition.

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REFERENCES

- Adolphs, R. (2003). Cognitive neuroscience of human social behaviour. *Nat. Rev. Neurosci.* 4, 165–178.
- Atkinson, A. P., Dittrich, W. H., Gemmel, A. J., and Young, A. W. (2004). Emotion perception from dynamic and static body expressions in point-light and full-light displays. *Perception* 33, 717–746.
- Biele, C., and Grabowska, A. (2006). Sex differences in perception of emotion intensity in dynamic and static facial expressions. *Exp. Brain Res.* 171, 1–6.
- Blank, P. D., Rosenthal, R., Snodgrass, S. E., DePaulo, B. M., and Zuckerman, M. (1981). Sex differences in eavesdropping on non-verbal cues: developmental changes. *J. Pers. Soc. Psychol.* 41, 391–396.
- Bourne, V. J. (2005). Lateralised processing of positive facial emotion: sex differences in strength of hemispheric dominance. *Neuropsychologia* 43, 953–956.
- Cahill, L. (2006). Why sex matters for neuroscience? *Nat. Rev. Neurosci.* 7, 477–484.
- Chouchourelou, A., Toshihiko, M., Harber, K., and Shiffrar, M. (2006). The visual analysis of emotional actions. *Soc. Neurosci.* 1, 63–74.
- Clarke, T. J., Bradshaw, M. F., Field, D. T., Hampson, S. E., and Rose, D. (2005). The perception of emotion from body movement in point-light displays of interpersonal dialogue. *Perception* 34, 1171–1180.
- De Gelder, B. (2006). Towards the neurobiology of emotional body language. *Nat. Rev. Neurosci.* 7, 242–249.
- De Gelder, B. (2009). Why bodies? Twelve reasons for including bodily expressions in affective neuroscience. *Philos. Trans. R. Soc. Lond., B.* 364, 3475–3484.
- De Vries, G. J. (2004). Sex differences in adult and developing brains: compensation, compensation, compensation. *Endocrinology* 145, 1603–1608.
- Derntl, B., Habel, U., Windischberger, C., Robinson, S., Kryspin-Exner, I., Gur, R. C., and Moser, E. (2009a). General and specific responsiveness of the amygdala during explicit emotion recognition in females and males. *BMC Neurosci.* 10, 91. doi: 10.1186/1471-2202-10-91
- Derntl, B., Windischberger, C., Robinson, S., Kryspin-Exner, I., Gur, R. C., Moser, E., and Habel, U. (2009b). Amygdala activity to fear and anger in healthy young males is associated with testosterone. *Psychoneuroendocrinology* 34, 687–693.
- Dittrich, W. H., Troscianko, T., Lea, S. E., and Morgan, D. (1996). Perception of emotion from dynamic point-light displays represented in dance. *Perception* 25, 727–738.
- Farris, C., Treat, T. A., Vilken, R. J., and McFall, R. M. (2008). Perceptual mechanisms that characterize gender differences in decoding women's sexual intent. *Psychol. Sci.* 19, 348–354.
- Gasbarri, A., Arnone, B., Pompili, A., Pacitti, C., and Cahill, L. (2007). Sex-related hemispheric lateralization of electrical potentials evoked by arousing negative stimuli. *Brain Res.* 1138, 178–186.
- Golan, O., Baron-Cohen, S., and Hill, J. (2006). The Cambridge Mindreading (CAM) Face-Voice Battery: the complex emotion recognition in adults with and without Asperger syndrome. *J. Autism Dev. Dis.* 36, 169–183.
- Grèzes, J., Frith, C. D., and Passingham, R. E. (2004a). Brain mechanisms for inferring deceit in the actions of others. *J. Neurosci.* 24, 5500–5505.
- Grèzes, J., Frith, C. D., and Passingham, R. E. (2004b). Inferring false beliefs from the actions of oneself and others: an fMRI study. *Neuroimage* 21, 744–750.
- Grossman, E. D., and Blake, R. (2002). Brain areas active during visual perception of biological motion. *Neuron* 35, 1167–1175.
- Heberlein, A. S., Adolphs, R., Tranel, D., and Damasio, H. (2004). Cortical regions for judgments of emotions and personality from point-light walkers. *J. Cogn. Neurosci.* 16, 1143–1158.
- Hubert, B., Wicker, B., Moore, D. G., Monfardini, E., Duverger, H., Da Fonseca, D., and Deruelle, C. (2007). Brief report: recognition of emotional and non-emotional biological motion in individuals with autistic spectrum disorders. *J. Autism Dev. Dis.* 37, 1386–1392.
- Ikeda, H., and Watanabe, K. (2009). Anger and happiness are linked differently to the explicit detection of biological motion. *Perception* 38, 1002–1011.
- Jazin, E., and Cahill, L. (2010). Sex differences in molecular neuroscience:

- from fruit flies to humans. *Nat. Rev. Neurosci.* 11, 9–17.
- Killgore, W. D., and Yurgelun-Todd, D. A. (2001). Sex differences in amygdala activation during the perception of facial affect. *Neuroreport* 12, 2543–2547.
- Kret, M. E., Pichon, S., Grèzes, J., and de Gelder, B. (2010). Similarities and differences in perceiving threat from dynamic faces and bodies. An fMRI study. *Neuroimage* 54, 1755–1762.
- Meeren, H. K., van Heijnsbergen, C. C., and de Gelder, B. (2005). Rapid perceptual integration of facial expression and emotional body language. *Proc. Natl. Acad. Sci. U.S.A.* 102, 16518–16523.
- Melamed, N., Yogeve, Y., and Glezerman, M. (2010). Fetal gender and pregnancy outcome. *J. Matern. Fetal. Neonatal. Med.* 23, 338–344.
- Montagne, B., Kessels, R. P., Frigerio, E., de Haan, E. H., and Perrett, D. I. (2005). Sex differences in perception of affective facial expressions: do men really lack emotional sensitivity? *Cogn. Process.* 6, 136–141.
- Moore, D. G., Hobson, R. P., and Lee, A. (1997). Components of person perception: an investigation with autistic, non-autistic retarded and typically developing children and adolescents. *Br. J. Dev. Psychol.* 15, 401–423.
- Newschaffer, C. J., Croen, L. A., Daniels, J., Giarelli, E., Grether, J. K., Levy, S. E., Mandell, D. S., Miller, L. A., Pinto-Martin, J., Reaven, J., Reynolds, A. M., Rice, C. E., Schendel, D., and Windham, G. C. (2007). The epidemiology of autism spectrum disorders. *Annu. Rev. Publ. Health* 28, 235–258.
- Orozco, S., and Ehlers, C. L. (1998). Gender differences in electrophysiological responses to facial stimuli. *Biol. Psychiatry* 44, 281–289.
- Parron, C., Da Fonseca, D., Santos, A., Moore, D. G., Monfardini, E., and Deruelle, C. (2008). Recognition of biological motion in children with autistic spectrum disorders. *Autism* 12, 2161–2174.
- Pavlova, M. (2009). Perception and understanding of intentions and actions: does gender matter? *Neurosci. Lett.* 499, 133–136.
- Pavlova, M., Guerreschi, M., Lutzenberger, W., Sokolov, A. N., and Krägeloh-Mann, I. (2010a). Cortical response to social interaction is affected by gender. *Neuroimage* 50, 1327–1332.
- Pavlova, M., Wecker, M., Krombholz, K., and Sokolov, A. A. (2010b). Perception of intentions and actions: gender stereotype susceptibility. *Brain Res.* 1311, 81–85.
- Pavlova, M., Lutzenberger, W., Sokolov, A., and Birbaumer, N. (2004). Dissociable cortical processing of recognizable and non-recognizable biological movement: analyzing gamma MEG activity. *Cereb. Cortex* 14, 181–188.
- Pavlova, M., Sokolov, A. N., Birbaumer, N., and Krägeloh-Mann, I. (2008). Perception and understanding of others' actions and brain connectivity. *J. Cogn. Neurosci.* 20, 494–504.
- Pelphrey, K. A., Morris, J. P., and McCarthy, G. (2004). Grasping the intentions of others: the perceived intentionality of an action influences activity in the superior temporal sulcus during social perception. *J. Cogn. Neurosci.* 16, 1706–1716.
- Pollick, F. E., Lestou, V., Ryu, J., and Cho, S. B. (2002). Estimating the efficiency of recognizing gender and affect from biological motion. *Vision Res.* 42, 2345–2355.
- Pollick, F. E., Paterson, H. M., Bruderlin, A., and Sanford, A. J. (2001). Perceiving affect from arm movement. *Cognition* 82, B51–B61.
- Proverbio, A. M., Riva, F., Martin, E., and Zani, A. (2010). Face coding is bilateral in the female brain. *PLoS One* 5, e11242. doi: 10.1371/journal.pone.0011242
- Proverbio, A. M., Riva, F., and Zani, A. (2009). Observation of static pictures of dynamic actions enhances the activity of movement-related brain areas. *PLoS One* 4, e5389. doi: 10.1371/journal.pone.0005389
- Proverbio, A. M., Riva, F., and Zani, A. (2010). When neurons do not mirror the agent's intentions: sex differences in neural coding of goal-directed actions. *Neuropsychologia* 48, 1454–1463.
- Proverbio, A. M., Zani, A., and Adorni, R. (2008). Neural markers of a greater female responsiveness to social stimuli. *BMC Neurosci.* 9, 56. doi: 10.1186/1471-2202-9-56
- Rose, D., and Clarke, T. J. (2009). Look who's talking: visual detection of speech from whole-body biological motion cues during emotive interpersonal conversation. *Perception* 38, 153–156.
- Runeson, S., and Frykholm, G. (1983). Kinematic specification of dynamics as information basis for the person-and-action perception: expectation, gender recognition, and deceptive intention. *J. Exp. Psychol.* 112, 585–615.
- Sabattinelli, D., Flaisch, T., Bradley, M. M., Fitzsimmons, J. R., and Lang, P. J. (2004). Affective picture perception: gender differences in visual cortex? *NeuroReport* 15, 1109–112.
- Sokolov, A. A., Gharabaghi, A., Tatagiba, M., and Pavlova, M. (2010). Cerebellar engagement in an action observation network. *Cereb. Cortex* 20, 486–491.
- Tamietto, M., and de Gelder, B. (2010). Neural bases of the non-conscious perception of emotional signals. *Nat. Rev. Neurosci.* 11, 697–709.
- Wrase, J., Klein, S., Gruesser, D. M., Hermann, D., Flor, H., Mann, K., Braus, D. F., and Heinz, A. (2003). Gender differences in the processing of standardized emotional visual stimuli in humans: a functional magnetic resonance imaging study. *Neurosci. Lett.* 348, 41–45.

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3. Emotion through locomotion: gender impact

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Emotion through Locomotion: Gender Impact

Samuel Krüger¹, Alexander N. Sokolov^{2,3}, Paul Enck², Ingeborg Krägeloh-Mann^{1,4}, Marina A. Pavlova^{1,5*}

1 Department of Pediatric Neurology and Developmental Medicine, Children's Hospital, Medical School, Eberhard Karls University of Tübingen, Tübingen, Germany, **2** Department of Psychosomatic Medicine and Psychotherapy, Medical School, Eberhard Karls University of Tübingen, Tübingen, Germany, **3** Center for Pediatric Clinical Studies, Children's Hospital, Medical School, Eberhard Karls University of Tübingen, Tübingen, Germany, **4** Werner Reichardt Center for Integrative Neuroscience, Eberhard Karls University of Tübingen, Tübingen, Germany, **5** Institute for Women's Health Baden-Württemberg, Eberhard Karls University of Tübingen, Tübingen, Germany

Abstract

Body language reading is of significance for daily life social cognition and successful social interaction, and constitutes a core component of social competence. Yet it is unclear whether our ability for body language reading is gender specific. In the present work, female and male observers had to visually recognize emotions through point-light human locomotion performed by female and male actors with different emotional expressions. For subtle emotional expressions only, males surpass females in recognition accuracy and readiness to respond to happy walking portrayed by female actors, whereas females exhibit a tendency to be better in recognition of hostile angry locomotion expressed by male actors. In contrast to widespread beliefs about female superiority in social cognition, the findings suggest that gender effects in recognition of emotions from human locomotion are modulated by emotional content of actions and opposite actor gender. In a nutshell, the study makes a further step in elucidation of gender impact on body language reading and on neurodevelopmental and psychiatric deficits in visual social cognition.

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* E-mail: marina.pavlova@uni-tuebingen.de

Introduction

Every single day we are watching strangers passing by. We automatically determine not only speed, trajectory, and direction of their locomotion in order to avoid collisions and safely get through a crowd, but also spontaneously judge mood, intentions, dispositions and personality traits of walkers, which may be useful for a potential social interaction. Adult perceivers discern emotions and dispositions of others conveyed by point-light displays that reduce other kinds of information except for body motion [1–7]. Yet this ability seems to require a period of maturation during childhood [7]. In one of the initial studies in the field [8], youthful point-light gaits were reported to appear as more powerful and happier. Later a few attempts had been made to identify body motion parameters that are associated with the perceived social and personality traits [9–12]. Visual sensitivity to camouflaged point-light locomotion is modulated by the emotional content of gait with the highest sensitivity to angry locomotion [13], and the ability to recognize anger in displays portraying masked human locomotion is related to gait detection [14]. Moreover, in agreement with the assumption that biological motion processing serves a hallmark of social cognition [15], in typically developing adults and individuals with autistic disorders, the ability to reveal emotions from point-light body motion may be related to more basic capability for discrimination between canonical and scrambled biological motion [16,17].

