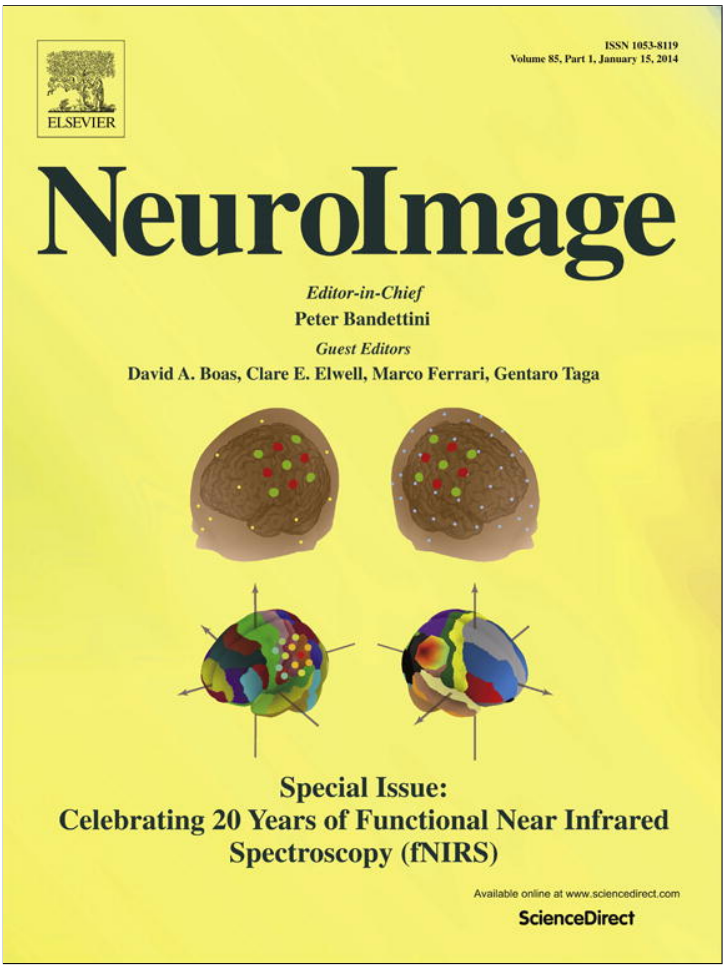

NeuroImage 85 (2014) 380–390

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

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

Sabrina Schneider [a,*,1], Andrea Christensen [b,c], Florian B. Häußinger [a], Andreas J. Fallgatter [a], Martin A. Giese [b,c,2], Ann-Christine Ehlis [a,2]

[a] University Clinic of Psychiatry and Psychotherapy, Department of General Psychiatry, University of Tuebingen, 72076, Germany
[b] Section for Computational Sensomotorics, Department of Cognitive Neurology, Hertie Institute for Clinical Brain Research, University Clinic Tuebingen, 72076, Germany
[c] Centre for Integrative Neuroscience, University Clinic Tuebingen, 72076, Germany

ARTICLE INFO

Article history:
Accepted 29 July 2013
Available online 3 August 2013

Keywords:
Emotion perception
Bodily expressions
Human gait
Near-infrared spectroscopy

ABSTRACT

The ability to recognize and adequately interpret emotional states in others plays a fundamental role in regulating social interaction. Body language presents an essential element of nonverbal communication which is often perceived prior to mimic expression. However, the neural networks that underlie the processing of emotionally expressive body movement and body posture are poorly understood.

33 healthy subjects have been investigated using the optically based imaging method functional near-infrared spectroscopy (fNIRS) during the performance of a newly developed emotion discrimination paradigm consisting of faceless avatars expressing fearful, angry, sad, happy or neutral gait patterns. Participants were instructed to judge (a) the presented emotional state (emotion task) and (b) the observed walking speed of the respective avatar (speed task).

We measured increases in cortical oxygenated haemoglobin (O_2HB) in response to visual stimulation during emotion discrimination. These O_2HB concentration changes were enhanced for negative emotions in contrast to neutral gait sequences in right occipito-temporal and left temporal and temporo-parietal brain regions. Moreover, fearful and angry bodies elicited higher activation increases during the emotion task compared to the speed task. Haemodynamic responses were correlated with a number of behavioural measures, whereby a positive relationship between emotion regulation strategy preference and O_2HB concentration increases after sad walks was mediated by the ability to accurately categorize sad walks.

Our results support the idea of a distributed brain network involved in the recognition of bodily emotion expression that comprises visual association areas as well as body/movement perception specific cortical regions that are also sensitive to emotion. This network is activated less when the emotion is not intentionally processed (i.e. during the speed task). Furthermore, activity of this perceptive network is, mediated by the ability to correctly recognize emotions, indirectly connected to active emotion regulation processes. We conclude that a full understanding of emotion perception and its neural substrate requires the investigation of dynamic representations and means of expression other than the face.

Introduction

The ability to correctly detect and recognize emotional states in others represents a fundamental requirement for adequate social interaction. It enables us to appropriately interpret social situations and to adapt our own behaviour to given conditions. Impaired emotion recognition is thus related to prominent deficits in social functioning. Accordingly, emotion recognition deficits have been observed in a variety of psychiatric syndromes, such as affective diseases (Gur et al., 1992; Mandal and Bhattacharya, 1985; Milders et al., 2010; Schaefer et al., 2010), eating disorders (Ridout et al., 2012), and different types of personality disorders (Dickey et al., 2011; Levine et al., 1997; Marissen et al., 2012). They are also central in schizophrenia (Chan et al., 2010; Edwards et al., 2002; Hellewell and Whittaker, 1998), and in the case of autism, they even represent the core deficit (Hobson et al., 1988; Philip et al., 2010).

Over a period of several decades, emotion recognition was investigated predominantly by means of facial stimuli. Neurobiological research on facial emotion perception revealed that emotion related activation increases in brain areas associated with face perception, such as the fusiform face area (FFA; Ganel et al., 2005; Jacob et al.,

* Corresponding author at: Psychophysiology & Optical Imaging, Department of Psychiatry and Psychotherapy, University of Tuebingen, Calwerstrasse 14, 72076 Tuebingen, Germany. Fax: +49 7071 29 4141.
E-mail address: S.Schneider@med.uni-tuebingen.de (S. Schneider).
[1] This work is part of the dissertation of Sabrina Schneider.
[2] A.-C. Ehlis and M. A. Giese contributed equally to this work.

1053-8119/$ – see front matter © 2013 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.neuroimage.2013.07.078

2012; Vuilleumier and Pourtois, 2007; Vuilleumier et al., 2001), superior temporal sulcus (Haxby et al., 2000; Winston et al., 2004), and inferior occipital gyrus (Fusar-Poli et al., 2009). Moreover, emotional face expressions have been reported to trigger neural activation within a distributed network, including the amygdala, the insula, the cerebellum, and prefrontal as well as orbitofrontal brain regions, (see Fusar-Poli et al., 2009), whereupon regional activation increases partly depend on the respective emotion perceived.

Although facial expression plays – without question – a crucial role in human social function, there are good reasons to broaden emotion recognition research by additionally studying body language expressions. First, in a number of daily situations body language is more accessible than facial expressions, e.g. if the face is averted or a person is observed from a distance. It has further been shown that the perception of facially expressed emotions is significantly affected by whole-body expressions (Meeren et al., 2005; Van den Stock et al., 2007). Moreover, although traditional and widely accepted approaches assume separate processing of facial identity and emotion following an initial stage of structural encoding (Breen et al., 2000; Bruce and Young, 1986), there is some evidence that the recognition of facial expression and identity is not entirely independent (Atkinson et al., 2005; Ellamil et al., 2008; Schweinberger and Soukup, 1998). While to our knowledge no studies have so far investigated interaction effects of emotion and identity for body movements, there are some studies showing that identity recognition and discrimination from moving bodies is, though possible, associated with very poor performance (Kozlowski and Cutting, 1977; Westhoff and Troje, 2007), indicating that identity is unlikely to strongly affect emotion processing from body language. Considering that facial emotion recognition, in contrast, may indeed be affected by identity, a holistic view of neural and cognitive mechanisms underlying emotion perception from body language appears even more reasonable.

Against this background, an increasing number of functional brain imaging studies have addressed the anatomical and functional substrates of emotion perception based on body expressions. Beyond face selective areas, circumscribed brain regions have been reported that are specialized in processing human body posture, body movements and/or body expressions, partially overlapping with those areas associated with the recognition of facial expressions: ventral parts of the fusiform gyrus (fusiform body area, FBA; Peelen and Downing, 2005, 2007; Schwarzlose et al., 2005), a region within the lateral occipitotemporal cortex (extrastriate body area, EBA; Downing et al., 2001), and the superior temporal sulcus (STS; Grossman et al., 2000; Krakowski et al., 2011). Using anatomical landmarks, a recent study further identified the inferior temporal gyrus (ITG), which is directly neighboured to the lateral fusiform cortex, as a relevant region for the perception of human bodies and limbs (Weiner and Grill-Spector, 2011). Recent studies explicitly assessing the neural processing of body expressions indicate that emotions indeed modulate brain activity within these brain regions. In addition to enhanced amygdala activity (Hadjikhani and de Gelder, 2003; Peelen et al., 2007), emotion-related increases in brain activation after the presentation of body expressions have been observed in the FBA (Hadjikhani and de Gelder, 2003; Kret et al., 2011; Pichon et al., 2008; van de Riet et al., 2009), the ITG (De Gelder et al., 2004b; Prochnow et al., 2013), the EBA (Atkinson et al., 2012; see de Gelder et al., 2010 for an overview; Grèzes et al., 2007; Kret et al., 2011; Peelen et al., 2007; Pichon et al., 2008), the STS (Grèzes et al., 2007; Kret et al., 2011; Peelen et al., 2010; Van den Stock et al., 2011), the temporo-parietal junction (TPJ; Grèzes et al., 2007; Pichon et al., 2009; Sinke et al., 2009) and frontal brain regions (de Gelder et al., 2004a; Peelen et al., 2010; van de Riet et al., 2009; Van den Stock et al., 2011). It has to be noted, that these effects strongly depend on whether the affective state was presented by means of static vs. dynamic body expressions. Recent research indicates that activation in the STS, a region that is known for its crucial role in social information perception (Kreifelts et al., 2009, 2010), is enhanced by emotional compared to neutral body expressions only if dynamic stimuli are presented (Grèzes et al., 2007). Moreover, emotional modulation of the EBA, in particular, is only evident in studies using dynamic, but not static, body expressions (de Gelder et al., 2010).

Human gait reflects a specific type of dynamic body motion which provides sufficient information for the perception of expressed motivational or emotional states (Karg et al., 2010; Montepare et al., 1987, 1999; Roether et al., 2009a,b). Using biological motion stimuli in terms of animated point-light displays, previous studies showed that emotions from point-light walkers can be reliably discriminated (Atkinson et al., 2004; Clarke et al., 2005; Dittrich et al., 1996) and, moreover, it has been demonstrated that emotional content facilitates gait identification (Chouchourelou et al., 2006; Ikeda and Watanabe, 2009). Until now, only very few brain imaging studies on the neurofunctional substrates of the perception of dynamic body expressions from gait patterns exist. Heberlein et al. (2004) used dynamic point-light stimuli that were based on walking actors expressing four different emotions (happiness, anger, fear, and sadness) to determine cortical regions that are involved in emotion recognition in healthy subjects and patients with brain damage. Their findings suggest a crucial role of the right parietal cortex in emotion recognition from point-light walkers (Heberlein et al., 2004). Using similar stimulus material, Atkinson et al. (2007) reported a case in which a patient showed normal emotion discrimination during the spot-light walkers' paradigm despite complete bilateral amygdala lesion that was accompanied by strong impairments in recognizing emotions from facial expressions (Atkinson et al., 2007), indicating that additional cerebral areas, such as cortical structures, may be crucially involved in emotion perception from point-light walkers.

Unlike in studies using point-light stimuli, many previous studies addressing the emotional modulation of body selective brain activity often drew on visual stimuli that were either restricted with respect to external validity (e.g., headless bodies were presented) or confounded with information other than bodily emotion perception (e.g. age, gender, or even facial expression). In order to counteract such confounding factors, the present study used whole body avatars that were established by Roether et al. (2009a). They recorded 25 individuals expressing different emotional states during walking by motion capture. Resulting recordings were computationally transformed into three-dimensional avatars using (see Materials and methods section). The appearance of these avatars does not unveil information about the representative's age, sex, ethnicity, or facial expression while validly displaying the recorded emotional gait pattern and, by being more "human-like", reflecting higher ecological validity compared to point-light walkers.

During the last decade, near-infrared spectroscopy (NIRS) has been proven to reliably depict cortical activation changes based on vascular responses in a broad range of emotion perception tasks (Herrmann et al., 2003, 2008; Köchel et al., 2011; Minati et al., 2009; Nakato et al., 2011). In a recent study, for example, Köchel et al. (2011) reported emotional modulation of oxygenation changes in the left occipital cortex: Both the perception as well as the imagery of happy and disgusting pictures were associated with stronger increases in oxygenated haemoglobin (O_2Hb) compared to neutral stimuli.

In order to investigate neurophysiological correlates of emotion recognition from gait patterns expressed by avatars, we conducted 52-channel near-infrared spectroscopy (NIRS) measurements in a group of healthy subjects. Due to its frequently quoted advantages (Ernst et al., 2012; Fallgatter et al., 2004), especially its quick and easy applicability in a noise-free, highly naturalistic setting, NIRS offers the opportunity to assess a large number of different subject groups characterized by certain needs or limitations, such as children or patients suffering from psychiatric diseases. While some fMRI studies already targeted cerebral processing of dynamic body expressions (see above), developmental aspects or pathologic

alterations of brain activity in this context are rather unexplored so far. As NIRS can be a useful tool in order to examine this new research field, we plan to investigate potential alterations within the bodily emotion perception cortical network, focussing on their classificational and predictive potency in different psychiatric syndromes (Major Depression, Schizophrenia, Anxiety Disorders). In order to have a solid basis that is fundamental for these large-scale NIRS investigations, the core aim of the present study is to investigate whether emotion specific cortical activation patterns related to human gait perception can be reliably detected using NIRS measurements. Based on recent literature on the cortical representation of dynamic body expressions and emotion modulation of cortical haemodynamic responses (see above), we hypothesize that avatars displaying emotional (i.e. fearful, sad, angry, or happy) gait patterns provoke higher O_2Hb increases compared to neutral gait within the EBA, the ITG, the STS, and the TPJ. The posterior part of the ITG, specifically, has been chosen because it has been associated with body perception and it is directly adjacent to the Fusiform Gyrus (FG). The FG as a typical region of interest in emotional body perception studies is, in turn, located on the ventral surface of the temporal lobe and the central/medial FG is hence unlikely to be directly assessable using fNIRS. Therefore, the present study will focus on peripheral areas of the FBA together with the neighboured posterior ITG. We also expect emotion discrimination accuracy as well as self-rated discriminability to correlate with cortical activation measured with near-infrared spectroscopy.

Materials and methods

Subjects

A total of 31 Caucasian and 2 Asian subjects (10 males, 23 females) were enrolled in the present study. Participants were recruited via email announcements and postings at the Departments of Psychology and General Psychiatry at the University of Tuebingen. Mean age was 28.9 (range: 18–51) years. All participants were right handed, as assessed by means of the Edinburgh Handedness Inventory (Oldfield, 1971) and did not exhibit current or past psychiatric illness. Further exclusion criteria were severe neurological disease (e.g., epilepsy, encephalitis), untreated diabetes or instable/untreated hypertension. Permission for the study was obtained from the local Ethics Committee of the University of Tuebingen; all study procedures were in line with the Declaration of Helsinki in its latest version. After complete description of the study to the participants, written informed consent was obtained.

Stimuli

The dynamic body stimuli used in the present study were provided by the Section of Computational Sensomotorics (Head: Prof. Martin A. Giese) at the Hertie Institute for Clinical Brain Research Tuebingen, Germany (Roether et al., 2008, 2009a,b). Avatar videos were created in three steps: First, gait sequences of 13 lay theatre actors were recorded using a VICON optical motion capture system (VICON, Oxford, UK) with eight cameras which can be utilized to track and record bodies in motion based on infrared camera recordings. The actors were instructed to walk straight within a proscribed area of approximately 5 m in length, during neutral walking and emotionally expressive walking (anger, sadness, fear, and happiness), and they were explicitly encouraged to avoid gestures that would have interrupted their rhythmic walking pattern. The actors' involvement in each affective state was ensured using a mood-induction paradigm based on the imagination of sentimental past life events. In order to capture neutral walking sequences that were speed matched to the – by nature – slower (e.g., sad walk) or faster (e.g., angry walk) emotionally expressive gait patterns, some actors were required to express neutral walk of three different speeds: At first, they were instructed to move at their customary walking speed followed by walking sequences of increased (instruction: “Walk faster than normal.”) or decreased (instruction: “Walk slower than normal.”) walking speed, respectively.

The motion captured walking data was animated using custom build software. The resulting video clips showed grey, volumetric avatars that walked as on a treadmill. Walking direction was either slightly to the left or to the right (about 22°) to provide the observer with a more lateral view on the avatar which has been shown to be beneficial for emotion perception. Video clip duration was 3 s (see Supplementary material for example videos).

Experimental procedure

The emotion discrimination paradigm consisted of two tasks: In one-half of the experiment, participants had to identify the emotion expressed by the respective avatar (neutral, anger, sadness, fear, and happiness), whereas in a second task, the moving speed of each presented avatar had to be judged on a five-point scale (from “very slow” up to “very fast”) in order to achieve common scaling for both tasks. The latter task was implemented in order to investigate possible attentional effects, i.e. the influence of task/perceptual state (intended emotion discrimination vs. unattended emotion perception during speed judgements) on the cortical processing of the different emotion categories. Therefore, the same video stimuli were presented in both task blocks and task order was counterbalanced across subjects. For each task, subjects had to judge 120 video trials, with 24 videos per emotion category (neutral, anger, sadness, fear, and happiness). Hereby, each emotion category consisted of three different actor videos, of which each was presented in two different movement directions (avatar walking from left to right and from right to left) and was repeated four times, leading to 24 trials per stimulus category. To account for the fact that emotions expressed through gait patterns are usually confounded with speed (i.e., some emotions, such as sadness, are typically associated with slow walking speed, whereas others [e.g. anger] are linked to fast speeds), neutral walks were speed matched to the emotional walks by subdividing the neutral category into three different walking speeds (slow neutral walk, medium neutral walk, fast neutral walk).