Emotional gender stereotyping appears to affect decoding of biological motion displays. Point-light displays depicting angry throwing a ball are often judged to be performed by men, whereas displays depicting sad throwing are referred to portray women [18]. Yet it is unclear whether the ability for veridical body language reading is impacted by gender. According to popular beliefs about female superiority in social cognition, there are some indications for sex impact on biological motion processing in non-human primates, common marmosets (*Callithrix jacchus*): females only exhibit curiosity to point-light biological motion displays [19]. Newly hatched female chicks are reported to exhibit a stronger preference for point-light biological motion of a walking hen (even over a walking cat) than their male peers [20]. This preference presumably reflects stronger affiliate tendencies in females. Gender congruency between perceivers and actors affects visual priming of camouflaged point-light locomotion [21], whereas alterations in biological motion processing with age appears to be unaffected by observers' gender [22]. Functional magnetic resonance imaging, fMRI, reveals enhanced brain activation during point-light biological motion processing in adult females as compared to males over the regions involved in social cognition (such as the temporal pole and amygdala) [23]. These sex differences are reported to be less pronounced in school-age youth.

Females excel in body language reading through expressive full-light (neck to knees or ankles) body motion video clips [24]. The first study on reading of point-light body language made use of displays representing knocking at a door with different emotional

expressions [25]. In a three-alternative-forced choice paradigm, healthy female and male adults indicated whether a display portrayed happy, neutral, or angry knocking. The outcome shows that gender effects are modulated by emotional content of actions: Males excel in recognition accuracy of happy actions, whereas females tend to excel in recognition of hostile angry knocking and are substantially better in recognition of neutral knocking. Another study shows that females are more accurate in recognition of point-light activities (walking, jumping on the spot, kicking a ball, drinking from a bottle, and wiping the table), and tend to be faster in differentiation of canonical point-light biological motion from scrambled displays [16]. Most important, females are reported to surpass in some aspects of body language reading: they are faster in making judgments on whether point-light displays are happier, sadder, angrier, or not different from an emotionally neutral prime portraying the same activity, in other words, in discrimination of emotional from neutral body motion. The lack of gender impact on emotion discrimination accuracy may have been at least partly explained by a rather high performance level in both females and males. It appears plausible that gender effects are more evident in recognition of subtle rather than explicit, full-blown or exaggerated emotional expressions. For example, gender effects are reported to be more pronounced in recognition of facial emotional expressions of lower intensity [26] or in briefly exposed displays [27].

The present work intends to make a further step in clarification of whether gender affects body language reading by studying recognition of emotional human locomotion. More specifically, we ask (i) whether gender of observers affects recognition of emotions represented by human gaits; (ii) whether gender effects depend on emotional content of gait; and (iii) whether gender effects in recognition of human locomotion are impacted by actor gender. With this purpose in mind, healthy female and male adult observers were presented with point-light displays portraying human locomotion with different emotional expressions. We used a point-light methodology that helps to isolate information revealed by motion from other cues (shape, color, etc.). Perceivers saw only a few bright dots placed on the main joints of an invisible actor (Figure 1), so that all other clues except for motion characteristics were eliminated.

Materials and Methods

Participants

Fifty three adults, students of the University of Tübingen were enrolled in the study. Age of females (27 participants) was 23.15 ± 1.1 years (median; 95% confidence interval), and of males

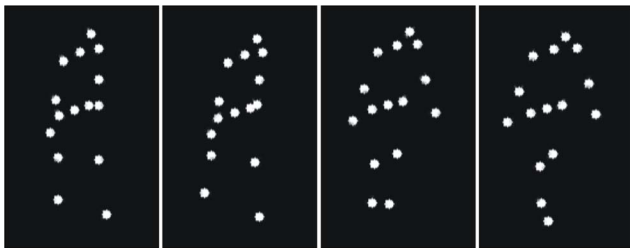


Figure 1. Illustration of stimuli. Four static images illustrating angry human walking as a set of dots placed on the main joints and head of an invisible actor body. Each display consists of 15 white dots presented against a black background. During locomotion, a walker was seen facing right in intermediate position (45°) between the frontal and sagittal view.

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(26 participants) was 24 ± 1.33 years. There was no age difference between female and male participants (Mann-Whitney test, $U = 407.5$, $p = 0.32$). All observers had normal or corrected-to-normal vision. None had head injuries or medication for anxiety or depression, and a history of neurological or psychiatric disorders including autistic spectrum disorders and schizophrenia. They were run individually. None had previous experience with such displays and tasks. The study was conducted in line with the Declaration of Helsinki and was approved by the local Ethics Committee at the University of Tübingen Medical School. Informed written consent was obtained from all participants. Participation was voluntary, and the data were processed anonymously.

Stimuli and procedure

Participants were presented with point-light displays portraying human locomotion. Display creation is described in detail elsewhere [28]. The displays were built up by using the Motion Capture Library. In brief, recording was performed using a 3D position measurement system at a rate of 60 Hz (Optotrak, Northern Digital Inc., Waterloo, ON, Canada). The matrix data for each frame was processed with MATLAB (The Mathworks Inc., Natick, MA, USA) into a video sequence. Each display consisted of 15 white dots visible against a black background (Figure 1). The dots were placed on the shoulder, elbow, and wrist of each arm; on the hip, knee and ankle of each leg; and on the head, neck, and pelvis of a human body. Each video consisted of 101 frames, and was presented at a rate of 60 frames per second. Each gait cycle was accomplished in 67 frames. As we supposed more pronounced gender effects would occur in recognition of subtle emotional expressions, we used brief stimulus duration. Each movie lasted for 1.68 s that corresponded to 1.5 walking cycle. During locomotion, a walker was seen facing right in intermediate position of 45° between the frontal and sagittal view. We used this intermediate trajectory of locomotion, because the sagittal view is often considered neutral in respect to possible social interactions, and the frontal view is reported to elicit ambiguous (facing backward or toward an observer) and often gender-dependent impressions of locomotion direction [29–32]. The walking figure was pelvis fixed to the middle of the screen.

Four females and four males served as actors. They were asked to walk with different emotional expressions (happy, angry, or neutral). All sets of stimuli were created from the same actors for avoiding variability in emotion portrayal. We chose to use animations with neutral, happy and angry motion primarily to enable comparison of the findings with the previous study on body language reading with a point-light knocking motion [25]. By using the Presentation software (Neurobehavioral Systems Inc., Albany, CA, USA), each video was displayed four times per experimental session resulting in 32 trials per emotion. The whole experimental session consisted of a set of 96 displays that were presented in a random order. A white fixation cross was displayed in the center of the screen for 3.32 s of inter-stimulus interval. Each session took about 10–15 min per participant. We used a three-alternative-forced choice paradigm. On each trial, participants indicated (by pressing one of three respective keys) whether the display portrayed happy, neutral or angry locomotion. No immediate feedback was given regarding performance.

Results

Individual rates of correct responses (proportion correct) were submitted to a $2 \times 3 \times 2$ repeated-measures analysis of variance, ANOVA (as assessed by the Shapiro-Wilk test, the data were

normally distributed) with factors Gender of observers (female/male), Emotional expression (happy/neutral/angry), and Gender of actors (female/male). The outcome revealed that main effects of Gender of observers ($F(1,51)=0.01$, ns) and Gender of actors ($F(1,51)=0.13$, ns.) were non-significant, whereas a main effect of Emotional expression ($F(2,102)=60.28$, $p<0.0001$) and interaction between the factors Emotional expression \times Gender of actors ($F(2,102)=3.43$, $p<0.036$) were significant. Post hoc analysis of simple effects revealed, however, that anger was not better recognized from displays portraying male as compared to female actors, and happiness from displays portraying female as compared to male actors. No difference was found in recognizability of neutral locomotion from movies portraying female and male actors. All other interactions were non-significant (Gender of observers \times Emotional expression ($F(2,102)=1.18$), Gender of observers \times Gender of actors ($F(1,51)=1.13$), Gender of observers \times Emotional expression \times Gender of actors ($F(2,102)=0.77$)).

As we expected more distinct gender impact on recognition of subtle emotional expressions (see Introduction), we set 41% cut-off (determined as a mean value of display recognizability) for recognition of emotions through human locomotion, and focused on analysis of the displays that were recognized below this level. No gender effects were found in recognition accuracy of displays that were recognized above the cut-off. All neutral displays were recognized above the cut-off, and, therefore, our analysis was limited to displays depicting angry and happy locomotion. Proportion of correct responses in emotion recognition is represented in Figure 2A. As can be seen, males surpass females in recognition of happy walking portrayed by female actors ($U=475.1$, $p<0.016$), whereas females exhibit a tendency to be better in recognition of angry locomotion expressed by male actors ($t(51)=1.68$, $p<0.098$). The data, therefore, reveal a lack of overall advantage of females in recognition of emotion through human locomotion.

To ensure that gender effects in emotion recognition were not due to gender-related bias for mistaking one emotion for another, we performed an error analysis. As seen in Figure 2B, in both females and males, happy locomotion expressed by female actors was primarily mistaken for neutral locomotion (mean error rate \pm standard deviation, 0.6 ± 0.04 and 0.6 ± 0.05 for females and males, respectively; gender difference: $t(51)=0.03$, $p=0.97$). When happy locomotion expressed by female actors was misperceived as angry locomotion, a lack of gender differences was also found (0.4 ± 0.04 and 0.4 ± 0.05 for females and males, respectively; $t(51)=0.03$, $p=0.97$). In turn, when angry locomotion portrayed by male actors was erroneously recognized, both females and males primarily mistook it for neutral locomotion without gender differences (0.59 ± 0.04 and 0.54 ± 0.04 for females and males, respectively; $t(51)=0.97$, $p=0.34$). When angry locomotion performed by male actors was misperceived for happy gait, no gender differences were found in error rate (0.41 ± 0.04 and 0.46 ± 0.04 for females and males, respectively; $t(51)=0.97$, $p=0.34$). The lack of gender differences in error rates suggests that gender effects in recognition accuracy of emotions through locomotion found in the present study are not due to gender-related bias for mistaking one emotion for another.

For response time analysis, a $2\times2\times2$ repeated-measures ANOVA was performed on individual values (as assessed by the Shapiro-Wilk test, the data were normally distributed) with factors Gender of observers (female/male), Emotional expression (happy/angry), and Gender of actors (female/male). This analysis reveals a main effect of Emotional expression ($F(1,51)=182.39$, $p<0.0001$). This outcome indicates that for both females and males, swiftness of response to emotional locomotion depends on its emotional

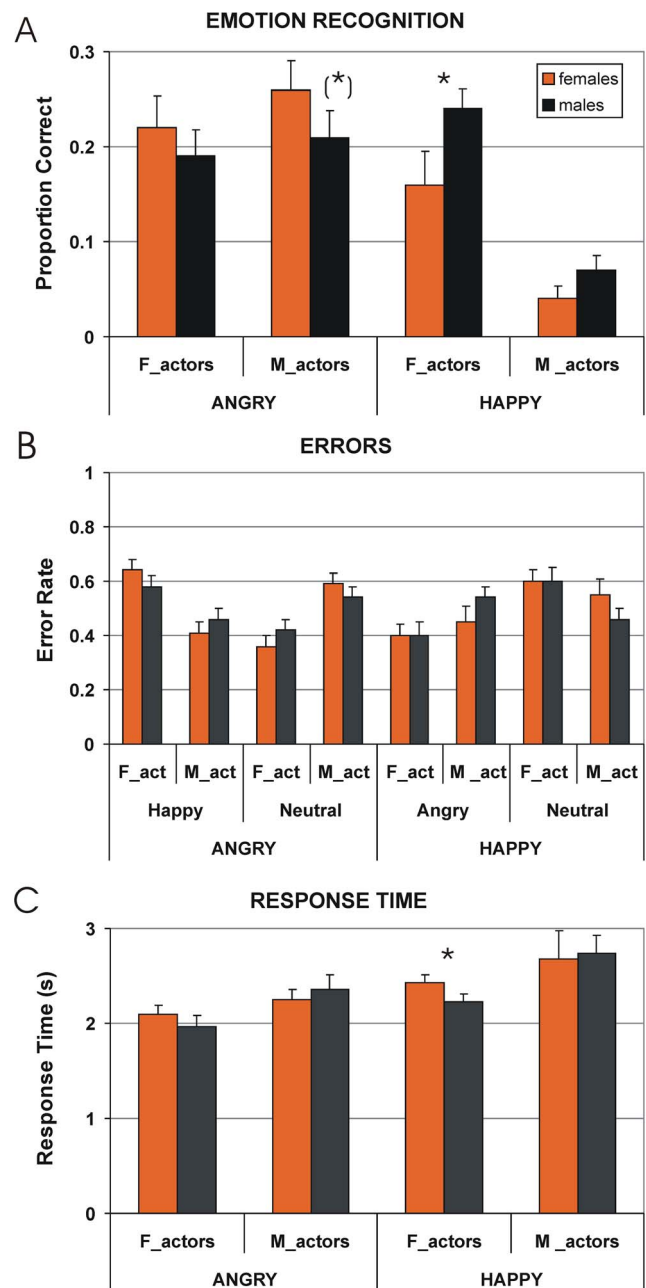


Figure 2. Recognition of subtle expressions of angry and happy point-light locomotion. **A)** Proportion correct: Males overperform females in recognition accuracy of happy walking portrayed by female actors, whereas females exhibit a tendency to be better in recognition of angry locomotion expressed by male actors. **B)** Error rate: The lack of gender differences in error rate indicates that gender differences are not caused by gender-related bias for mistaking one emotion for another. **C)** Response time: Males are faster than females in responding to happy walking portrayed by female actors. Asterisks indicate significant gender differences, whereas asterisks in brackets indicate a tendency. Vertical bars represent \pm SE. doi:10.1371/journal.pone.0081716.g002

content. As further seen from Figure 2C, the fastest response was given to angry locomotion represented by female actors, and the slowest response to happy locomotion represented by male actors. This suggests that for both female and male participants, displays representing subtle expression of a happy man were most difficult

to recognize, whereas recognition of subtle anger expressed by female actors was the easiest. A main effect of Gender of actor was significant ($F(1,51) = 109.09$, $p < 0.001$). On overall, emotions portrayed by female actors were more readily recognizable than emotions expressed by male walkers. Males were not only better in recognition of happy walking portrayed by female actors, but also faster in responses to these displays than females (Figure 2C; $t(51) = 2.42$, $p < 0.019$).