Participants were seated comfortably in a sound-attenuated room approximately 75 cm in front of a computer screen. They were instructed to watch all videos attentively and to either judge the expressed emotion (emotion task) or the respective walking speed of the avatar (speed task) via button press. The letters “Q”, “W”, “P”, “Ü” and the space-button on a German keyboard served as response buttons and key assignment was counterbalanced across participants. Each trial started with a fixation cross that was presented in the centre of the screen for 500 ms. After another 100 ms of blank screen, an avatar video was presented for 3000 ms. The video trial was again followed by a gap (blank screen) for 100 ms. After this gap, a response screen appeared that displayed the response options and their respective key assignment. This response screen remained until the key response was provided, whereby the maximal response time was set to 2000 ms in order to limit total experiment duration. Hence, each trial had a minimum duration of 3700 ms and a maximum duration of 5700 ms and there was a jittered inter-trial interval (ITI) of 4000–7000 ms which has been shown as a proper interval in previous NIRS studies (Telkemeyer et al., 2011; Tupak et al., 2013) while even much shorter stimulus-onset intervals (SOAs) have been reported recently (Heilbronner and Muente, 2013). At the beginning of each task, a practice block comprising 10 video trials (two per emotion category) was carried out. The maximum total duration of the experiment came up to 48 min without breaks, but the actual duration was usually shorter due to average response times of 490 ± 165 ms instead of 2000 ms. Breaks were implemented at three fixed time points

throughout the experiment and their duration could be determined by the participant.

Right after the experiment, participants were asked to rate the experimental material concerning its emotional content, emotion recognisability, and perceived arousal during stimulus perception. To this end, 30 videos (six per category) from the main experiment were presented again, and after each video subjects had to provide their judgements on a five-point Likert-scale for emotional content (1 = not at all; 5 = very, for sad, fearful, angry, and happy, respectively) as well as for recognisability (1 = not at all recognizable; 5 = very easily recognizable), and arousal (1 = not arousing; 5 = very arousing).

Several psychometric scales were additionally applied in order to assess subject's current emotional state (Beck Depression Inventory [BDI], Positive and Negative Affect Schedule [PANAS], and the State version of the State-Trait Anxiety Inventory [STAI]). The trait version of the STAI was used to further gather information about personality variations concerning anxiety. To assess interindividual preferences regarding emotion regulation strategies, the Emotion Regulation Questionnaire (ERQ) was also completed by each subject.

Near-infrared spectroscopy

NIRS measurements were conducted with the ETG-4000 Optical Topography System (Hitachi Medical Corporation, Tokyo, Japan) using a 52-channel array of optodes (17 light sources/emitters and 16 detectors) covering posterior (corresponding to occipital–parietal–temporal cortex regions) areas on the head. Emitter-detector distance was 30 mm for contiguous optodes and near-infrared light of two wavelengths (695 and 830 nm, respectively) was used. NIRS optodes were attached to the subject's head using a plastic array of optode holders in a rectangular shape that was placed on the occiput with respect to the international 10/20 system (Jasper, 1958) in such a way that channel 37 (the middle channel in the lowest of five channel rows) corresponded to the location of Oz (see Fig. 1), and the anterior NIRS channels 43 (left side) and 52 (right side) were equivalent to the temporal electrode positions T3 (T7) and T4 (T8), respectively.

To obtain anatomic channel assignment the plastic optode holder array was placed on a volunteer's head and respective optode positions were determined using a neuronavigation system [LOCALITE GmbH, St. Augustin, Germany]. The resulting optode coordinates were transferred from the volunteer's native MRI space to the standard MNI space by applying normalization routines from Statistic Parametric Mapping (SPM) 8 (http://www.fil.ion.ucl.ac.uk/spm/software/spm8/). The normalized coordinates were projected on a brain template in order to calculate estimates that indicate which brain region is most probably located below a certain channel. Fig. 1 displays the so-estimated cortical projection points of the NIRS channels and their probabilistic assignment to respective Brodmann Areas (Brodmann, 1909).

Data analyses

With the ETG-4000, changes in the concentration of oxygenated haemoglobin (O_2Hb) and deoxygenated haemoglobin (HHb) were recorded from a 10 s starting baseline continuously throughout the entire paradigm. Signals obtained from the 52 NIRS channels were measured with a sampling rate of 10 Hz, and analyzed and transformed according to their wavelength and location, resulting in values for the changes in the concentration of oxygenated and deoxygenated haemoglobin for each channel. Haemoglobin quantity is scaled in mmol∗mm, implying that all concentration changes depend on the path length of the NIR light in the brain. Subsequent analyses of the recorded data were performed using MATLAB 7.9.0 (The MathWorks Inc., Natick, USA) and IBM SPSS Statistics (Armonk, NY, USA). Firstly, data was filtered using a .008–.25 Hz band pass. The pre-processed data was then assessed by applying a General Linear Model (GLM) approach to the NIRS data time series (see Plichta et al., 2007). Hence, functional data can be modelled as:

$$\mathbf{Y} = \boldsymbol{X} * \boldsymbol{\beta} + \varepsilon,$$

with $\mathbf{Y}$ as a time × channel matrix consisting of the entire functional NIRS time series, whereas $\mathbf{X}$ constitutes the design matrix containing the respective modelled effects, further including $\boldsymbol{\beta}$ as the parameter matrix comprising the beta weights to be estimated and the error term ε. More precisely, the design matrix $\mathbf{X}$ of the type time × number of modelled effects comprises the predicted hemodynamic response function (stick function) for each experimental condition over time, with stimulus (i.e. avatar video) onset as starting point. This GLM based assessment represents a common analysis approach for fMRI data (Friston et al., 1995) and has also been increasingly described for NIRS data assessment (see Plichta et al., 2006, 2007; Schroeter et al., 2004). The hypothesized stick function was a Gaussian curve with a modelled peak time (PT) of 9 s after stimulus onset (corresponds to 6 s after stimulus offset, compare Fig. 2, upper panel) due to previous data showing that event-related haemodynamic response function (HRF) in striate areas peaks at around 6 s after an event (Aguirre et al., 1998; Buckner et al., 1996). As visual inspection of the averaged event-related haemodynamic responses revealed that actual PTs were delayed in a number of (particularly lateral) channels (see Fig. 2, lower panel), we decided to test a second model with a hypothesized PT of 11 s after stimulus onset. In both cases, beta weights were estimated using the method of least squares indicating the amplitude of brain activation. In order to identify channels with significant O_2Hb increases after stimulation, we performed separate one sample t-tests (contrast value: 0) for each condition and channel on the estimated beta weights. For the first GLM analyses (PT = 9 s), t-tests revealed significant O_2Hb activation increases, indicated by significantly positive beta weights, in channels 25, 28, 36, and 38 ($2.87 < t < 4.13$, $2.40 * e^{-4} < p < .007$, Bonferroni–Holm corrected) after neutral walks. Activation patterns for the four emotion categories were highly similar. Overall, the channels with significant and marginally significant ($t > 2.0$, $p < .05$) activation increases were restricted to occipital areas. In contrast, the second GLM analyses revealed significant increases of O_2Hb in channels 1–14, 16, 19–21, 23, 30–31, 33–34, 41, 43–44, 48, and 51–52 ($3.70 < t < 5.51$, $4.50 * e^{-6} < p < 7.98 * e^{-4}$, Bonferroni–Holm corrected), whereby these channels are located over visual association areas instead of the occipital pole/V1. This finding implies that different perceptual processes were assessed depending on the respectively modelled HRF peak time.

To account for (1) this variability in peak latencies between different brain regions (posterior-occipital vs. lateral/temporo-parietal) and (2) the fact that in some predominantly laterally located channels the O_2Hb time course seemed too complex to be modelled by a Gaussian haemodynamic response function (see Fig. 2, lower panel), an additional model-free analysis that abandons fixed unimodal HRF peak times was performed. This strategy enabled us to investigate the effects of emotional content on body movement perception instead of assessing different particular sub-processes within the complex mechanism of emotion perception and recognition. Hereby, data were analyzed in an event-related fashion, i.e., NIRS data segments were created according to each of the five stimulus emotion categories (neutral, sad, angry, fearful, and happy). Segments started 2 s prior to video presentation (baseline) and lasted until 20 s following the stimulus (stimulation period). Amplitude averages of the haemodynamic response functions (HRFs) of O_2Hb within a 6–14 s segment following the onset of the presented avatar video were calculated per subject per condition. Analogously, an automatic peak detection determining maximum values of the respective HRFs was performed within this time window. Visual data

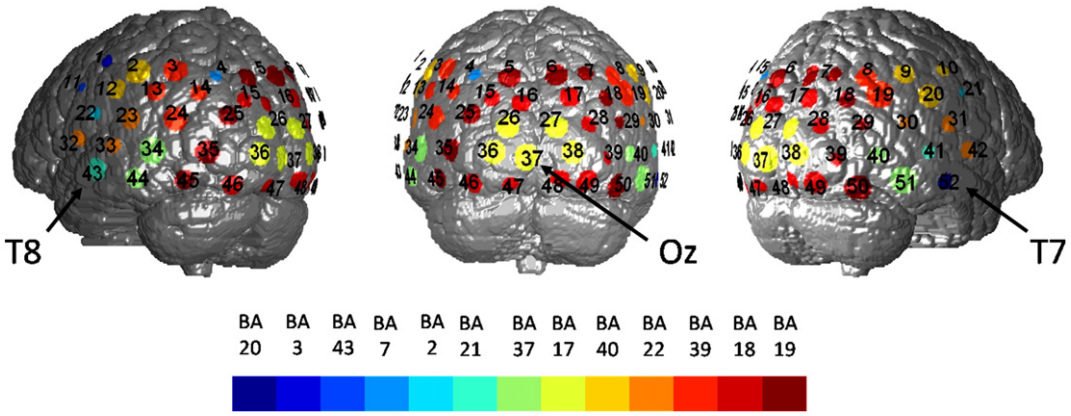

Fig. 1. 3D illustration of NIRS channel arrangement over the brain resulting from the neuronavigation procedure as described in the Materials and methods section. Colours indicate the respectively assigned Brodmann Area (BA). Blob size is associated with the probability of the respective channel-BA assignment.

inspection confirmed that HRF amplitudes and peaks were identifiable within this time window (see Fig. 2). Exact peak values as well as mean amplitude values were exported in order to perform subsequent statistical analysis. To reduce complexity, only mean amplitude results are presented here. However, it is important to note that resulting activation patterns were quite similar for peak values and mean amplitudes.