Discussion

The outcome of the present study suggests that gender impacts recognition of subtle emotions from human locomotion only, and this occurs in a complex way. The gender effects in recognition of subtle emotions are modulated by the emotional content of locomotion and opposite actor gender: Males surpass females in recognition accuracy and readiness to respond to subtle expressions of happiness performed by female actors, whereas females exhibit a tendency to be better in recognition of angry locomotion expressed by male actors. The lack of gender differences in error rates indicates that gender effects in recognition accuracy are not caused by gender-related bias for mistaking one emotional expression for another. The findings agree with previous evidence on gender effects in recognition of emotions from point-light displays portraying knocking: Male observers over-perform in recognition of happy knocking, whereas females tend to better recognize hostile angry motion [25]. This earlier study however, did not address the issue of whether gender effects are associated with gender of actors. The present work suggests that gender effects in body language reading can be modulated not only by emotional content of body motion, but also by (opposite) actor gender.

The present data appears to challenge the recent theoretical reasoning suggesting that production of actions may be intimately linked with understanding of intentions and actions of others [33,34]. From the mirror neuron system point of view, one would expect that observers would over-perform in recognition of emotions expressed by actors of the same gender (i.e., females would be better in recognition of emotions expressed by female actors, and males in recognition of emotions expressed by male actors), because they have common or more similar motor programs engaged in emotional expressions, and therefore can understand emotional locomotion of others “from the inside” [33, p.264]. Actually, such common motor programs may facilitate biological motion perception; gender congruency between an observer and a runner during the visual priming improves detection of direction of a point-light runner embedded into a complex simultaneous dynamical mask [21]. Motor expertise may enhance perception of point-light biological motion displays portraying dance [35]: female dance experts are better in similarity discrimination of point-light dance elements expressed by female actors (when observers and performers share not only visual experience, but also common motor program for dance performance) than male experts (when observers and performers share enriched visual experience only). Acquired motor skills in dance performance also specifically affect brain activity during action observation [36,37]. However, facilitation effect of gender congruency was not observed in the present study dealing with some aspects of social cognition.

Although social cognition is presumably associated with active interactions and immediate reactions, and, therefore, body language reading is likely associated with motor programs, we did not observe facilitation effects of gender congruency in recognition of subtle emotions from locomotion. Our findings

rather agree with assumptions based on the evolutionary or ecological accounts that imply gender-specific socio-cultural differences. Indeed, higher sensitivity of male observers even to subtle happiness expressed by female walkers might suggest perceptual significance of positive emotions in potential partner selection [38]. In addition, a considerable amount of research has documented that both female and male observers are especially tuned to anger expressions depicted in different kinds of point-light biological motion [1,3,13,14,25] and in faces and full-body displays [39], presumably because perceiving anger is of particular relevance for one’s own well-being and helps to avoid critical situations. Bearing in mind that from the evolutionary and socio-cultural points of view, female roles are often associated with offspring care providing, it appears that women might be not only more sensitive to anger expressions in body language, but also exhibit higher sensitivity than males even to subtle clues of anger expressed by males because they may signal potential danger. Future research should confirm whether gender effects in body language reading persist with other repertoires of body movements, and with other arrays of emotions.

At first glance, the outcome of the present study appears to contradict the findings reported by Alaerts and colleagues [16] about female superiority in some aspects of body language reading in point-light displays: although females do not differ from male observers in accuracy, they tend to be faster in discrimination of emotional (happy, angry, sad or neutral) point-light body motion from neutral displays. This apparent discrepancy may be explained by methodological differences in the tasks (discrimination vs. forced choice paradigm), movies duration, and variety of portrayed point-light actions.

Future research should be directed at uncovering sex differences in brain activity during body language reading. First of all, it is unclear whether the neural circuits underlying body language reading are sex specific. The existing findings on sex differences in the social brain are either limited to investigation of static and dynamic faces (for recent review, see [40]) or extremely sparse. In males, greater fMRI brain activation over the extrastriate body area, superior temporal sulcus, fusiform gyrus, pre-supplementary motor area, and premotor cortex (with a lack of behavioral differences) is reported for a full-body male threatening versus neutral displays [41]. 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 [42,43]. Yet sex differences are not manifested in the neural circuitry underpinning visual processing of social interaction in Heider-and-Simmel-like animations. Gender impact is evident only in the regions engaged in perceptual decision making: the magnetoencephalographic (MEG) oscillatory induced gamma response over the left prefrontal cortex boosts later in males [43]. Furthermore, the time delay in peak MEG activation in males corresponds to longer response time to the Heider-and-Simmel animations as compared with control stimuli [43].

Growing neuroimaging evidence points to sexual dimorphism of the brain [44–46], also in the white matter underlying brain connectivity between different areas [47,48]. Investigation of sex differences in body language reading would help to clarify 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 prevalence and clinical picture. Males have a higher risk for developing autistic spectrum disorders than females, with a sex ratio of about 4:1 [49]. Neuroanatomy of autism is

reported to differ between females and males [50]. For Down syndrome, the reported sex ratio is 1.28 [51], and for fragile X syndrome, the ratio is 2 [52]. Males are at a 14–20% higher risk for premature birth [53] and of its complications in the brain development and cognition [54]. On the other hand, depression is approximately twice as common in females as in males [55]. Females are more often affected by anxiety disorders with a ratio of 2:1 or even 3:1, and gender differences occur already in childhood increasing with age [56,57]. Although in most of these disorders some aspects of biological motion processing and body language reading are reported to be impaired [58–62], gender impact on these impairments is largely unknown. Clarification of gender effects in body language reading and underlying brain networks would provide novel insights into understanding of

gender vulnerability to psychiatric and neurodevelopmental deficits in social cognition [15].

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Author Contributions

Conceived and designed the experiments: MAP SK. Performed the experiments: SK. Analyzed the data: SK ANS MAP. Contributed reagents/materials/analysis tools: MAP, ANS, IKM, PE. Wrote the paper: SK ANS MAP.

References

- Atkinson AP, Dittrich WH, Gemmel AJ, Young AW (2004) Emotion perception from dynamic and static body expressions in point-light and full-light displays. *Perception* 33: 717–746.
- Clarke TJ, Bradshaw MF, Field DT, Hampson SE, Rose D (2005) The perception of emotion from body movement in point-light displays of interpersonal dialogue. *Perception* 34: 1171–1180.
- Dittrich WH, Troscianko T, Lea SE, Morgan D (1996) Perception of emotion from dynamic point-light displays represented in dance. *Perception* 25: 727–738.
- Heberlein AS, Adolphs R, Tranel D, Damasio H (2004) Cortical regions for judgments of emotions and personality from point-light walkers. *J Cogn Neurosci* 16: 1143–1158.
- Rose D, Clarke TJ (2009) Look who's talking: Visual detection of speech from whole-body biological motion cues during emotive interpersonal conversation. *Perception* 38: 153–156.
- Walk RD, Homan CP (1984) Emotion and dance in dynamic light displays. *Bull Psychon Soc* 22: 437–440.
- Ross PD, Polson L, Grosbras M-H (2012) Developmental changes in emotion recognition from full-light and point-light displays of body movement. *PLoS ONE* 7: e44815.
- Montepare JM, Zebrowitz-McArthur L (1988) Impressions of people created by age-related qualities of their gaits. *J Pers Soc Psychol* 55: 547–556.
- Pollick FE, Lestou V, Ryu J, Cho SB (2002) Estimating the efficiency of recognizing gender and affect from biological motion. *Vision Res* 42: 2345–2355.
- Pollick FE, Paterson HM, Bruderlin A, Sanford AJ (2001) Perceiving affect from arm movement. *Cognition* 82: B51–61.
- Roether CL, Omlor L, Christensen A, Giese MA (2009) Critical features for the perception of emotion from gait. *J Vis* 9: 15.1–32.
- Thoresen JC, Vuong QC, Atkinson AP (2012) First impressions: gait cues drive reliable trait judgements. *Cognition* 124: 261–271.
- Chouchourelou A, Toshihiko M, Harber K, Shiffrar M (2006) The visual analysis of emotional actions. *Soc Neurosci* 1: 63–74.
- Ikeda H, Watanabe K (2009) Anger and happiness are linked differently to the explicit detection of biological motion. *Perception* 38: 1002–1011.
- Pavlova MA (2012) Biological motion processing as a hallmark of social cognition. *Cereb Cortex* 22: 981–995.
- Alaerts K, Nackaerts E, Meyns P, Swinnen SP, Wenderoth N (2011) Action and emotion recognition from point light displays: an investigation of gender differences. *PLoS One* 6: e20989.
- Nackaerts E, Wagemans J, Helsen W, Swinnen SP, Wenderoth N, et al. (2012) Recognizing biological motion and emotions from point-light displays in autism spectrum disorders. *PLoS One* 7: e44473.
- Johnson KL, McKay LS, Pollick FE (2011) He throws like a girl (but only when he's sad): emotion affects sex-decoding of biological motion displays. *Cognition* 119: 265–280.
- Brown J, Kaplan G, Rogers IJ, Vallortigara G (2010) Perception of biological motion in common marmosets (*Callithrix jacchus*): by females only. *Anim Cogn* 13: 555–564.
- Miura M, Matsushima T (2012) Preference for biological motion in domestic chicks: sex-dependent effect of early visual experience. *Anim Cogn* 15: 871–879.
- Bidet-Ildi C, Chauvin A, Coello Y (2010) Observing or producing a motor action improves later perception of biological motion: evidence for a gender effect. *Acta Psychol (Amst)* 134: 215–224.
- Billino J, Bremmer F, Gegenfurtner KR (2008) Differential aging of motion processing mechanisms: evidence against general perceptual decline. *Vision Res* 48: 1254–1261.
- Anderson LC, Bolling DZ, Schelinski S, Coffman MC, Pelphrey KA, et al. (2013) Sex differences in the development of brain mechanisms for processing biological motion. *NeuroImage* 83C: 751–760.
- Blanck PD, Rosenthal R, Snodgrass SE, DePaulo BM, Zuckerman M (1981) Sex differences in eavesdropping on non-verbal cues: developmental changes. *J Pers Soc Psychol* 41: 391–396.
- Sokolov AA, Krüger S, Enck P, Krägeloh-Mann I, Pavlova MA (2011) Gender affects body language reading. *Front Psychol* 2: 16.
- Hoffmann H, Kessler H, Eppel T, Rukavina S, Traue HC (2010) Expression intensity, gender and facial emotion recognition: Women recognize only subtle facial emotions better than men. *Acta Psychol (Amst)* 135: 278–283.
- Hall JA, Matsumoto D (2004) Gender differences in judgments of multiple emotions from facial expressions. *Emotion* 4: 201–206.
- Ma Y, Paterson HM, Pollick FE (2006) A motion capture library for the study of identity, gender, and emotion perception from biological motion. *Behav Res Methods* 38: 134–141.
- Brooks A, Schouten B, Troje NF, Verfaillie K, Blanke O, et al. (2008) Correlated changes in perceptions of the gender and orientation of ambiguous biological motion figures. *Curr Biol* 18: R728–R729.
- Schouten B, Troje NF, Brooks A, van der Zwan R, Verfaillie K (2010) The facing bias in biological motion perception: effects of stimulus gender and observer sex. *Atten Percept Psychophys* 72: 1256–1260.
- Schouten B, Troje NF, Verfaillie K (2011) The facing bias in biological motion perception: structure, kinematics, and body parts. *Atten Percept Psychophys* 73: 130–143.
- Pollick FE, Kay JW, Heim K, Stringer R (2005) Gender recognition from point-light walkers. *J Exp Psychol Hum Percept Perform* 31: 1247–1265.
- Rizzolatti G, Sinigaglia C (2010) The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nat Rev Neurosci* 11: 264–274.
- Sinigaglia C, Rizzolatti G (2011) Through the looking glass: self and others. *Conscious Cogn* 20: 64–74.
- Calvo-Merino B, Ehrenberg S, Leung D, Haggard P (2010) Experts see it all: configural effects in action observation. *Psychol Res* 74: 400–406.
- Calvo-Merino B, Glaser DE, Grèzes J, Passingham RE, Haggard P (2005) Action observation and acquired motor skills: an fMRI study with expert dancers. *Cereb Cortex* 15: 1243–1249.
- Calvo-Merino B, Grèzes J, Glaser DE, Passingham RE, Haggard P (2006) Seeing or doing? Influence of visual and motor familiarity in action observation. *Curr Biol* 16: 1905–1910.
- Hugill N, Fink B, Neave N (2010) The role of human body movements in mate selection. *Evol Psychol* 8: 66–89.
- Kret ME, Stekelenburg JJ, Roelofs K, de Gelder B (2013) Perception of face and body expressions using electromyography, pupillometry and gaze measures. *Front Psychol* 4: 28.
- Kret ME, De Gelder B (2012) A review on sex differences in processing emotional signals. *Neuropsychologia* 50: 1211–1221.
- Kret ME, Pichon S, Grèzes J, de Gelder B (2011) Men fear other men most: gender specific brain activations in perceiving threat from dynamic faces and bodies - an fMRI study. *Front Psychol* 2: 3.
- Gobbini MI, Koralek AC, Bryan RE, Montgomery KJ, Haxby JV (2007) Two takes on the social brain: a comparison of theory of mind tasks. *J Cogn Neurosci* 19: 1803–1814.
- Pavlova M, Guerreschi M, Lutzenberger W, Sokolov AN, Krägeloh-Mann I (2010) Cortical response to social interaction is affected by gender. *NeuroImage* 50: 1327–1332.
- Cahill L (2006) Why sex matters for neuroscience. *Nat Rev Neurosci* 7: 477–484.
- Brain Development Cooperative Group (2012) Total and regional brain volumes in a population-based normative sample from 4 to 18 years: the NIH MRI study of normal brain development. *Cereb Cortex* 1: 1–12.
- McCarthy MM, Arnold AP, Ball GF, Blaustein JD, De Vries GJ (2012) Sex differences in the brain: the not so inconvenient truth. *J Neurosci* 32: 2241–2247.
- Menzler K, Belke M, Wehrmann E, Krakow K, Lengler U, et al. (2011) Men and women are different: diffusion tensor imaging reveals sexual dimorphism in the microstructure of the thalamus, corpus callosum and cingulum. *NeuroImage* 54: 2557–2562.