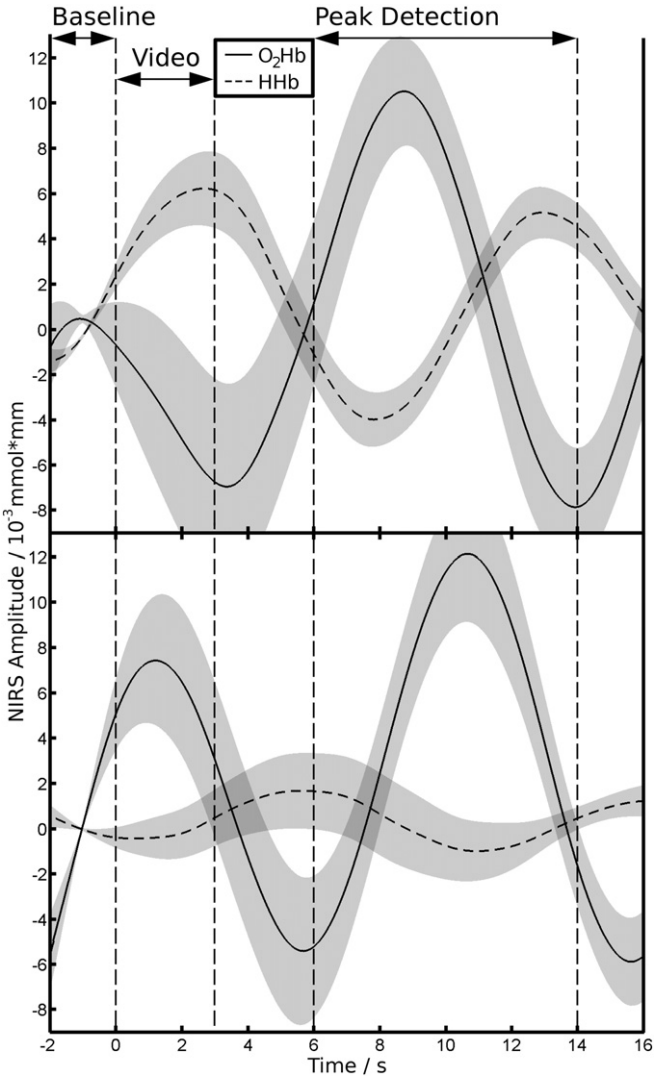

Fig. 2. Typical course of the haemodynamic response function (HRF) in the occipital pole (upper panel) and an exemplary ROI (left TPJ; lower panel) averaged over subjects (n = 33). Dashed vertical lines mark baseline period of the segment, avatar video onset and offset as well as the pre-defined peak-detection interval. Solid curve: oxygenated haemoglobin, dashed curve: deoxygenated haemoglobin. Greyed out thick lines in the time course indicate HRF standard deviations.

Regions of interest (ROI) definition

In order to perform hypotheses-based data analyses, certain cortical regions of interest (ROIs) were defined a priori according to recent findings from bodily emotion expression studies. According to state of the art research, at least four cortical regions are distinguishable that seem to be critically involved in the perception of bodily emotion expression: (1) the posterior part of the ITG (Brodmann Area 37) including the lateral–peripheral part of the FBA; (2) the EBA (e.g. Grèzes et al., 2007; Sinke et al., 2009), located at the junction of the visual association cortex (Brodmann Area 18) and the posterior angular gyrus (Brodmann Area 39); (3) The inferior part of the supramarginal gyrus (Brodmann Area 40), including the TPJ (e.g. Pichon et al., 2009); and (4) the posterior STS (e.g. Peelen et al., 2010). Table 1 contains the channels that formed each particular ROI with the respective MNI (Montreal Neurologic Institute) coordinates as determined by the neuro-navigation procedure (see Fig. 1).

Statistics

Behavioural data (accuracy and reaction times, recognition and arousal ratings) were analyzed by means of repeated measures analyses of variance (RM-ANOVAs) for repeated measures with the within-subject factors task (emotion vs. speed) and emotion (neutral, sad, fearful, angry, and happy). Ratings concerning emotional content were further analyzed performing univariate ANOVAs for repeated measures comprising the within-subject variable category which further considered different walking speeds of the avatars (neutral slow, neutral medium, neutral fast, sad, fearful, angry, and happy). Paired *t*-tests (with Bonferroni–Holm correction applied) were computed as post-hoc analyses whenever an ANOVA revealed significant effects.

Mean O_2Hb amplitudes were analyzed with 2×5 RM-ANOVAs comprising the within-subject variables task and emotion for each ROI. In order to verify whether potential effects of condition occur specifically within the pre-defined ROIs, mean O_2Hb amplitude values for all channels not included in one of the ROIs were computed and a final ANOVA for repeated measures (again including the factors task and emotion) on non-ROI channels was performed. Bonferroni–Holm (BH) correction procedure was used to correct for multiple analyses caused by the investigation of four different ROIs per hemisphere. Separate RM-ANOVAs for both tasks including the factor emotion, and paired one-sided *t*-tests, respectively, were performed whenever main

or interaction effects were significant in any of the computed ANOVAs. Once again, BH-correction was performed to adjust respective alpha levels, leading to adjusted alpha levels of $.0125 < p < .05$.

With respect to the psychometric data, a sum score was calculated for the BDI. Regarding the STAI, PANAS and ERQ, sum scores were created for the respective subscales. The STAI thus consisted of a state score and a trait score, the PANAS of a positive and a negative affect score, and the ERQ of the components "emotion suppression" and "re-evaluation of the situation/context". Eventually, Pearson's correlation coefficients were calculated between the ascertained psychometric scores and the emotion-dependent haemodynamic brain activation parameters (i.e., mean amplitudes of O_2Hb) within ROIs that previously revealed emotion category effects on mean O_2Hb amplitudes. We further correlated the haemodynamic parameters with emotion discrimination performance (accuracy and RTs in the emotion identification task), and subjective stimulus ratings (emotion recognisability and subjective arousal that was evoked by a certain stimulus condition) within each emotion category. For the sake of conciseness, only haemodynamic parameters from the relevant emotion discrimination task block were used for these correlation analyses. Hereby, two-sided testing procedures and Bonferroni–Holm correction were used, leading to a corrected alpha of .003–.05 for r(O_2Hb mean amplitudes, psychometric scales), and 0.125–.05 for correlations between O_2Hb mean amplitudes and behavioural performance (accuracy, RTs) as well as subjective ratings (emotion recognisability, subjectively elicited arousal) per emotion category.

Results

Behavioural data

Table 2 contains arithmetic means and standard deviations (SDs) for accuracy and RTs during the emotion and the speed task blocks for each emotion category. With respect to response accuracy, the RM-ANOVA revealed significant main effects of emotion ($F(4,128) = 39.60$, $p < .001$, $\eta^2 = .55$) and task ($F(1,32) = 135.40$, $p < .001$, $\eta^2 = .81$) as well as a significant interaction of both factors ($F(4,128) = 15.68$, $p < .001$, $\eta^2 = .33$). Post-hoc t-tests showed that response accuracy was similar in both tasks for fearful avatars ($t(32) = 0.20$; $p = .85$) whereas task performance differed with respect to the other emotion categories ($-9.36 < t < -2.87$, $p < .05$; BH-corrected): Within the emotion discrimination task, emotion recognition accuracy was highest for sad and fearful, followed by angry and happy avatars ($-11.53 < t < 6.28$, $p < .05$; BH-corrected), while accuracy for neutral avatars was lowest ($-10.19 < t_{neutral–others} < -4.10$, $p < .05$; BH-corrected). For the speed judgements, response accuracy was highest for sad and happy ($t(32) = -1.20$; $p = .24$), followed by all other categories ($1.90 < t < 4.92$, $p < .05$; $p < .05$; BH-corrected). Regarding RTs for trials with correctly identified emotions, there were significant main effects for both task ($F(1,32) = 9.48$, $p < .01$, $\eta^2 = .23$) and emotion ($F(4,128) = 4.75$, $p < .01$, $\eta^2 = .13$). Responses were provided faster in the speed judgement than in the emotion discrimination task ($p < .01$). Post-hoc t-tests investigating the emotion effect revealed fastest reaction times for angry followed by neutral, sad, and happy walks ($2.16 < t < 4.37$, $p < .05$; BH-corrected) and slowest responses overall for fearful walks ($2.42 < t < 4.37$, $p < .05$; BH-corrected).