48. Chou KH, Cheng Y, Chen IY, Lin CP, Chu WC (2011) Sex-linked white matter microstructure of the social and analytic brain. *NeuroImage* 54: 725–733.
49. Newschaffer CJ, Croen LA, Daniels J, Giarelli E, Grether JK, et al. (2007) The epidemiology of autism spectrum disorders. *Ann Rev Publ Health* 28: 235–258.
50. Lai MC, Lombardo MV, Suckling J, Ruigrok AN, Chakrabarti B, et al. (2013) Biological sex affects the neurobiology of autism. *Brain* 136: 2799–2815.
51. Bishop J, Huether CA, Torfs C, Lorey F, Deddens J (1997) Epidemiologic study of Down syndrome in a racially diverse California population, 1989–1991. *Am J Epidemiol* 145: 134–147.
52. Crawford DC, Acuña JM, Sherman SL (2001) FMR1 and the fragile X syndrome: human genome epidemiology review. *Genet Med* 3: 359–371.
53. Melamed N, Yogeve Y, Glezerman M (2010) Fetal gender and pregnancy outcome. *J Matern Fetal Neonatal Med* 23: 338–344.
54. Pavlova MA, Krägeloh-Mann I (2013) Limitations on the developing preterm brain: Impact of periventricular white matter lesions on brain connectivity and cognition. *Brain* 136: 998–1011.
55. Difflorio A, Jones I (2010) Is sex important? Gender differences in bipolar disorder. *Int Rev Psych* 22: 437–452.
56. Craske MG (2003) *Origins of phobias and anxiety disorders: Why more women than men?* Amsterdam (Netherlands): Elsevier.
57. Beesdo-Baum K, Knappe S (2012) Developmental epidemiology of anxiety disorders. *Child Adolesc Psychiatr Clin N Am* 21: 457–478.
58. Kim J, Blake R, Park S, Shin YW, Kang DH, et al. (2008) Selective impairment in visual perception of biological motion in obsessive-compulsive disorder. *Depress Anxiety* 25: E15–25.
59. Klin A, Lin DJ, Gorrindo P, Ramsay G, Jones W (2009) Two-year-olds with autism orient to non-social contingencies rather than biological motion. *Nature* 459: 257–261.
60. Pavlova M, Sokolov A, Birbaumer N, Krägeloh-Mann I (2006) Biological motion processing in adolescents with early periventricular brain damage. *Neuropsychologia* 44: 586–593.
61. Taylor NM, Jakobson LS, Maurer D, Lewis TL (2009) Differential vulnerability of global motion, global form, and biological motion processing in full-term and preterm children. *Neuropsychologia* 47: 2766–2778.
62. Virji-Babul N, Kerns K, Zhou E, Kapur A, Shiffar M (2006) Perceptual-motor deficits in children with Down syndrome: implications for intervention. *Down Syndr Res Pract* 10: 74–82.

4. GENERAL DISCUSSION

Previous research concentrated on emotion recognition of static affective faces or body language reading in static images of body postures. In the present work consisted of two studies, for the first time, we investigated gender differences in body language reading by using point-light movies portraying human actions (knocking on a door) and locomotion. The main advantage of these stimuli is that they eliminate other possible sources of information (such as outfit, age cues, and body shape) except of body motion cues.

The aim of the present work was to clarify whether, and, if so, how gender of observer affects body language reading (recognition of emotions in point-light displays of knocking motion and human locomotion). We intended to clarify whether, and, if so, how perceiver's gender affects recognition of emotional expressions conveyed by actions of others or more specifically (i) whether gender affects recognition of emotions represented by BM, or, in other words, whether females excel in recognition of emotional actions; and (ii) whether gender effects depend on emotional content of actions.

The outcome of both studies together indicated that gender of observer affects the accuracy of body language reading, but not response time (i.e., processing speed). Observer gender affects body language reading in point-light movies depicting knocking on a door, but the effects are modulated by emotional content of actions: males surpass females in recognition accuracy of happy actions, whereas females tend to excel in recognition of angry knocking ([Sokolov et al., 2011](#)). The advantage of women in recognition accuracy of neutral actions suggested that females are better tuned to the lack of emotional content of actions. A similar pattern of results was found for subtle emotions expressed by point-light human locomotion ([Krüger et al., 2013](#)). The gender effects are modulated by the emotional content of locomotion and opposite actor gender: males surpass females in recognition accuracy and readiness to respond to expressions of happiness performed by female actors, whereas females exhibit a tendency to be better in recognition of angry locomotion expressed by male actors (an opposite gender effect).

In a nutshell, the gender effect in body language reading is modulated (i) by the emotional content, e.g. females tend to surpass males in recognition of angry hostile action, whereas men exhibit an advance in the performance on the recognition of happy action. (ii) Actor gender also has an influence on the performance, e.g. females show a tendency to perform better when an angry action is presented by a male actor, whereas men over-perform (more accurate and faster) in the recognition of happy female point-light walkers.

4.1 POSSIBLE MECHANISMS UNDERLYING GENDER DIFFERENCES

4.1.1 Sex specific brain structures and functions. The question arises, what are the sources of gender differences in body language reading. One possibility would be the existence of sex specific brain structures (see, e.g., [Pavlova, 2017b](#); [Ritchie et al., 2018](#)). Indeed, based on the analysis of 949 human brains (428 male and 521 female), it has been reported that males exhibit greater within-hemisphere connectivity, whereas between-hemispheric connectivity predominates in females ([Ingalhalikar et al., 2014](#)). During the first 30 years of life, TD females tend to have greater gray matter volume relative to brain size and a lower white-to-gray matter ratio than males ([Groeschel et al., 2010](#)). In children aged 4.5–18 years (325 total brains), developmental trajectories of brain tissue volumes are predominantly curvilinear in females but linear in males ([Brain Development Cooperative Group, 2012](#)). The social cognition network involves the parieto-temporal junction, temporal cortices and the superior temporal sulcus (STS), orbitofrontal cortices and the amygdala (e.g., [Adolphs, 2003](#)). In fMRI studies, full-light (whole-body) BM stimuli depicting threat or anger elicit higher activation in the STS and linked regions compared to neutral stimuli ([Grèzes et al., 2007](#); [Pichon et al., 2008](#); [2009](#)).

However, findings on sex specificity of the social brain are controversial. For example, BOLD responses of the amygdala show a sex-specific effect only towards happy faces with a higher activation of the right amygdala than the left in men, but not women. Fearful content activated the left amygdala more than the right for both male and female ([Killgore, 2001](#)). Otherwise, a significant correlation between fMRI activity of the amygdala and behavioral response to

fearful faces is observed in males only (Derntl, 2009a,b). Other findings indicate that there are morphological sex-dependent differences in the brain structure and connectivity (Cahill, 2006; Brain Development Cooperative Group, 2012; Menzler et al., 2011; Chou et al., 2011).

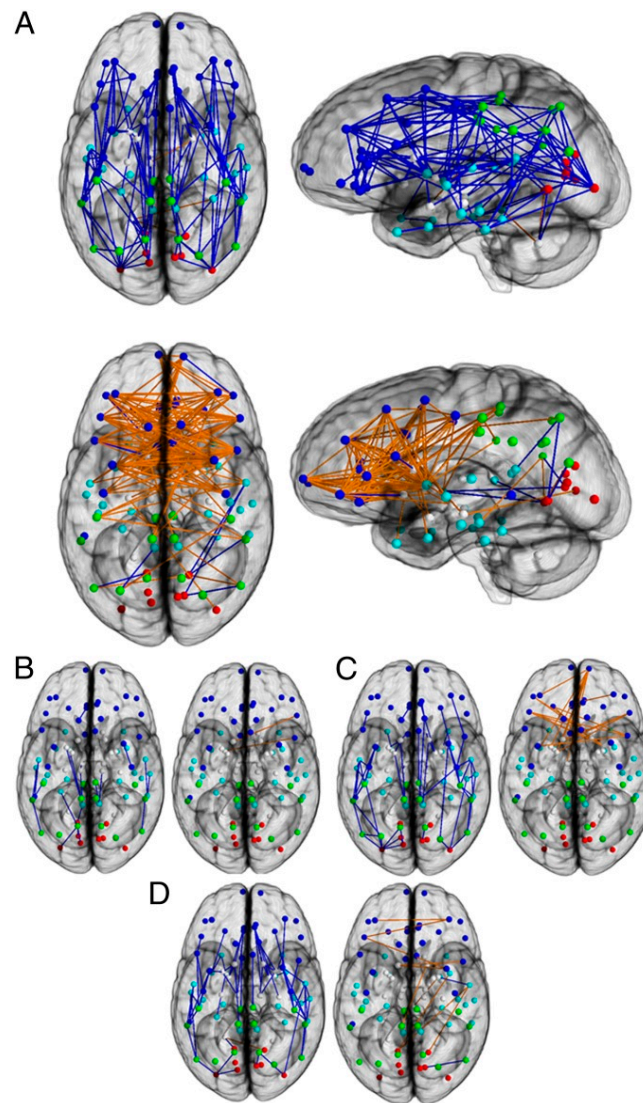


Figure 3. (A) Brain connectivity in males (upper panel) and females (lower panel) as revealed by connection-wise analysis. Brain connectivity in child (B), adolescent (C), and young adult (D). Intrahemispheric connections are shown in blue, and interhemispheric connections in orange. Node color representations are: light blue, frontal; cyan, temporal; green, parietal; red, occipital; white, subcortical. From Ingahlakar et al. (2014). Sex differences in the structural connectome of the human brain. *Proceedings of the National Academy of Sciences of the USA* 111 (2): 823-828; <https://doi.org/10.1073/pnas.1316909110>.

Previous findings on sex specificity of the social brain in relation to processing of body motion and body language reading are extremely sparse and only a few recent studies are available (e.g., [Burke et al., 2019](#)). In females, increased fMRI activation is found during passive viewing of point-light BM displays (waving, pat-a-cake, and peek-a-boo) over the regions belonging to the social brain, in particular, the temporal pole, medial temporal gyrus, cerebellum, and amygdala ([Anderson et al., 2013](#)). Brain fMRI activity elicited by threatening facial and whole-body expressions is modulated by the observer's gender ([Kret et al., 2011](#)). By judging emotions represented by stick-figure human body postures, healthy adults express sex specific patterns of fMRI activity ([Kana and Travers, 2012](#)).

MEG work revealed sex dependent modes in the time course and topography of the neural circuitry underpinning visual processing of neutral point-light BM, even in the absence of behavioral differences ([Pavlova et al., 2015b](#)). At early latencies, females exhibit a greater activation than males over the right parietal, left temporal, and right temporal cortices, a core of the social brain. In males, the boosts of activation are greater at later latencies over the right frontal and occipital cortices that likely reflect back-propagating influences from the areas involved in higher order cognitive processing. The findings deliver the first evidence for gender-dependent modes in the time course and topography of the circuitry for BM processing. In light of the absence of differences at the behavioral level, it is plausible that sex differences in the cortical response may prevent behavioral differences if they are maladaptive. Moreover, by using MEG, temporal characteristics and topography of the network engaged in visual processing of social interaction in Heider-and-Simmel-like animations of geometric shapes were identified ([Pavlova et al., 2010a](#)). Stronger activity in the left Crus I and lobule VI of the cerebellum was associated with a greater tendency to describe the Heider-and-Simmel movies in affective rather than motion-related terms, and psychophysiological interaction analysis indicates preferential effective connectivity between the right pSTS and the left Crus II ([Jack and Pelphrey, 2015](#)). Contrary to popular wisdom, gender effects were evident in the neural circuitry underpinning perceptual decision making rather

than in visual social perception ([Pavlova et al., 2010b](#)): The gamma oscillatory MEG response over the left prefrontal cortex, a region implicated in perceptual decision making, peaked earlier in females.

4.1.2 The mirror neuron system. The other possible mechanism that can explain gender impact on body language reading is the mirror neuron system. It is proclaimed that the mirror neuron system is a key-player in the recognition, understanding and performance of actions and embedded emotions (for reviews, see [Rizzolatti and Sinigaglia, 2010](#); [Sinigaglia and Rizzolatti, 2011](#)): observers better understand and recognize actions of others, if they can perform these actions themselves. It is reported that even infants aged 9-11 weeks exhibit links between perception and production of actions ([Reid et al., 2019](#)). As pointed earlier ([Krüger et al., 2013](#)), from the mirror neuron system point of view, one would expect that observers would over-perform in recognition of emotions expressed by actors of the same gender (i.e., females would be better in recognition of emotions expressed by female actors, and males in recognition of emotions expressed by male actors), because they have common or similar motor programs. Previous findings show that visual priming elevates the direction detection of a masked runner only in observers of the same gender, who possess similar motor programs with a runner ([Bidet-Ildei et al., 2010](#)). Motor experience in performance of certain movements (for example, dancing) also leads to a better recognition of these movements: female dance experts are better in discrimination of point-light dance elements expressed by female actors (when observers and performers share common motor program for dance performance) than male experts (when observers and performers share visual experience only) ([Calvo-Merino et al., 2010](#)).