Stimulus rating analyses revealed significant main effects of emotion category with respect to subjective emotion recognisability ($F(6,192) = 23.14$, $p < .001$, $\eta^2 = .42$), perceived arousal ($F(6,192) = 9.26$, $p < .001$, $\eta^2 = .22$), and each of the emotional content ratings ($82.41 < F_{ratings} < 263.43$). Further analyses indicated that sad walks were most easily recognizable ($M = 4.19 \pm .54$), followed by angry walks ($M = 3.90 \pm .41$; $t_{sad–angry} = 3.06$, $p < .05$; BH-corrected), followed by fearful ($M = 3.66 \pm .55$; $t_{angry–fearful} = 2.31$; $p < .05$; BH-corrected) and happy ($M = 3.51 \pm .57$; $t_{angry–happy} = 4.23$, $p < .05$; BH-corrected) walks, and with lowest recognisability rates for all types of neutral walks ($M_{neutral–slow} = 3.04 \pm 0.73$; $M_{neutral–medium} = 2.82 \pm 0.68$; $M_{neutral–fast} = 3.14 \pm 0.92$, $-8.56 < t_{neutral–sad/angry/fear/happy} < -2.50$, $p < .05$; BH-corrected). While arousal ratings were generally low, highest arousal was elicited by sad walks ($M = 1.77 \pm .65$) followed by fearful ($M = 1.53 \pm .67$; $t_{sad–fearful} = 3.02$, $p < .05$; BH-corrected), angry ($M = 1.45 \pm .65$; $t_{sad–fearful} = 3.12$, $p < .05$; BH-corrected) and slow neutral walks ($M = 1.46 \pm .67$; $t_{sad–fearful} = 3.33$, $p < .05$; BH-corrected); medium speed ($M = 1.23 \pm .37$) and fast neutral ($M = 1.17 \pm .39$) as well as happy ($M = 1.32 \pm .54$) walks were associated with lowest arousal rates.

Neurophysiological data

The 2×5 RM-ANOVAs revealed BH-corrected significant main effects of emotion for the right EBA ($F(4,128) = 3.00$, $p < .0167$, $\eta^2 = .10$), the right ITG ($F(4,128) = 2.67$, $p < .025$, $\eta^2 = .08$), the left TPJ ($F(4,128) = 3.00$, $p < .0167$, $\eta^2 = .09$), and the left posterior STS (pSTS, $F(4,128) = 3.03$, $p < .01$, $\eta^2 = .10$). A significant main effect of task was only found in the right EBA with overall higher activation increases during the emotion discrimination compared to the speed judgement task ($F(4,128) = 4.27$, $p < .025$, $\eta^2 = .12$). Moreover, with respect to the right EBA and the left TPJ there was a significant task × emotion interaction ($2.27 < F < 2.81$, $p < .05$). Therefore, separate RM-ANOVAs for the emotion discrimination and the speed judgement task were conducted. Respective results showed that a main effect of emotion was only apparent in the emotion discrimination task ($3.88 < F < 4.08$, $p < .01$) but not in the speed judgement task ($1.19 < F < 1.60$, $p > .10$) within the EBA and TPJ. During the emotion task block, right EBA and left TPJ activity was enhanced for sad, fearful, and angry compared to neutral walks ($2.35 < t < 3.36$, $p < .05$; BH-corrected) while there was no difference between the happy and neutral condition ($t_{EBA}(32) = 0.84$, $p = .41$, $t_{TPJ}(32) = 0.96$, $p = .35$). To further analyze the main effect of emotion regarding the right ITG and

Table 1
NIRS channel assignment to the present regions of interest (ROIs) and respective MNI coordinates.

Left hemisphere			Right hemisphere		
ROI	Channels	MNI coordinates (x, y, z)	ROI	Channels	MNI coordinates (x, y, z)
EBA	14	−79, 41, 36	EBA	18	−82, −43, 32
	24	−69, 54, 21		29	−78, −50, 18
ITG	34	−60, 62, 3	ITG	40	−71, −57, 1
	44	−52, 67, −12		51	−58, −63, −14
pSTS	23	−47, 65, 22	pSTS	30	−58, −63, 20
	33	−38, 70, 6		41	−46, −70, 3
TPJ	12	−34, 64, 36	TPJ	19	−67, −55, 34
	13	−57, 58, 36		20	−42, −66, 35
	22	−23, 66, 25		31	−8, 65, 5

Table 2
Arithmetic mean values and standard deviations (SD) for accuracy and reaction times (RTs) within the emotion task block and the speed task block, respectively. Accuracy reflects the relative frequency of correct responses.

	Emotion task block				Speed task block			
	Accuracy		Reaction rimes (RTs) in ms		Accuracy		Reaction rimes (RTs) in ms	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Neutral	.60	.14	555	203	.84	.16	433	141
Sad	.92	.11	542	225	.98	.04	430	135
Angry	.73	.08	496	192	.91	.10	419	157
Fearful	.92	.08	540	199	.92	.17	484	161
Happy	.74	.14	525	203	.97	.05	437	150

the left STS, subsequently calculated paired t-tests showed that mean amplitudes of O_2Hb concentration changes in the right ITG were generally higher for sad, fearful, and angry vs. neutral walks ($2.35 < t < 3.36$, $p < .05$; BH-corrected). With respect to the left pSTS, increased O_2Hb peak values were observed for sad and fearful as compared to neutral stimuli ($2.14 < t < 3.22$, $p < .05$; BH-corrected). Again, there was no O_2Hb concentration difference between the neutral and happy category ($t(32) = 1.85$, $p = .08$).

Eventually, 2×5 RM ANOVAs for the mean activation of all non-ROI channels did not reveal any significant main or interaction effects ($0.8 < F < 3.9$, $p > .05$). Fig. 3 displays differential O_2HB concentration changes for sad, angry, fearful, and happy walks as contrasted to the neutral walks (control condition).

Relationship of neurophysiological data, behavioural, and subjective measures

There were significant positive correlations between the preference for a favourable emotion regulation strategy (re-evaluation of the situation) and haemodynamic responses within the left posterior STS after angry walks ($r = .42$, $p < .0167$) and the left TPJ after angry ($r = .51$, $p < .0125$) or sad avatars ($r = .35$, $p < .05$) were presented. None of the other psychometric measures correlated significantly with NIRS activation within one of the ROIs. Interestingly, however, explorative calculations revealed that emotion regulation further correlated positively with sadness identification accuracy ($r = .49, p < .0125$). Sadness identification accuracy, again, was strongly correlated with O_2Hb concentration changes within the right ITG ($r = .43$, $p < .0125$), marginally significant within the EBA ($r = .33$, $p = .058$), and highly significant regarding the left posterior STS, and left TPJ (both: $r = .53$, $p < .01$) after viewing sad avatars. Hence, in order to clarify whether the above reported correlation between left temporal brain activation and emotion regulation strategy preference was mediated by emotion recognition accuracy, the partial correlation coefficient $r_{X,Y,Z}$ was correlated, with X = emotion regulation strategy preference, Y = O_2Hb concentration increases after sad walks in the left TPJ, and Z = sadness identification accuracy. Keeping Z constant, the relation between emotion regulation and cortical activation vanished ($r = .11$, n.s.; see Fig. 4).

Analogue to the accuracy–brain response correlations, we found significantly negative correlations between RTs and cortical activation parameters for sad avatars: $r_{RT,left\ TPJ} = -.46$, $p < .01$; $r_{RT,left\ STS} = -.40$, $p = .019$. There was also a trend for such a negative correlation in the angry condition ($r_{RT,left\ TPJ} = -.41, p = .018$) that did, however, not meet Bonferroni–Holm significance level correction. For sad avatars, subjective recognisability tended to correlate positively with haemodynamic responses ($r_{Recogn,left\ TPJ} = .40$, $p = .02$; $r_{Recogn,left\ STS} = .33$, $p = .05$).

Discussion

The present study addressed the question whether fNIRS is a reliable method for depicting activity changes in cortical regions that are associated with emotion perception from human body movements. As fNIRS is known for its great advantages in the field of psychiatry research (Ehlis et al., 2014), the NIRS paradigm investigated and presented in the present study will be the method of choice for future applications within big samples of psychiatric patients suffering from different psychological syndromes. In order to elucidate the method's potential to investigate the activity of a distributed brain network involved in bodily emotion expression, the present study investigated the effects of emotion modulation on cortical haemodynamic responses elicited by the perception of dynamic human gait patterns and assessed via fNIRS. This study constitutes the first approach using functional NIRS in combination with newly developed dynamic body stimuli that are characterized by high ecologic validity and simultaneously allow to control for a number of possibly confounding factors (such as walking speed or actor's gender). Our results suggest that activation within a cortical network, involving right and left occipito-temporo-parietal areas, is enhanced when negative emotional gaits (sad, fearful or angry) are observed. There was no such effect for positive emotions (i.e. happy walks).