Facilitation effect of gender congruency, however, was not observed in the present study dealing with some aspects of social cognition. We obtained an opposite gender effect, i.e., better female performance of female observers when recognizing male angry actors and better performance of male observers by recognition of female happy actors ([Krüger et al., 2013](#)). This may reflect evolutionary significance of the opposite gender appearance with higher tuning

of males to happiness communicated through body motion of females and higher tuning of females to possible (even subtle) signals of threat or danger in body language of males.

Future work is required to clarify the origin of gender impact on social cognition, and on body language reading. Clarification of complex interaction of neurobiological sex and sociocultural gender, and its influence on the social brain would provide novel insights for understanding gender vulnerability to psychiatric and neurodevelopmental deficits ([Pavlova, 2017a](#)).

4.2 CLINICAL RELEVANCE

The clinical relevance of research on gender differences in body language reading is based on the following interconnected reasons: (i) most of neurodevelopmental, psychiatric, psychosomatic, and neurological disorders are characterized by aberrant visual social cognition and body language reading; and (ii) most of these disorders are gender specific with a skewed sex ratio: females and males are affected differently in terms of clinical picture, prevalence, and severity ([Pavlova, 2017ab](#)). Causes of this gender specificity are largely unknown, but may be of neurobiological as well as socio-cultural (different social roles and images of females and males, such as ‘males should be stronger than females and don’t usually show their sensibility and depressive mood’).

Anxiety disorders, for instance, show a female to male ratio of 2:1. New evidence indicate that there are two anatomically and functionally different serotonergic circuits involved in modulating anxiety (for review, see [Donner, 2013](#)). Depression occurs significantly more often in females, with a ratio of 2:1 ([Diflorio and Jones, 2010](#)). Many other neuropsychiatric disorders (such as ASD or schizophrenia) show male prevalence. Individuals with autism [prevalence is close to 6 per 1000 ([Newschaffer et al., 2007](#)); or even higher (but cf. [Pantelis and Kennedy, 2016](#))] may be considered as a key population for understanding the relationship between BM processing and aberrant social cognition. Neurodevelopmental disorders are also often gender/sex specific: Down

syndrome possesses a sex ratio of 1.28 (Bishop et al., 1997), Fragile X syndrome has a ratio of 2:1 (Crawford et al., 2001) and is characterized by some unique gender-dependent differences in cognitive and clinical profiles (Rinehart et al., 2011). Male fetuses are at 14-20% higher risk of premature birth (Melamed et al., 2010) with complications for further brain development and cognition (for review, see Pavlova and Krägeloh-Mann, 2013).

Deficits in BM processing and/or body language reading are reported in individuals who were born preterm and suffer congenital brain lesions (Pavlova and Krägeloh-Mann, 2013), with Alzheimer (Henry et al., 2012; Insch et al., 2017) and Parkinson diseases (Cao et al., 2015; Jaywant et al., 2016a,b; Kloeters et al., 2017), epilepsy (Bala et al., 2018), and eating disorders such as anorexia nervosa and bulimia (Zucker et al., 2013; Lang et al., 2015; Dapelo et al., 2017). Some aspects of BM processing and body language reading are aberrant in ASD (e.g., Klin et al., 2009; Nackaerts et al., 2012; Jack et al., 2017; Metcalfe et al., 2019) or in individuals with elevated autistic traits (Burling et al., 2019), schizophrenia (e.g., Hastings et al., 2013; Kim et al., 2011; Spencer et al., 2013; Hashimoto et al., 2014; Vaskinn et al., 2016; Engelstad et al., 2017, 2018; Egeland et al., 2019) or schizotypal personality disorder (Hur et al., 2016), bipolar disorders (Vaskinn et al., 2017), ADHD (Kröger et al., 2014), anxiety disorders or in individuals with elevated anxiety (van der Cruys et al., 2013; Heenan and Troje, 2014), obsessive compulsive disorders (Kim et al., 2008), and unipolar depression (Loi et al., 2013; Kaletsch et al., 2014).

Revealing gender differences requires specifically targeted work. This work will contribute to better understanding of gender-specific disorders related to social cognition and sex-specific functioning of the social brain. Further steps towards understanding of gender impact on social cognition have prospective clinical significance and implications.

5. CONCLUSIONS

The outcome of the presented work could be summarized as follows: Gender affects the accuracy, but not processing speed (response time) of body

language reading. This effect is modulated (i) by the emotional content of action: females tend to surpass males in recognition of angry hostile action, whereas males exhibit an advance in the performance on the recognition of happy action. (ii) Actor gender also has an influence on performance: females show a tendency to perform better when an angry action is presented by a male actor, whereas men over perform on the recognition of happy female walkers.

These findings could be helpful for creating, developing and validation of clinical tests on the ability of body language reading. In addition, better understanding of the neural processes underlying emotion recognition could reveal possible points of attack in the treatment of diseases associated with aberrant social cognition.

6.1 SUMMARY

Body motion is a rich and reliable source of information for daily life social cognition, interaction and non-verbal communication. Yet gender effects in body language reading are largely unknown, and a few previous findings are sparse and controversial. Investigation of gender impact on body language reading is of substantial value for clarification of the nature of neurodevelopmental and psychiatric disorders (such as autism, attention deficit hyperactivity disorder, eating and anxiety disorders) characterized by aberrant social cognition. Many of these disorders are gender-specific: females and males are differently affected in terms of clinical picture, prevalence, and severity. The motivation of the present work was to clarify whether, and, if so, how gender affects body language reading in typically developing adults. We intended to make a step toward a framework for evaluation gender differences in the social brain in psychiatric and neurodevelopmental disorders. In our experiments, body motion was 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 visual cues (e.g., color, shape). *In the first study* (Sokolov et al., 2011), by using a three alternative-forced choice paradigm, participants had to indicate whether a display portrayed happy, neutral or angry knocking at a door. The findings show that gender affects accuracy rather than speed of body language reading. This effect, however, is modulated by emotional content of actions: males surpass in recognition accuracy of happy actions, whereas females tend to excel in recognition of hostile angry knocking movement. *In the second study* (Krüger et al., 2013), 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 happy walking portrayed by female actors, whereas females tend to be better in recognition of angry locomotion expressed by male actors. In contrast to widespread beliefs about female superiority in social cognition, this work suggests that gender effects in body language reading are largely modulated by emotional content of actions. Further research should combine methods of social neuroscience to uncover neural circuits underlying gender differences in the social brain.

6.2 ZUSAMMENFASSUNG

Körpersprache ist eine wichtige und verlässliche Informationsquelle bei sozialer Wahrnehmung, Interaktion und non-verbaler Kommunikation im Alltag. Bisher sind jedoch Geschlechtereffekte bei der Wahrnehmung von Körpersprache weitestgehend unbekannt, die wenigen vorhandenen Erkenntnisse sind dürftig und widersprüchlich. Die Erforschung des Einflusses des Geschlechts auf die Wahrnehmung von Körpersprache ist wichtig für ein tieferes Verständnis für entwicklungsneurologische und psychiatrische Erkrankungen (wie zum Beispiel Autismus, Aufmerksamkeits-Defizit-Hyperaktivitäts-Syndrom, Ess- und Angststörungen), die durch eine veränderte Sozialwahrnehmung gekennzeichnet sind. Viele dieser Erkrankungen sind geschlechtsspezifisch: Frauen und Männer sind hinsichtlich klinischer Ausprägung, Häufigkeit und Schweregrad in unterschiedlichem Ausmaß betroffen. Das Ziel dieser Arbeit war es zu klären, ob, und wenn ja, welchen Einfluss das Geschlecht bei normal entwickelten Erwachsenen auf die Körpersprachenwahrnehmung hat. In unseren Experimenten wurde Körpersprache mittels Lichtpunkt-Technik dargestellt mit mehreren Leuchtpunkten, die die Gelenke eines ansonsten unsichtbaren Körpers repräsentieren. Dadurch kann der durch Körperbewegung erzeugte Informationsgehalt von anderen visuellen Informationen (zum Beispiel Farben, Formen) isoliert werden. *In der ersten Studie* (Sokolov et al., 2011) mussten die Teilnehmer bestimmen, ob ein Video entweder ein fröhliches, neutrales oder ärgerliches Klopfen an eine Tür zeigt. Es konnte gezeigt werden, dass das Geschlecht eher die Genauigkeit als die Geschwindigkeit bei der Körpersprachenerkennung beeinflusst. Dieser Effekt variierte jedoch je nach Emotion der gezeigten Handlung: Männer erkennen fröhliches Klopfen besser, Frauen eher aggressiv ärgerliches Klopfen. *In der zweiten Studie* (Krüger et al., 2013) zeigte sich ein ähnliches Ergebnis für durch Punktlicht dargestellte subtile Emotionen bei menschlichem Gehen: Männer erkennen besser und schneller fröhliches Laufen, das von weiblichen Schauspielern dargestellt wird, Frauen sind jedoch eher besser in der Erkennung von ärgerlichem Gehen von männlichen Schauspielern. Im Gegensatz zum weitverbreiteten Glauben an die weibliche Überlegenheit bei sozialer Wahrnehmung zeigt diese Arbeit, dass

Geschlechtsunterschiede bei der Körpersprachenerkennung zu einem großen Teil vom emotionalen Inhalt der gezeigten Handlung abhängen. Zur Identifizierung neuronaler Netzwerke, die den Geschlechtsunterschieden in der sozialen Wahrnehmung zugrunde liegen, sollte die weitere Forschung auch neurowissenschaftliche Methoden einbinden.

7. REFERENCES

- Actis-Grosso R, Bossi F, Ricciardelli P. (2015). Emotion recognition through static faces and moving bodies: a comparison between typically developed adults and individuals with high level of autistic traits. *Front Psychol.* 23: 1570.
- Adolphs, R. (2003). Cognitive neuroscience of human social behaviour. *Nat. Rev. Neurosci.* 4: 165–178.
- Alaerts K, Nackaerts E, Meyns P, Swinnen SP, Wenderoth N. (2011). Action and emotion recognition from point light displays: an investigation of gender differences. *PLoS One* 6: e20989.
- Andersen GJ, Atchley P. (1995). Age-related differences in the detection of three-dimensional surfaces from optic flow. *Psychol Aging.* 10: 650-8.
- Anderson LC, Bolling DZ, Schelinski S, Coffman MC, Pelphrey KA, et al. (2013). Sex differences in the development of brain mechanisms for processing biological motion. *NeuroImage* 83C: 751–760.
- Annaz D, Remington A, Milne E, Coleman M, Campbell R, Thomas MS, Swettenham J. (2010). Development of motion processing in children with autism. *Dev Sci.* 13: 826-38.
- Atkinson AP, Dittrich WH, Gemmel AJ, Young AW. (2004). Emotion perception from dynamic and static body expressions in point-light and full-light displays. *Perception* 33: 717–746.
- Atkinson AP, Vuong QC, Smithson HE. (2012). Modulation of the face- and body-selective visual regions by the motion and emotion of point-light face and body stimuli. *Neuroimage.* 59: 1700-12.
- Bala A, Okruszek Ł, Piejka A, Głębigicka A, Szewczyk E, Bosak K, Szantroch M, Hyniewska S, Rysz A, Marchel A. (2018). Social Perception in Mesial Temporal Lobe Epilepsy: Interpreting Social Information From Moving Shapes and Biological Motion. *J Neuropsychiatry Clin Neurosci.* 30: 228-235.
- Ball K, Sekuler R. (1986). Improving visual perception in older observers. *J Gerontol.* 41: 176-82.
- Beauchamp MS, Lee KE, Haxby JV, Martin A. (2003). fMRI responses to video and point-light displays of moving humans and manipulable objects. *J Cogn Neurosci.* 15: 991-1001.
- Beesdo-Baum K, Knappe S. (2012). Developmental epidemiology of anxiety disorders. *Child Adolesc Psychiatr Clin N Am* 21: 457–478.
- Bernaerts S, Berra E, Wenderoth N, Alaerts K. (2016). Influence of oxytocin on emotion recognition from body language: A randomized placebo-controlled trial. *Psychoneuroendocrinology* 72: 182-189.
- Bertenthal BI, Pinto J. (1994). Global processing of biological motions. *Psychological Science* 5: 221-225.
- Bidet-Ildei C, Chauvin A, Coello Y. (2010). Observing or producing a motor action improves later perception of biological motion: evidence for a gender effect. *Acta Psychol (Amst)* 134: 215–224.