In more detail, significant activation increases were observed for sad, angry, and fearful gait patterns within the right EBA, the right ITG, and the left TPJ during the emotion task. Angry and fearful walks further elicited brain activation increases in the left posterior STS. We interpret this finding in terms of emotion recognition processes. Viewing the body movements already enhances O_2 metabolism, as indicated by increases in O_2HB concentration that also occurred when neutral walks were observed. However, differentially pronounced O_2HB concentration increases for sad, angry, and fearful compared to neutral gait

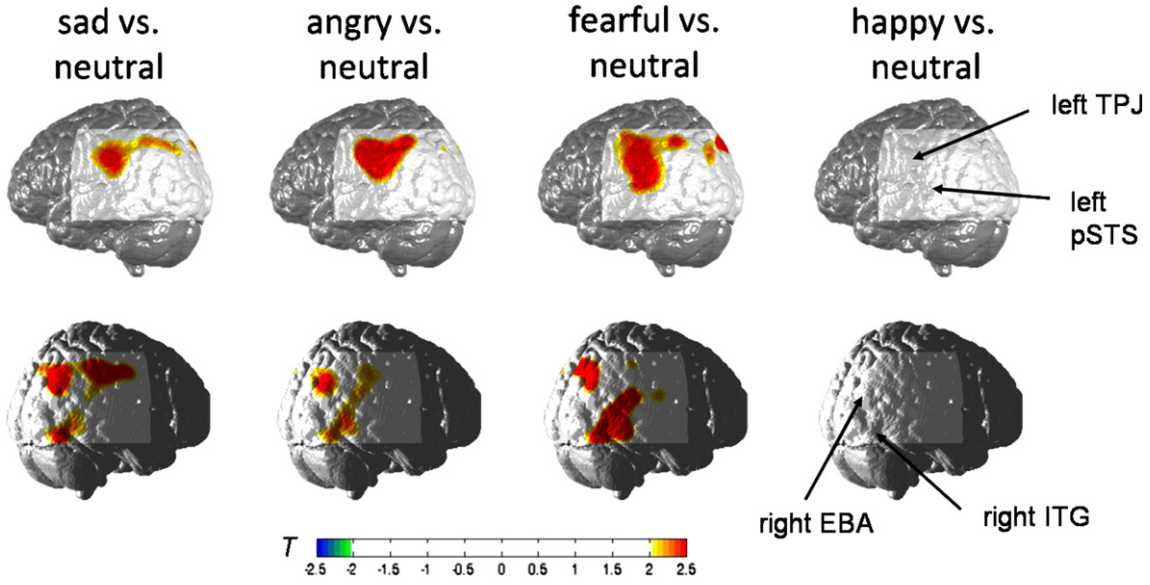

Fig. 3. Contrast maps illustrating the differential O_2HB concentration changes for sad, angry, fearful, and happy walks, each contrasted to the control condition (neutral walks). T-values for the respective differences in O_2HB amplitude values (emotional–neutral) are depicted. For reasons of simplification, only T-values > ±2 are displayed. Arrows indicate the location of the following regions of interest (ROIs): left TPJ, left posterior STS (pSTS), right EBA, and right ITG. Contrast maps were created using MATLAB (The MathWorks Inc.).

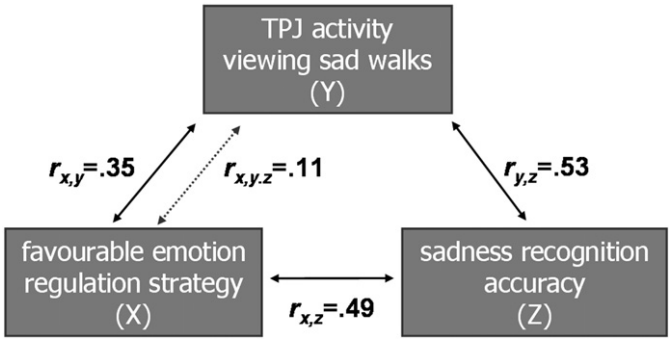

Fig. 4. Graphical illustration of the relationship between O_2HB amplitudes in the left TPJ after sad walks, emotion recognition accuracy after sad walks, and preference of favourable emotion regulation. Pearson correlation coefficients ($r_{x,y}/r_{x,z}/r_{y,z}$) and the partial correlation coefficient $r_{x,y,z}$ are provided.

patterns suggest that functional activity within these cortical areas is linked to the perception of negative emotions. This interpretation is particularly supported by the finding that mean O_2HB concentration increases in all non-ROI channels did not differ between emotional and neutral body movements, implying that activity in these non-ROI cortical areas was not modulated by emotional expressions. As the neutral avatar videos were speed matched to the emotional stimuli, we conclude that the observed brain activation pattern reflects neurophysiological processes that are specific for the emotional content of the gait pattern rather than speed sensitive. In sum, we could show that emotional modulation of cerebral activation in body sensitive cortical areas can be (1) demonstrated for basic types of body movements (gait) and (2) depicted using NIRS measurements. Interestingly, the present study further indicated that for NIRS paradigms involving videos of emotional body movements such as the one implemented in the present experiment, different analysis strategies may lead to very different outcomes and therefore need to be considered carefully. In detail, model-based (GLM) NIRS data analyses were found to be less appropriate to assess our haemodynamic data for two main reasons: First, while model-based topographical analyses require one specific peak-time that will be equally modelled for all channels, a relatively high variability in peak latencies between different brain regions of interest (occipital vs. temporo-parietal) was observed here. Second, event-related averages of the haemodynamic responses further showed that, especially within laterally located channels, the O_2Hb time course was too complex to be simulated by a Gaussian haemodynamic response function (see lower panel of Fig. 2) which, therefore, would have been rather inappropriate to model the HRF in the present data. This complex time course of O_2Hb, in some channels already apparent during the baseline period, may be attributed to the occurrence of complex evaluative processes that are involved in the perception of (especially emotional) body movements. This interpretation is further supported by the fact that a rather pure NIRS signal (no baseline signal change, only one clear HRF peak) can be observed in primary visual areas associated with rather basic encoding of visual input. However, an alternative explanation for the complex O_2Hb course observed in some temporo-parietal channels that cannot be entirely ruled out refers to the somewhat short ITI used in the present study which may have led to an affection of a given HRF by the respectively proceeding trial. Although similar ITIs have been reported in previous NIRS studies (e.g., Telkemeyer et al., 2011; Tupak et al., 2013), it cannot be conclusively clarified whether video triggered HRFs could have somewhat influenced the subsequent trial. Further studies using a smaller number of experimental conditions but extended ITIs may help to elucidate this question.

Consistent with the present results, previous studies addressing the anatomic and functional correlates of emotion perception from whole body movements identified different cortical brain regions that may be involved, such as the EBA, the ITG/FBA, the STS, and the TPJ (e.g., Grèzes et al., 2007; Kret et al., 2011; see also Introduction). Especially for fearful and angry body movements, brain activation increases have been reported in these areas (e.g., Kret et al., 2011; Pichon et al., 2009). Although certain deeper brain regions (amygdala, insula) have been shown to be also sensitive for emotion expressed in bodies and/or body movements (Hadjikhani and de Gelder, 2003; Peelen et al., 2007), by now the majority of studies focus on the main cortical regions, such as the EBA, FBA, or the STS. Enhanced cortical haemodynamic responses, however, were observed only for negative but not positive (i.e. happy) emotional walks in the present study. This finding may a) reflect a valence effect of emotional stimulation on regional brain activation patterns or b) be attributed to restricted expressiveness of the specific type of stimulation material (avatar gait patterns) for positive emotions. Although findings from other neuroimaging studies could help to clarify the background of this lacking effect for happy walks, the neurophysiological response to happy whole body movements has been poorly investigated so far, as most experiments used stimuli of negative valence. Peelen et al. (2007) and Atkinson et al. (2012) reported enhanced activity in the EBA and FBA for both angry and happy body movements compared to neutral stimuli. These studies suggest that body sensitive cortical regions such as the EBA or the FBA are sensitive for both negative and positive emotion categories. In contrast to the present experiment, these studies used point-light instead of full-light stimuli showing typical emotional gestures instead of emotional walks. Moreover, analyses of the stimulus ratings revealed that happy walks were most difficult to identify by our subjects. The positive correlation between emotion recognition accuracy and activation in the right ITG, left TPJ, left posterior STS, and, to a lesser degree, in the right EBA, suggests that easier and better emotion recognition was associated with higher cortical activation within respective areas. Emotion recognition accuracy, in turn, is related to the emotional expressiveness of a given stimulus. We therefore conclude that happy avatar walks in particular may have lacked emotional expressiveness and were thus not associated with a significant increase in cortical brain activation in contrast to the negative emotion categories. Moreover, there is another feature in which happy walks may differ from the other three emotional gait patterns, that is related to emotional and behavioural implications of the perceived emotional body expression for the observer. Whereas sad and also fearful body expressions may trigger secondary emotional reactions, such as empathy, in the observer, threatening (i.e. angry) walks may be associated with an activation of our internal defence or avoidance system. In both cases, the perceived emotion has relevant implications for the observer. A number of theories emphasize the communicative function of emotional expressions and postulate a direct link between perceiving other's emotional states and own motivational and action tendencies, including approach and avoidance behaviour (see for example Fischer and Manstead, 2008; Frijda, 2010; Lang and Bradley, 2010; Niedenthal and Brauer, 2012; Reis and Gray, 2009). In contrast to sad, fearful and angry body movements, the observation of happy walks may initiate less personal involvement due to their, compared with negative walks, reduced personal relevance and implications for the observer's behaviour. Whereas happy faces have been shown to induce approach behaviour during behavioural studies (Rotteveel and Phaf, 2004; Seidel et al., 2010; Stins et al., 2012), we propose that happy walking patterns may be less crucial for indicating reward and thus trigger appetitive behaviour to a lesser extent than happy, smiling faces. This could, at least in part, explain the missing haemodynamic effect of happy avatar walks in the present study. This interpretation is strongly supported by a behavioural study conducted by Ikeda and Watanabe (2009), who investigated emotion recognition in point-light walkers using neutral, angry and happy biological motion stimuli that were embedded in dynamic noise (moving dots). Participants had to a) judge whether moving dot stimuli contained biological motion (gait identification task) and b) identify the expressed emotion in these trials containing

biological motion (emotion recognition task). Results revealed that emotion detection performance was higher for angry compared to happy walks and correlation analyses revealed that only for angry – but not for happy – biological motion emotion recognition performance was clearly linked to gait detection performance. The authors suggest that it may be more crucial for the observer to identify walks of aggressive rather than happy persons. Our present results support this hypothesis.