- Bidet-Ildes C, Kitromilides E, Orliaguet JP, Pavlova M, Gentaz E. (2014). Preference for point-light human biological motion in newborns: contribution of translational displacement. *Dev Psychol.* 50: 113-20.
- Biehl SC, Andersen M, Waiter GD, Pilz KS. (2017). Neural changes related to motion processing in healthy aging. *Neurobiol Aging.* 57: 162-169.
- Biele C, Grabowska A. (2006). Sex differences in perception of emotion intensity in dynamic and static facial expressions. *Exp. Brain Res.* 171: 1–6.
- Billino J, Braun DI, Böhm KD, Bremmer F, Gegenfurtner KR. (2009). Cortical networks for motion processing: effects of focal brain lesions on perception of different motion types. *Neuropsychologia.* 47: 2133-44.
- Billino J, Bremmer F, Gegenfurtner KR. (2008). Differential aging of motion processing mechanisms: evidence against general perceptual decline. *Vision Res.* 48: 1254–1261.
- Bishop J, Huether CA, Torfs C, Lorey F, Deddens J. (1997). Epidemiologic study of Down syndrome in a racially diverse California population, 1989-1991. *Am J Epidemiol* 145: 134–147.
- Blanck PD, Rosenthal R, Snodgrass SE, DePaulo BM, Zuckerman M. (1981). Sex differences in eavesdropping on non-verbal cues: developmental changes. *J Pers Soc Psychol.* 41: 391–396.
- Boone RT, Cunningham JG. (1998). Children's decoding of emotion in expressive body movement: the development of cue attunement. *Dev Psychol.* 34: 1007–1016.
- Bourne, V. J. (2005). Lateralised processing of positive facial emotion: sex differences in strength of hemispheric dominance. *Neuropsychologia.* 43: 953–956.
- Boyatzis CJ, Chazan E, Ting CZ. (1993). Preschool children's decoding of facial emotions. *J Genet Psychol.* 154: 375-82.
- Brain Development Cooperative Group (2012). Total and regional brain volumes in a population-based normative sample from 4 to 18 years: the NIH MRI study of normal brain development. *Cereb Cortex* 1: 1–12.
- Brooks A, Schouten B, Troje NF, Verfaillie K, Blanke O, et al. (2008). Correlated changes in perceptions of the gender and orientation of ambiguous biological motion figures. *Curr Biol* 18: R728–R729.
- Brown J, Kaplan G, Rogers LJ, Vallortigara G. (2010). Perception of biological motion in common marmosets (*Callithrix jacchus*): by females only. *Anim Cogn* 13: 555–564.
- Burke SL, Hu T, Fava NM, Li T, Rodriguez MJ, Schuldiner KL, Burgess A, Laird A. (2019). Sex differences in the development of mild cognitive impairment and probable Alzheimer's disease as predicted by hippocampal volume or white matter hyperintensities. *J Women Aging.* 31: 140-164.
- Burling JM, Kadambi A, Safari T, Lu H. (2019). The Impact of Autistic Traits on Self-Recognition of Body Movements. *Front Psychol.* 9: 2687.

Cahill L. (2006). Why sex matters for neuroscience. *Nat Rev Neurosci* 7: 477–484.

Calvo-Merino B, Ehrenberg S, Leung D, Haggard P. (2010). Experts see it all: configural effects in action observation. *Psychol Res* 74: 400–406.

Calvo-Merino B, Glaser DE, Grèzes J, Passingham RE, Haggard P. (2005). Action observation and acquired motor skills: an fMRI study with expert dancers. *Cereb Cortex* 15: 1243–1249.

Calvo-Merino B, Grèzes J, Glaser DE, Passingham RE, Haggard P (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Curr Biol* 16: 1905–1910.

Cao R, Ye X, Chen X, Zhang L, Chen X, Tian Y, Hu P, Wang K. (2015). Exploring Biological Motion Processing in Parkinson's Disease Using Temporal Dilation. *PLoS One*. 10: e0138502.

Chou KH, Cheng Y, Chen IY, Lin CP, Chu WC et al. (2011). Sex-linked white matter microstructure of the social and analytic brain. *NeuroImage* 54: 725–733.

Chouchourelou A, Toshihiko M, Harber K, Shiffrar M. (2006). The visual analysis of emotional actions. *Soc Neurosci* 1: 63–74.

Clarke TJ, Bradshaw MF, Field DT, Hampson SE, Rose D. (2005). The perception of emotion from body movement in point-light displays of interpersonal dialogue. *Perception* 34: 1171–1180.

Craske MG (2003). *Origins of phobias and anxiety disorders: Why more women than men?* Amsterdam (Netherlands): Elsevier.

Crawford DC, Acuna JM, Sherman SL (2001). FMR1 and the fragile X syndrome: human genome epidemiology review. *Genet Med* 3: 359–371.

Dapelo MM, Surguladze S, Morris R, Tchanturia K. (2017). Emotion Recognition in Face and Body Motion in Bulimia Nervosa. *Eur Eat Disord Rev*. 25: 595-600.

Dasgupta S, Tyler SC, Wicks J, Srinivasan R, Grossman ED. (2017). Network Connectivity of the Right STS in Three Social Perception Localizers. *J Cogn Neurosci*. 29: 221-234.

De Gelder B. (2006). Towards the neurobiology of emotional body language. *Nat. Rev. Neurosci*. 7: 242–249.

De Gelder B. (2009). Why bodies? Twelve reasons for including bodily expressions in affective neuroscience. *Philos. Trans. R. Soc. Lond., B*. 364, 3475–3484.

De Vries G. J. (2004). Sex differences in adult and developing brains: compensation, compensation, compensation. *Endocrinology* 145: 1603–1608.

Derntl B, Habel U, Windischberger C, Robinson S, Kryspin-Exner I, Gur RC, and Moser E. (2009a). General and specific responsiveness of the amygdala during explicit emotion recognition in females and males. *BMC Neurosci*. 10: 91.

Derntl B, Windischberger C, Robinson S, Kryspin-Exner I, Gur RC, Moser E,

Habel U. (2009b). Amygdala activity to fear and anger in healthy young males is associated with testosterone. *Psychoneuroendocrinology* 34: 687–693.

Diflorio A, Jones I. (2010). Is sex important? Gender differences in bipolar disorder. *Int Rev Psych* 22: 437–452.

Dittrich WH, Troscianko T, Lea SE, Morgan D. (1996). Perception of emotion from dynamic point-light displays represented in dance. *Perception* 25: 727–738.

Donner NC, Lowry CA. (2013). Sex differences in anxiety and emotional behavior. *Pflugers Arch*. 465: 601-26.

Egeland J, Holmen TL, Bang-Kittilsen G, Bigseth TT, Vaskinn A, Engh JA. (2019). Body language reading of emotion and outcome in schizophrenia. *Cogn Neuropsychiatry*. 24: 54-64.

Elsner C, Falck-Ytter T, Gredebäck G. (2012). Humans anticipate the goal of other people's point-light actions. *Front Psychol*. 3: 120.

Engell AD, McCarthy G. (2013). Probabilistic atlases for face and biological motion perception: an analysis of their reliability and overlap. *Neuroimage* 74: 140-51.

Engelstad KN, Sundet KS, Andreassen OA, Vaskinn A. (2017). Body language reading of emotion in schizophrenia: Associations with symptoms and functional outcome. *Scand J Psychol*. 58: 359-366.

Engelstad KN, Vaskinn A, Torgalsbøen AK, Mohn C, Lau B, Rund BR. (2018). Impaired neuropsychological profile in homicide offenders with schizophrenia. *Compr Psychiatry*. 85: 55-60.

Farris C, Treat TA, Vilken RJ, McFall RM. (2008). Perceptual mechanisms that characterize gender differences in decoding women's sexual intent. *Psychol. Sci*. 19: 348–354.

Freire A, Lewis TL, Maurer D, Blake R. (2006). The development of sensitivity to biological motion in noise. *Perception* 35: 647-57.

Furuhata N, Shirai N. (2015). The development of gaze behaviors in response to biological motion displays. *Infant Behav Dev*. 38: 97-106.

Gasbarri A, Arnone B, Pompili A, Pacitti C, Cahill L. (2007). Sex-related hemispheric lateralization of electrical potentials evoked by arousing negative stimuli. *Brain Res*. 1138: 178–186.

Gobbini MI, Koralek AC, Bryan RE, Montgomery KJ, Haxby JV. (2007). Two takes on the social brain: a comparison of theory of mind tasks. *J Cogn Neurosci* 19: 1803–1814.

Golan O, Baron-Cohen S, Hill J. (2006). The Cambridge Mindreading (CAM) Face-Voice Battery: the complex emotion recognition in adults with and without Asperger syndrome. *J. Autism Dev. Dis.* 36: 169–183.

Goldberg H, Christensen A, Flash T, Giese MA, Malach R. (2015). Brain activity correlates with emotional perception induced by dynamic avatars. *Neuroimage*. 122: 306-17.

Grèzes J, Frith CD, Passingham RE (2004a). Brain mechanisms for inferring deceit in the actions of others. *J. Neurosci.* 24: 5500–5505.

Grèzes J, Frith CD, Passingham RE. (2004b). Inferring false beliefs from the actions of oneself and others: an fMRI study. *Neuroimage* 21: 744–750.

Grèzes J, Pichon S, de Gelder B. (2007). Perceiving fear in dynamic body expressions. *Neuroimage* 35: 959-67.

Groeschel S, Vollmer B, King MD, Connelly A. (2010). Developmental changes in cerebral grey and white matter volume from infancy to adulthood. *Int J Dev Neurosci.* 28: 481-9.

Grosbras MH, Beaton S, Eickhoff SB. (2012). Brain regions involved in human movement perception: a quantitative voxel-based meta-analysis. *Hum Brain Mapp.* 33: 431-54.

Grossman ED, Blake R. (2002). Brain areas active during visual perception of biological motion. *Neuron* 35: 1167–1175.

Grossman ED, Donnelly M, Price R, Pickens D, Morgan V, Neighbor G, Blake R. (2000). Brain Areas Involved in Perception of Biological Motion. *Journal of Cognitive Neuroscience* 12: 711-720.

Hall JA, Matsumoto D (2004). Gender differences in judgments of multiple emotions from facial expressions. *Emotion* 4: 201–206.

Han Z, Bi Y, Chen J, Chen Q, He Y, Caramazza A. (2013). Distinct regions of right temporal cortex are associated with biological and human-agent motion: functional magnetic resonance imaging and neuropsychological evidence. *J Neurosci.* 33: 15442-53.

Hashimoto N, Toyomaki A, Hirai M, Miyamoto T, Narita H, Okubo R, Kusumi I. (2014). Absent activation in medial prefrontal cortex and temporoparietal junction but not superior temporal sulcus during the perception of biological motion in schizophrenia: a functional MRI study. *Neuropsychiatr Dis Treat.* 10: 2221-30.

Hastings CN, Brittain PJ, Ffytche DH. (2013). An asymmetry of translational biological motion perception in schizophrenia. *Front Psychol.* 4: 436.

Heberlein AS, Adolphs R, Tranel D, Damasio H. (2004). Cortical regions for judgments of emotions and personality from point-light walkers. *J Cogn Neurosci* 16: 1143–1158.

Heenan A, Troje NF. (2014). Both physical exercise and progressive muscle relaxation reduce the facing-the-viewer bias in biological motion perception. *PLoS One.*9: e99902.

Henry MS, Passmore AP, Todd S, McGuinness B, Craig D, Johnston JA. (2012). The development of effective biomarkers for Alzheimer's disease: a review. *Int J Geriatr Psychiatry.* 28: 331-40.

Herrington JD, Nymberg C, Schultz RT. (2011). Biological motion task performance predicts superior temporal sulcus activity. *Brain Cogn.* 77: 372-81.

Hirai M, Fukushima H, Hiraki K. (2003). An event-related potentials study of

biological motion perception in humans. *Neurosci Lett.* 344: 41-4.

Hirai M, Senju A. (2020) The two-process theory of biological motion processing. *Neurosci Biobehav Rev.* 111: 114-124.

Hoffmann H, Kessler H, Eppel T, Rukavina S, Traue HC (2010). Expression intensity, gender and facial emotion recognition: Women recognize only subtle facial emotions better than men. *Acta Psychol (Amst)* 135: 278–283.

Hubert B, Wicker B, Moore DG, Monfardini E, Duverger H, Da Fonseca D, Deruelle C. (2007). Brief report: recognition of emotional and non-emotional biological motion in individuals with autistic spectrum disorders. *J. Autism Dev. Dis.* 37: 1386–1392.

Hugill N, Fink B, Neave N. (2010). The role of human body movements in mate selection. *Evol Psychol* 8: 66–89.

Hur JW, Blake R, Cho KI, Kim J, Kim SY, Choi SH, Kang DH, Kwon JS. (2016). Biological Motion Perception, Brain Responses, and Schizotypal Personality Disorder. *JAMA Psychiatry.* 73: 260-7.

Ikeda H, Blake R, Watanabe K. (2005). Eccentric perception of biological motion is unscalably poor. *Vision Res.* 45: 1935-43.

Ikeda H, Watanabe K (2009). Anger and happiness are linked differently to the explicit detection of biological motion. *Perception* 38: 1002–1011.

Ingalhalikar M, Smith A, Parker D, Satterthwaite TD, Elliott MA, Ruparel K, Hakonarson H, Gur RE, Gur RC, Verma (2014). Sex differences in the structural connectome of the human brain. *Proc Natl Acad Sci.* 111: 823–828.

Insch PM, Bull R, Phillips LH, Allen R, Slessor G. (2012). Adult aging, processing style, and the perception of biological motion. *Exp Aging Res.* 38: 169-185.

Insch PM, Slessor G, Warrington J, Phillips LH. (2017). Gaze detection and gaze cuing in Alzheimer's disease. *Brain Cogn.* 116: 47-53.

Isernia S, Sokolov AN, Fallgatter AJ, Pavlova MA. (2020). Untangling the Ties Between Social Cognition and Body Motion: Gender Impact. *Front Psychol.* 11:128.

Jack A, Keifer CM, Pelphrey KA. (2017). Cerebellar contributions to biological motion perception in autism and typical development. *Hum Brain Mapp.* 38:1914-1932.

Jack A, Pelphrey KA. (2015). Neural Correlates of Animacy Attribution Include Neocerebellum in Healthy Adults. *Cereb Cortex.* 25: 4240-7.

Jastorff J, Abdollahi RO, Fasano F, Orban GA. (2015). Seeing biological actions in 3D: An fMRI study. *Hum Brain Mapp.* 37: 203-19.

Jaywant A, Shiffrar M, Roy S, Cronin-Golomb A. (2016b). Impaired perception of biological motion in Parkinson's disease. *Neuropsychology.* 30: 720-30.

Jaywant A, Wasserman V, Kempainen M, Nearing S, Cronin-Golomb A. (2016a). Perception of Communicative and Non-communicative Motion-Defined

- Gestures in Parkinson's Disease. *J Int Neuropsychol Soc.* 22: 540-50.
- Jazin E, Cahill L. (2010). Sex differences in molecular neuroscience: from fruit flies to humans. *Nat. Rev. Neurosci.* 11: 9–17.
- Johansson G. (1973). Visual perception of biological motion and a model for its analysis. *Perception & Psychophysics* 14: 201-211.
- Johnson KL, McKay LS, Pollick FE (2011). He throws like a girl (but only when he's sad): emotion affects sex-decoding of biological motion displays. *Cognition* 119: 265–280.
- Jokisch D, Daum I, Suchan B, Troje NF. (2005). Structural encoding and recognition of biological motion: evidence from event-related potentials and source analysis. *Behav Brain Res.* 157: 195-204.
- Kaiser MD, Delmolino L, Tanaka JW, Shiffrar M. (2010). Comparison of visual sensitivity to human and object motion in autism spectrum disorder. *Autism Res.* 4: 191-5.
- Kaletsch M, Pilgramm S, Bischoff M, Kindermann S, Sauerbier I, Stark R, Lis S, Gallhofer B, Sammer G, Zentgraf K, Munzert J, Lorey B. (2014). Major depressive disorder alters perception of emotional body movements. *Front Psychiatry.* 20: 4.
- Kana RK, Travers BG. (2012). Neural substrates of interpreting actions and emotions from body postures. *Soc Cogn Affect Neurosci.* 7: 446-56.
- Killgore WD, Yurgelun-Todd DA (2001). Sex differences in amygdala activation during the perception of facial affect. *Neuroreport* 12: 2543–2547.
- Kim J, Blake R, Park S, Shin YW, Kang DH, et al. (2008). Selective impairment in visual perception of biological motion in obsessive-compulsive disorder. *Depress Anxiety* 25: E15–25.
- Kim J, Jung EL, Lee SH, Blake R. (2015). A new technique for generating disordered point-light animations for the study of biological motion perception. *J Vis.* 15: 13.
- Kim J, Park S, Blake R. (2011). Perception of biological motion in schizophrenia and healthy individuals: a behavioral and fMRI study. *PLoS One* 6: e19971.
- Klin A, Lin DJ, Gorrindo P, Ramsay G, Jones W. (2009). Two-year-olds with autism orient to non-social contingencies rather than biological motion. *Nature* 459: 257–261.
- Kloeters S, Hartmann CJ, Pundmann VD, Schnitzler A, Südmeyer M, Lange J. (2017). Impaired perception of human movements in Parkinson's disease. *Behav Brain Res.* 317: 88-94.
- Krakowski AI, Ross LA, Snyder AC, Sehatpour P, Kelly SP, Foxe JJ. (2011). The neurophysiology of human biological motion processing: a high-density electrical mapping study. *Neuroimage.* 56: 373-83.
- Kret ME, De Gelder B. (2012). A review on sex differences in processing emotional signals. *Neuropsychologia* 50: 1211–1221.

Kret ME, Pichon S, Grèzes J, de Gelder B. (2010). Similarities and differences in perceiving threat from dynamic faces and bodies. An fMRI study. *Neuroimage* 54: 1755–1762.

Kret ME, Pichon S, Grèzes J, de Gelder B. (2011). Men fear other men most: gender specific brain activations in perceiving threat from dynamic faces and bodies - an FMRI study. *Front Psychol* 2: 3.

Kret ME, Stekelenburg JJ, Roelofs K, de Gelder B (2013). Perception of face and body expressions using electromyography, pupillometry and gaze measures. *Front Psychol* 4: 28.

Kröger A, Hof K, Krick C, Siniatchkin M, Jarczok T, Freitag CM, Bender S. (2014). Visual processing of biological motion in children and adolescents with attention-deficit/hyperactivity disorder: an event related potential-study. *PLoS One*. 9: e88585.

Krüger S, Sokolov AN, Enck P, Krägeloh-Mann I, Pavlova MA. (2013). Emotion through locomotion: gender impact. *PLoS ONE* 8: e81716.

Kutsuki A, Kuroki M, Egami S, Ogura T, Itakura S; Japan Children's Study Group. (2009). Individual differences in changes in infants' interest in social signals in relation to developmental index. *Infant Behav Dev*. 32: 381-91.

Lagerlof I, Djerf M. (2009). Children's understanding of emotion in dance. *Eur J Dev Psychol* 6: 409–431.

Lai MC, Lombardo MV, Suckling J, Ruigrok AN, Chakrabarti B, et al. (2013). Biological sex affects the neurobiology of autism. *Brain* 136: 2799–2815.

Lambrecht L, Kreifelts B, Wildgruber D. (2012). Age-related decrease in recognition of emotional facial and prosodic expressions. *Emotion*. 12: 529-39.

Lang K, Dapelo MM, Khondoker M, Morris R, Surguladze S, Treasure J, Tchanturia K. (2015). Exploring emotion recognition in adults and adolescents with anorexia nervosa using a body motion paradigm. *Eur Eat Disord Rev*. 23: 262-8.

Lee H, Kim J. (2017). Facilitating Effects of Emotion on the Perception of Biological Motion: Evidence for a Happiness Superiority Effect. *Perception*. 46: 679-697.

Legault I, Faubert J. (2012). Perceptual-cognitive training improves biological motion perception: evidence for transferability of training in healthy aging. *Neuroreport*. 23: 469-73.

Legault I, Troje NF, Faubert J. (2012). Healthy older observers cannot use biological-motion point-light information efficiently within 4m of themselves. *Iperception* 3: 104-11.

Loi F, Vaidya JG, Paradiso S. (2013). Recognition of emotion from body language among patients with unipolar depression. *Psychiatry Res*. 30: 40-9.

Lorey B, Kaletsch M, Pilgramm S, Bischoff M, Kindermann S, Sauerbier I, Stark R, Zentgraf K, Munzert J. (2012). Confidence in emotion perception in point-light displays varies with the ability to perceive own emotions. *PLoS One*. 7:

e42169.

Ma Y, Paterson HM, Pollick FE. (2006). A motion capture library for the study of identity, gender, and emotion perception from biological motion. *Behav Res Methods* 38: 134-141.

Manera V, Becchio C, Schouten B, Bara BG, Verfaillie K. (2011). Communicative interactions improve visual detection of biological motion. *PLoS One*. 6: e14594.

Manera V, Schouten B, Becchio C, Bara BG, Verfaillie K. (2010). Inferring intentions from biological motion: a stimulus set of point-light communicative interactions. *Behav Res Methods*. 42: 168-78.

Manera V, Schouten B, Verfaillie K, Becchio C. (2013). Time will show: real time predictions during interpersonal action perception. *PLoS One*. 8: e54949.

Mazzoni N, Jacobs C, Venuti P, Silvanto J, Cattaneo L. (2017). State-Dependent TMS Reveals Representation of Affective Body Movements in the Anterior Intraparietal Cortex. *J Neurosci*. 37: 7231-7239.

McCarthy MM, Arnold AP, Ball GF, Blaustein JD, De Vries GJ (2012). Sex differences in the brain: the not so inconvenient truth. *J Neurosci* 32: 2241–2247.

Meeren HK, van Heijnsbergen CC, de Gelder B. (2005). Rapid perceptual integration of facial expression and emotional body language. *Proc. Natl. Acad. Sci. U.S.A.* 102: 16518–16523.

Melamed N, Yogev Y, Glezerman M. (2010). Fetal gender and pregnancy outcome. *J Matern Fetal Neonatal Med* 23: 338–344.

Menzler K, Belke M, Wehrmann E, Krakow K, Lengler U. (2011). Men and women are different: diffusion tensor imaging reveals sexual dimorphism in the microstructure of the thalamus, corpus callosum and cingulum. *NeuroImage* 54: 2557–2562.

Metcalfe D, McKenzie K, McCarty K, Pollet TV. (2019). Emotion recognition from body movement and gesture in children with Autism Spectrum Disorder is improved by situational cues. *Res Dev Disabil*. 86: 1-10.

Michels L, Kleiser R, de Lussanet MH, Seitz RJ, Lappe M. (2009). Brain activity for peripheral biological motion in the posterior superior temporal gyrus and the fusiform gyrus: Dependence on visual hemifield and view orientation. *Neuroimage*. 45: 151-9.

Michels L, Lappe M, Vaina LM. (2005). Visual areas involved in the perception of human movement from dynamic form analysis. *Neuroreport*. 16: 1037-41.

Miura M, Matsushima T (2012). Preference for biological motion in domestic chicks: sex-dependent effect of early visual experience. *Anim Cogn* 15: 871–879.

Montagne B, Kessels RP, Frigerio E, de Haan EH, Perrett DI. (2005). Sex differences in perception of affective facial expressions: do men really lack emotional sensitivity? *Cogn. Process*. 6: 136–141.

Montepare JM, Zebrowitz-McArthur L (1988). Impressions of people created by age-related qualities of their gaits. *J Pers Soc Psychol* 55: 547–556.

Moore DG, Hobson RP, Lee A. (1997). Components of person perception: an investigation with autistic, non-autistic retarded and typically developing children and adolescents. *Br. J. Dev. Psychol.* 15: 401–423.

Nackaerts E, Wagemans J, Helsen W, Swinnen SP, Wenderoth N, et al. (2012). Recognizing biological motion and emotions from point-light displays in autism spectrum disorders. *PLoS One* 7: e44473.

Newschaffer CJ, Croen LA, Daniels J, Giarelli E, Grether JK, et al. (2007). The epidemiology of autism spectrum disorders. *Ann Rev Publ Health* 28: 235–258.

Norman JF, Dawson TE, Butler AK. (2000). The effects of age upon the perception of depth and 3-D shape from differential motion and binocular disparity. *Perception* 29: 1335-59.

Norman JF, Payton SM, Long JR, Hawkes LM. (2004). Aging and the perception of biological motion. *Psychol Aging* 19: 219-25.

Norman JF, Ross HE, Hawkes LM, Long JR. (2003). Aging and the perception of speed. *Perception*. 32: 85-96.

Okruszek Ł, Piejka A, Wysokiński A, Szczepocka E, Manera V. (2019). The second agent effect: Interpersonal predictive coding in people with schizophrenia. *Soc Neurosci.* 14: 208-213.

Orozco S, Ehlers CL. (1998). Gender differences in electrophysiological responses to facial stimuli. *Biol. Psychiatry* 44: 281–289.

Oullier O, Basso F. (2010). Embodied economics: how bodily information shapes the social coordination dynamics of decision-making. *Philos Trans R Soc Lond B Biol Sci* 365: 291-301.

Pantelis PC, Kennedy DP. (2016). Estimation of the prevalence of autism spectrum disorder in South Korea, revisited. *Autism.* 20: 517-27.

Parkinson C, Walker TT, Memmi S, Wheatley T. (2017). Emotions are understood from biological motion across remote cultures. *Emotion* 17: 459-477.

Parron C, Da Fonseca D, Santos A, Moore DG, Monfardini E, Deruelle C. (2008). Recognition of biological motion in children with autistic spectrum disorders. *Autism* 12: 2161–2174.

Pavlova MA, Erb M, Hagberg GE, Loureiro J, Sokolov AN, Scheffler K. (2017). "Wrong Way Up": Temporal and Spatial Dynamics of the Networks for Body Motion Processing at 9.4 T. *Cereb Cortex.* 27: 5318-5330.

Pavlova MA, Guerreschi M, Lutzenberger W, Sokolov AN, Krägeloh-Mann I. (2010a). Cortical response to social interaction is affected by gender. *NeuroImage* 50: 1327–1332.

Pavlova MA, Krägeloh-Mann I, Sokolov A, Birbaumer N. (2001). Recognition of point-light biological motion displays by young children. *Perception* 30: 925-33.