A detailed review of the recent literature concerning neurobiological emotion perception from whole-body movements revealed emotion-specific brain activation increases in cortical regions that are associated with body perception during various different task designs and paradigms. In some studies, subjects had to explicitly name the observed emotion (Pichon et al., 2009; Sinke et al., 2009; van de Riet et al., 2009), whereas other investigations used oddball paradigms containing up-right and inverted body stimuli (Grèzes et al., 2007; Kret et al., 2011; Pichon et al., 2008). Again other studies had participants provide intensity ratings for each seen emotion (Peelen et al., 2007, 2010). Brain activation patterns in respective brain regions, such as the EBA, FBA, TPJ, and the STS, therefore appear to be independent of task type. Taking the factor task block into account, our statistical analyses revealed mixed results: Although we found similar O_2HB concentration increases within the pre-defined ROIs after viewing emotional vs. neutral avatars, significant task-by-emotion interactions for the right EBA and the left TPJ indicated that for these two areas, emotion related signal increases were significant only for the emotion discrimination task. Hence, additional processes of conscious emotion recognition occurring during the emotion task block may have reinforced the emotion specific cortical activation within the EBA and the TPJ. With respect to the STS and ITG, however, emotion triggered brain activation increases took place even when the emotional content is perceived unintentionally. This finding is well-consistent with the observation made by de Gelder and Hadjikhani (2006) in a patient with unilateral striatal cortex damage: presentation of happy vs. neutral body images to the patient's blind hemifield triggered activation increases within the STS and the inferior temporal sulcus, pointing towards possible implicit bodily emotion perception in those areas.

In order to investigate certain relationships between the observed cerebral activation patterns and behavioural outcomes, additional correlation analyses were computed. Hereby, a crucial role of particularly the sad avatars was reflected in the various correlations that were found for O_2HB concentration increases and emotion recognition performance, subjective recognisability and personal emotion regulation strategies. Whereby high positive correlations between O_2HB amplitudes and emotion regulation were also observed for angry avatars, we found an interesting threefold relationship between cortical haemodynamic responses, emotion recognition performance, and emotion regulation preferences only for sad walks (see Fig. 4): High preference for functional emotion regulation strategies (trying to re-evaluate a situation whenever bad feelings occur in order to cheer up) was associated with better recognition performance and higher brain activation increases, which were themselves positively correlated with emotion recognition performance. The computation of partial correlation coefficients showed that the relationship between emotion regulation behaviour and brain activation in the TPJ after sad avatars was entirely mediated by the ability to correctly recognize sad walks. This correlation pattern illustrates the connection between interindividual differences concerning the ability to recognize sadness from pure gait and personal emotion regulation tendencies as well as the neurophysiological counterpart of sadness recognition. This leads us to the hypothesis that certain populations showing dysfunctional emotion regulation strategies – such as psychiatric patients – may show impaired sadness recognition from gait patterns and may thus be linked to accordingly lowered cortical responses to sad body movements. Future studies investigating respective patient groups are needed to further investigate this hypothesis.

Despite these interesting findings that leave much room for interpretation and raise possible future research questions, there are some limitations in this study that need to be kept in mind. An important restriction is the limitation of neurophysiological data acquisition to temporo-parietal and occipital areas. Different studies have reported an involvement of frontal brain areas, especially the inferior frontal gyrus (IFG) and premotor cortex (PMC), in emotion processing from whole-body movements (Grèzes et al., 2007; Pichon et al., 2009; Sinke et al., 2009). Amoruso et al. (2011) proposed a model of an integrative brain network, including the prefrontal cortex, that might be critical for contextual emotion recognition from human action (Amoruso et al., 2011). The present investigation primarily focussed on posterior regions of interest, for which the most robust effects have been reported in previous research. In future studies, however, another probeset arrangement or even the simultaneous use of two NIRS systems (in order to double the number of assessable channels) should be considered.

Conclusions

The present study provides a new and innovative approach to investigate neurophysiological correlates of emotion recognition from human gait. For both stimulation material (computer-animated avatar videos that were created from motion-captured actors) and neurophysiological assessments (NIRS measurements), methods of particularly high ecological validity were used. We showed that negative emotional gait patterns, but not happy walks, were associated with brain activation increases in the right EBA, right ITG, left TPJ and left STS, cortical regions that have been consistently shown to respond to dynamic body expressions (other than gait) in previous studies using different stimuli and imaging techniques. Our results further indicate that these cortical activation patterns were confirmed for sad gait patterns even if the emotional content was unattended, and that they are related to emotion recognition performance and, at least indirectly, to emotion regulation tendencies. We conclude that fNIRS is now ready for further applications to assess functional alterations in the here reported cortical activation patterns in people suffering from psychiatric diseases. Future studies should therefore explore cortical activity in different neuropsychiatric disorders linked to alterations in affective processing. NIRS has been proven to be a useful tool aiming at these perspectives.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2013.07.078.

Acknowledgments

The present study was supported by the Medical Faculty of the University of Tuebingen (*f*ortüne programme, no. 2013-0-0) and the EC FP7 Project TANGO (Grant FP7-249858-TP3). We thank Hitachi Medical Co., Japan for their skilled technical support whenever needed. Moreover, we would particularly like to thank Elke Stefanie Smith for her perseveringly support during the data acquisition phase as well as Ramona Taeglich and Betti Schopp for their trustworthy and proficient technical assistance. Saskia Deppermann, Katja Hagen, and Agnes Kroczek contributed significantly with their patient and flexible support during data acquisition.

Conflict of interest

The authors have no conflicts of interest to declare for the current submission.

References

Aguirre, G.K., Zarahn, E., D'Esposito, M., 1998. The variability of human, BOLD hemodynamic responses. NeuroImage 8, 360–369.

Amoruso, L., Couto, J.B., Ibanez, A., 2011. Beyond extrastriate body area (EBA) and fusiform body area (FBA): context integration in the meaning of actions. Front. Hum. Neurosci. 5.

Atkinson, A.P., Dittrich, W.H., Gemmell, A.J., Young, A.W., 2004. Emotion perception from dynamic and static body expressions in point-light and full-light displays. Perception 33, 717–746.

Atkinson, A.P., Tipples, J., Burt, D.M., Young, A.W., 2005. Asymmetric interference between sex and emotion in face perception. Percept. Psychophys. 67, 1199–1213.

Atkinson, A.P., Heberlein, A.S., Adolphs, R., 2007. Spared ability to recognise fear from static and moving whole-body cues following bilateral amygdala damage. Neuropsychologia 45, 2772–2782.

Atkinson, A.P., Vuong, Q.C., Smithson, H.E., 2012. Modulation of the face- and body-selective visual regions by the motion and emotion of point-light face and body stimuli. NeuroImage 59, 1700–1712.

Breen, N., Caine, D., Coltheart, M., 2000. Models of face recognition and delusional misidentification: a critical review. Cogn. Neuropsychol. 17, 55–71.

Brodmann, K., 1909. Vergleichende Lokalisationslehre der Grosshirnrinde. Barth, Leipzig.

Bruce, V., Young, A., 1986. Understanding face recognition. Br. J. Psychol. 77, 305–327.

Buckner, R.L., Bandettini, P.A., O'Craven, K.M., Savoy, R.L., Petersen, S.E., Raichle, M.E., Rosen, B.R., 1996. Detection of cortical activation during averaged single trials of a cognitive task using functional magnetic resonance imaging. Proc. Natl. Acad. Sci. U. S. A. 93, 14878–14883.

Chan, R.C.K., Li, H., Cheung, E.F.C., Gong, Q.-y, 2010. Impaired facial emotion perception in schizophrenia: a meta-analysis. Psychiatry Res. 178, 381–390.

Chouchourelou, A., Matsuka, T., Harber, K., 2006. The visual analysis of emotional actions. Soc. Neurosci. 1, 63–74.