- Pavlova MA, Krägeloh-Mann I. (2013). Limitations on the developing preterm brain: Impact of periventricular white matter lesions on brain connectivity and cognition. *Brain* 136: 998–1011.
- Pavlova MA, Lutzenberger W, Sokolov A, Birbaumer N. (2004). Dissociable cortical processing of recognizable and non-recognizable biological movement: analyzing gamma MEG activity. *Cereb. Cortex* 14: 181–188.
- Pavlova MA, Sokolov A, Birbaumer N, Krägeloh-Mann I. (2006). Biological motion processing in adolescents with early periventricular brain damage. *Neuropsychologia* 44: 586–593.
- Pavlova MA, Sokolov A. (2003). Prior knowledge about display inversion in biological motion perception. *Perception* 32: 937-46.
- Pavlova MA, Sokolov AN, Bidet-Iledei C. (2015b). Sex Differences in the Neuromagnetic Cortical Response to Biological Motion. *Cereb Cortex*. 25: 3468-74.
- Pavlova MA, Sokolov AN, Birbaumer N, Krägeloh-Mann I. (2008). Perception and understanding of others' actions and brain connectivity. *J. Cogn. Neurosci.* 20: 494–504.
- Pavlova MA, Wecker M, Krombholz K, Sokolov, AA. (2010b). Perception of intentions and actions: gender stereotype susceptibility. *Brain Res.* 1311: 81–85.
- Pavlova MA. (2012). Biological motion processing as a hallmark of social cognition. *Cereb Cortex* 22: 981–995.
- Pavlova MA. (2017a). Sex and gender affect the social brain: Beyond simplicity. *J Neurosci Res.* 95: 235-250.
- Pavlova MA. (2017b). Emotion Science in the Twenty-First Century. Time, Sex, and Behavior in Emotion Science: Over and Above. *Front Psychol.* 8: 1211.
- Pavlova, MA. (2009). Perception and understanding of intentions and actions: does gender matter? *Neurosci. Lett.* 499: 133–136.
- Peelen MV, Caramazza A. (2010). What body parts reveal about the organization of the brain. *Neuron.* 4; 68: 331-3.
- Pelphrey KA, Morris JP, McCarthy G. (2004). Grasping the intentions of others: the perceived intentionality of an action influences activity in the superior temporal sulcus during social perception. *J. Cogn. Neurosci.* 16: 1706–1716.
- Pichon S, de Gelder B, Grezes J. (2008). Emotional modulation of visual and motor areas by dynamic body expressions of anger. *Soc Neurosci* 3: 199-212.
- Pichon S, de Gelder B, Grezes J. (2009). Two different faces of threat. Comparing the neural systems for recognizing fear and anger in dynamic body expressions. *Neuroimage* 47: 1873-83.
- Pilz KS, Vuong QC, Bülthoff HH, Thornton IM. (2010). Walk this way: approaching bodies can influence the processing of faces. *Cognition.* 118: 17-31.
- Pollick FE, Kay JW, Heim K, Stringer R. (2005). Gender recognition from point-

- light walkers. *J Exp Psychol Hum Percept Perform* 31: 1247–1265.
- Pollick FE, Lestou V, Ryu J, Cho SB. (2002). Estimating the efficiency of recognizing gender and affect from biological motion. *Vision Res* 42: 2345–2355.
- Pollick FE, Paterson HM, Bruderlin A, Sanford AJ. (2001). Perceiving affect from arm movement. *Cognition* 82: B51–61.
- Pollux PM, Hermens F, Willmott AP. (2016). Age-congruency and contact effects in body expression recognition from point-light displays. *PeerJ*. 4: e2796.
- Proverbio AM, Riva F, Martin E, Zani A. (2010). Face coding is bilateral in the female brain. *PLoS One* 5: e11242.
- Proverbio AM, Riva F, Zani A. (2009). Observation of static pictures of dynamic actions enhances the activity of movement-related brain areas. *PLoS One* 4: e5389
- Proverbio AM, Riva F, Zani A. (2010). When neurons do not mirror the agent's intentions: sex differences in neural coding of goal-directed actions. *Neuropsychologia* 48: 1454–1463.
- Proverbio AM, Zani A, Adorni R. (2008). Neural markers of a greater female responsiveness to social stimuli. *BMC Neurosci*. 9: 56.
- Puce A, Perrett D. (2003). Electrophysiology and brain imaging of biological motion. *Philos Trans R Soc Lond B Biol Sci*. 358 (1431): 435-45.
- Reid VM, Kaduk K, Lunn J. (2019). Links between action perception and action production in 10-week-old infants. *Neuropsychologia*. 126: 69-74.
- Rinehart NJ, Cornish KM, Tonge BJ. (2011). Gender differences in neurodevelopmental disorders: autism and fragile x syndrome. *Curr Top Behav Neurosci.*: 209-29.
- Ritchie SJ, Cox SR, Shen X, Lombardo MV, Reus LM, Alloza C, Harris MA, Alderson HL, Hunter S, Neilson E, Liewald DCM, Auyeung B, Whalley HC, Lawrie SM, Gale CR, Bastin ME, McIntosh AM, Deary IJ. (2018). Sex Differences in the Adult Human Brain: Evidence from 5216 UK Biobank Participants. *Cereb Cortex*. 28: 2959-2975.
- Rizzolatti G, Sinigaglia C. (2010). The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nat Rev Neurosci* 11: 264–274.
- Roether CL, Omlor L, Christensen A, Giese MA. (2009). Critical features for the perception of emotion from gait. *J Vis* 9: 15.1–32.
- Rose D, Clarke TJ. (2009). Look who's talking: Visual detection of speech from whole-body biological motion cues during emotive interpersonal conversation. *Perception* 38: 153–156.
- Ross PD, Polson L, Grosbras M-H. (2012) Developmental changes in emotion recognition from full-light and point-light displays of body movement. *PLoS One* 7: e44815.
- Runeson S, Frykholm G. (1983). Kinematic specification of dynamics as

information basis for the person-and-action perception: expectation, gender recognition, and deceptive intention. *J. Exp. Psychol.* 112,: 585–615.

Sabattineli D, Flaisch T, Bradley MM, Fitzsimmons JR, Lang PJ. (2004). Affective picture perception: gender differences in visual cortex? *NeuroReport* 15: 1109–112.

Saygin AP. (2007). Superior temporal and premotor brain areas necessary for biological motion perception. *Brain.* 130: 2452-61.

Schneider S, Christensen A, Häußinger FB, Fallgatter AJ, Giese MA, Ehlis AC. (2014). Show me how you walk and I tell you how you feel - a functional near-infrared spectroscopy study on emotion perception based on human gait. *Neuroimage.* 85 Pt 1: 380-90.

Schouten B, Troje NF, Brooks A, van der Zwan R, Verfaillie K. (2010). The facing bias in biological motion perception: effects of stimulus gender and observer sex. *Atten Percept Psychophys* 72: 1256–1260.

Schouten B, Troje NF, Verfaillie K. (2011). The facing bias in biological motion perception: structure, kinematics, and body parts. *Atten Percept Psychophys* 73: 130–143.

Sevdalis V, Keller PE. (2011). Captured by motion: dance, action understanding, and social cognition. *Brain Cogn.* 77: 231-6.

Simion F, Regolin L, Bulf H. (2008). A predisposition for biological motion in the newborn baby. *Proc Natl Acad Sci USA.* 105: 809-13.

Simion F, Di Giorgio E, Leo I, Bardi L. (2011). The processing of social stimuli in early infancy: from faces to biological motion perception. *Prog Brain Res.* 189:173-93.

Sinigaglia C, Rizzolatti G. (2011). Through the looking glass: self and others. *Conscious Cogn* 20: 64–74.

Sokolov AA, Erb M, Gharabaghi A, Grodd W, Tatagiba MS, Pavlova MA. (2012). Biological motion processing: the left cerebellum communicates with the right superior temporal sulcus. *Neuroimage.* 59: 2824-30.

Sokolov AA, Erb M, Grodd W, Pavlova MA. (2014a). Structural loop between the cerebellum and the superior temporal sulcus: evidence from diffusion tensor imaging. *Cereb Cortex* 24: 626-32.

Sokolov AA, Erb M, Grodd W, Tatagiba MS, Frackowiak RS, Pavlova MA. (2014b). Recovery of biological motion perception and network plasticity after cerebellar tumor removal. *Cortex.* 59: 146-52.

Sokolov AA, Gharabaghi A, Tatagiba M, Pavlova M. (2010). Cerebellar engagement in an action observation network. *Cereb. Cortex* 20: 486–491.

Sokolov AA, Krüger S, Enck P, Krägeloh-Mann I, Pavlova MA. (2011). Gender affects body language reading. *Front Psychol* 2: 16.

Sokolov AA, Zeidman P, Erb M, Pollick FE, Fallgatter AJ, Ryvlin P, Friston KJ, Pavlova MA. (2020). Brain circuits signaling the absence of emotion in body language. *Proc Natl Acad Sci U S A.* 117: 20868-20873.

- Sokolov AA, Zeidman P, Erb M, Ryvlin P, Friston KJ, Pavlova MA. (2018). Structural and effective brain connectivity underlying biological motion detection. *Proc Natl Acad Sci USA*. 115: E12034-E12042.
- Spencer JM, Sekuler AB, Bennett PJ, Christensen BK. (2013). Contribution of coherent motion to the perception of biological motion among persons with Schizophrenia. *Front Psychol*. 4: 507.
- Spencer JM, Sekuler AB, Bennett PJ, Giese MA, Pilz KS. (2016). Effects of aging on identifying emotions conveyed by point-light walkers. *Psychol Aging*. 31: 126-138.
- Strauss GP, Keller WR, Koenig JI, Sullivan SK, Gold JM, Buchanan RW. (2015). Endogenous oxytocin levels are associated with the perception of emotion in dynamic body expressions in schizophrenia. *Schizophr Res*. 162: 52-6.
- Sumi S. (1984). Upside-down presentation of the Johansson moving light-spot pattern. *Perception* 13: 283-286.
- Tamietto M, de Gelder B. (2010). Neural bases of the non-conscious perception of emotional signals. *Nat. Rev. Neurosci*. 11: 697–709.
- Taylor NM, Jakobson LS, Maurer D, Lewis TL (2009). Differential vulnerability of global motion, global form, and biological motion processing in full-term and preterm children. *Neuropsychologia* 47: 2766–2778.
- Thoresen JC, Vuong QC, Atkinson AP (2012). First impressions: gait cues drive reliable trait judgements. *Cognition* 124: 261–271.
- Vaina LM, Solomon J, Chowdhury S, Sinha P, Belliveau JW. (2001). Functional neuroanatomy of biological motion perception in humans. *Proc Natl Acad Sci* 98: 11656-61.
- Van de Cruys S, Schouten B, Wagemans J. (2013). An anxiety-induced bias in the perception of a bistable point-light walker. *Acta Psychol (Amst)*. 144: 548-53.
- Van Meel J, Verburch H, DeMeijer M. (1993). Children's interpretation of dance expressions. *Empirical Studies of the Arts* 11: 117–133.
- Vaskinn A, Lagerberg TV, Bjella TD, Simonsen C, Andreassen OA, Ueland T, Sundet K. (2017). Impairment in emotion perception from body movements in individuals with bipolar I and bipolar II disorder is associated with functional capacity. *Int J Bipolar Disord*. 5: 13.
- Vaskinn A, Sundet K, Østefjells T, Nymo K, Melle I, Ueland T. (2016). Reading Emotions from Body Movement: A Generalized Impairment in Schizophrenia. *Front Psychol*. 6: 2058.
- Virji-Babul N, Kerns K, Zhou E, Kapur A, Shiffrar M. (2006). Perceptual-motor deficits in children with Down syndrome: implications for intervention. *Down Syndr Res Pract* 10: 74–82.
- Vonck S, Swinnen SP, Wenderoth N, Alaerts K. (2015). Effects of Transcranial Direct Current Stimulation on the Recognition of Bodily Emotions from Point-

Light Displays. *Front Hum Neurosci.* 9: 438.

Walk RD, Homan CP. (1984). Emotion and dance in dynamic light displays. *Bull Psychon Soc* 22: 437–440.

White NC, Fawcett JM, Newman AJ. (2014). Electrophysiological markers of biological motion and human form recognition. *Neuroimage.* 84: 854-67.

Wrase J, Klein S, Gruesser DM, Hermann D, Flor H, Mann K, Braus DF, Heinz A. (2003). Gender differences in the processing of standardized emotional visual stimuli in humans: a functional magnetic resonance imaging study. *Neurosci. Lett.* 348: 41–45.

Wynn JK, Green MF, Helleman G, Reavis EA, Marder SR. (2019). A dose-finding study of oxytocin using neurophysiological measures of social processing. *Neuropsychopharmacology* 44: 289-294.

Yoon JM, Johnson SC. (2009). The development of gaze behaviors in response to biological motion displays. *Child Dev.* 80: 1069-75.

Zucker N, Moskovich A, Bulik CM, Merwin R, Gaddis K, Losh M, Piven J, Wagner HR, LaBar KS. (2013). Perception of affect in biological motion cues in anorexia nervosa. *Int J Eat Disord.* 46: 12-22.

8. DECLARATION OF AUTHORS' CONTRIBUTION

1. GENDER AFFECTS BODY LANGUAGE READING

Sokolov AA, Krüger S, Enck P, Krägeloh-Mann I, Pavlova MA
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Arseny A. Sokolov (Department of Neurosurgery, Medical School, Eberhard Karls University of Tübingen) contributed to the design and supervised the experiments. He was responsible for the data analysis and wrote the manuscript.

Samuel Krüger contributed to the performance of the experiments, data analysis, preparing and writing of the manuscript.

Paul Enck (Department of Psychosomatic Medicine and Psychotherapy, Medical School, Eberhard Karls University of Tübingen) provided guidance in the design of the stimuli and for the analysis tools.

Ingeborg Krägeloh-Mann (Department of Pediatric Neurology and Developmental Medicine, Children's Hospital, Medical School, Eberhard Karls University of Tübingen) participated in designing and supervision of the study.

Marina A. Pavlova (Department of Pediatric Neurology and Developmental Medicine, Children's Hospital, Medical School, Eberhard Karls University of Tübingen) contributed to the study design; she guided data analysis and interpretation of the data and supervised the whole project.

2. EMOTION THROUGH BODY MOTION: GENDER IMPACT

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Samuel Krüger conceived and designed the study and stimuli creation; he was responsible for conducting experiments and participants recruitment. He contributed to data analysis and preparing and writing the paper.

Alexander N. Sokolov (Department of Psychosomatic Medicine and Psychotherapy, Medical School, Eberhard Karls University of Tübingen) contributed to the data analysis and statistical tools used. He also contributed to the writing.

Paul Enck (Department of Psychosomatic Medicine and Psychotherapy, Medical School, Eberhard Karls University of Tübingen) provided guidance in the design of the stimuli and for the analysis tools.

Ingeborg Krägeloh-Mann (Department of Pediatric Neurology and Developmental Medicine, Children's Hospital, Medical School, Eberhard Karls University of Tübingen) participated in design of the study.

Marina A. Pavlova (Department of Pediatric Neurology and Developmental Medicine, Children's Hospital, Medical School, Eberhard Karls University of Tübingen) contributed to the study design; she guided data analysis and interpretation of the data; she supervised the whole work.

All authors agree with the use and publication of the manuscript in Samuel Krüger's doctoral thesis entitled 'Emotion revealed through body motion: gender impact'

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