Clarke, T.J., Bradshaw, M.F., Field, D.T., Hampson, S.E., Rose, D., 2005. The perception of emotion from body movement in point-light displays of interpersonal dialogue. Perception 34, 1171–1180.

de Gelder, B., Hadjikhani, N., 2006. Non-conscious recognition of emotional body language. NeuroReport 17, 583–586.

de Gelder, B., Snyder, J., Greve, D., Gerard, G., Hadjikhani, N., 2004a. Fear fosters flight: a mechanism for fear contagion when perceiving emotion expressed by a whole body. Proc. Natl. Acad. Sci. U. S. A. 101, 16701–16706.

De Gelder, B., Snyder, J., Greve, D., Gerard, G., Hadjikhani, N., 2004b. Fear fosters flight: amechanism for fear contagion when perceiving emotion expressed by a whole body. Proc. Natl. Acad. Sci. U. S. A. 101, 16701–16706.

de Gelder, B., Van den Stock, J., Meeren, H.K.M., Sinke, C.B.A., Kret, M.E., Tamietto, M., 2010. Standing up for the body. Recent progress in uncovering the networks involved in the perception of bodies and bodily expressions. Neurosci. Biobehav. Rev. 34, 513–527.

Dickey, C.C., Panych, L.P., Voglmaier, M.M., Niznikiewicz, M.A., Terry, D.P., Murphy, C., Zacks, R., Shenton, M.E., McCarley, R.W., 2011. Facial emotion recognition and facial affect display in schizotypal personality disorder. Schizophr. Res. 131, 242–249.

Dittrich, W.H., Troscianko, T., Lea, S.E., Morgan, D., 1996. Perception of emotion from dynamic point-light displays represented in dance. Perception 25, 727–738.

Downing, P.E., Jiang, Y., Shuman, M., Kanwisher, N., 2001. A cortical area selective for visual processing of the human body. Science 293, 2470–2473.

Edwards, J., Jackson, H.J., Pattison, P.E., 2002. Emotion recognition via facial expression and affective prosody in schizophrenia: a methodological review. Clin. Psychol. Rev. 22.

Ehlis, A.-C., Schneider, S., Dresler, T., Fallgatter, A.J., 2014. Application of functional near-infrared spectroscopy in psychiatry. NeuroImage 85, 478–488.

Ellamil, M., Susskind, J.M., Anderson, A.K., 2008. Examinations of identity invariance in facial expression adaptation. Cogn. Affect. Behav. Neurosci. 8, 273–281.

Ernst, L.H., Schneider, S., Ehlis, A.C., Fallgatter, A.J., 2012. Functional near infrared spectroscopy in psychiatry: a critical review. JNIRS 20, 93–105.

Fallgatter, A.J., Ehlis, A.C., Wagener, A., Michel, T., Herrmann, M.J., 2004. Nah-Infrarot-Spektroskopie in der Psychiatrie. Nervenarzt 75, 911–916.

Fischer, A.H., Manstead, A.S.R., 2008. Social functions of emotions. In: Lewis, M., Haviland-Jones, J.M., Barrett, L. (Eds.), Handbook of Emotions. Guilford Press, New York, pp. 456–470.

Frijda, N.H., 2010. Impulsive action and motivation. Biol. Psychol. 84, 570–579.

Friston, K.J., Holmes, A.P., Poline, J.B., Grasby, P.J., Williams, S.C.R., Frackowiak, R.S.J., Turner, R., 1995. Analysis of fMRI time-series revisited. NeuroImage 2, 45–53.

Fusar-Poli, P., Placentino, A., Carletti, F., Landi, P., Allen, P., Surguladze, S., Benedetti, F., Abbamente, M., Gasparotti, R., Barale, F., Perez, J., McGuire, P.K., Politi, P., 2009. Functional atlas of emotional faces processing: a voxel-based meta-analysis of 105 functional magnetic resonance imaging studies. J. Psychiatry Neurosci. 34, 418–432.

Ganel, T., Valyear, K.F., Goshen-Gottstein, Y., Goodale, M.A., 2005. The involvement of the "fusiform face area" in processing facial expression. Neuropsychologia 43, 1645–1654.

Grèzes, J., Pichon, S., de Gelder, B., 2007. Perceiving fear in dynamic body expressions. NeuroImage 35, 959–967.

Grossman, E., Donnelly, M., Price, R., Picikens, D., Morgan, V., Neighbor, G., Blake, R., 2000. Brain areas involved in perception of biological motion. J. Cogn. Neurosci. 12, 711–720.

Gur, R.C., Erwin, R.J., Gur, R.E., Zwil, A.S., Heimberg, C., Kraemer, H.C., 1992. Facial emotion discrimination: II. Behavioral findings in depression. Psychiatry Res. 42, 241–251.

Hadjikhani, N., de Gelder, B., 2003. Seeing fearful body expressions activates the fusiform cortex and amygdala. Curr. Biol. 13, 2201–2205.

Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2000. The distributed human neural system for face perception. Trends Cogn. Sci. 4, 223–233.

Heberlein, A.S., Adolphs, R., Tranel, D., Damasio, H., 2004. Cortical regions for judgments of emotions and personality traits from point-light walkers. J. Cogn. Neurosci. 16, 1143–1158.

Heilbronner, U., Muente, T.F., 2013. Rapid event-related near-infrared spectroscopy detects age-related qualitative changes in the neural correlates of response inhibition. NeuroImage 65, 408–415.

Hellewell, J.S.E., Whittaker, J.F., 1998. Affect perception and social knowledge in schizophrenia. In: Mueser, K.T., Tarrier, N. (Eds.), Handbook of Social Functioning in Schizophrenia. Allyn and Bacon, Needham Heigths.

Herrmann, M.J., Ehlis, A.C., Fallgatter, A.J., 2003. Prefrontal activation through task requirements of emotional induction measured with NIRS. Biol. Psychol. 64, 255–263.

Herrmann, M.J., Huter, T., Plichta, M.M., Ehlis, A.-C., Alpers, G.W., Mühlberger, A., Fallgatter, A.J., 2008. Enhancement of activity of the primary visual cortex during processing of emotional stimuli as measured with event-related functional near-infrared spectroscopy and event-related potentials. Hum. Brain Mapp. 29, 28–35.

Hobson, R.P., Ouston, J., Lee, A., 1988. Emotion recognition in autism: coordinating faces and voices. Psychol. Med. 18, 911–923.

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

Jacob, H., Kreifelts, B., Brueck, C., Erb, M., Hoesl, F., Wildgruber, D., 2012. Cerebral integration of verbal and nonverbal emotional cues: impact of individual nonverbal dominance. NeuroImage 61, 738–747.

Jasper, H.H., 1958. The ten-twenty electrode system of the International Federation. Electroencephalogr. Clin. Neurophysiol. 10, 371–375.

Karg, M., Kühnlenz, K., Buss, M., 2010. Recognition of affect based on gait patterns. IEEE Trans. Syst. Man Cybern. 40, 1050–1061.

Köchel, A., Plichta, M.M., SchÃ¤fer, A., Leutgeb, V., ScharmÃ¼ller, W., Fallgatter, A.J., Schienle, A., 2011. Affective perception and imagery: a NIRS study. Int. J. Psychophysiol. 80, 192–197.

Kozlowski, L., Cutting, J., 1977. Recognizing the sex of a walker from a dynamic point-light display. Percept. Psychophys. 21, 575–580.

Krakowski, A.I., Ross, L.A., Snyder, A.C., Sehatpour, P., Kelly, S.P., Foxe, J.J., 2011. The neurophysiology of human biological motion processing: a high-density electrical mapping study. NeuroImage 56, 373–383.

Kreifelts, B., Ethofer, T., Shiozawa, T., Grodd, W., Wildgruber, D., 2009. Cerebral representation of non-verbal emotional perception: fMRI reveals audiovisual integration area between voice- and face-sensitive regions in the superior temporal sulcus. Neuropsychologia 47, 3059–3066.

Kreifelts, B., Ethofer, T., Huberle, E., Grodd, W., Wildgruber, D., 2010. Association of trait emotional intelligence and individual fMRI-activation patterns during the perception of social signals from voice and face. Hum. Brain Mapp. 31, 979–991.

Kret, M.E., Pichon, S., Grèzes, J., de Gelder, B., 2011. Similarities and differences in perceiving threat from dynamic faces and bodies. An fMRI study. NeuroImage 54, 1755–1762.

Lang, P.J., Bradley, M.M., 2010. Emotion and the motivational brain. Biol. Psychol. 84, 437–450.

Levine, D., Marziali, E., Hood, J., 1997. Emotion processing in borderline personality disorders. J. Nerv. Ment. Dis. 185, 240–246.

Mandal, M.K., Bhattacharya, B.B., 1985. Recognition of facial affect in depression. Percept. Mot. Skills 61, 13–14.

Marissen, M.A.E., Deen, M.L., Franken, I.H.A., 2012. Disturbed emotion recognition in patients with narcissistic personality disorder. Psychiatry Res. 198, 269–273.

Meeren, H.K.M., van Heijnsbergen, C.C.R.J., de Gelder, B., 2005. Rapid perceptual integration of facial expression and emotional body language. Proc. Natl. Acad. Sci. U. S. A. 102, 16518–16523.

Milders, M., Bell, S., Platt, J., Serrano, R., Runcie, O., 2010. Stable expression recognition abnormalities in unipolar depression. Psychiatry Res. 179, 38–42.

Minati, L., Jones, C.L., Gray, M.A., Medford, N., Harrison, N.A., Critchley, H.D., 2009. Emotional modulation of visual cortex activity: a functional near-infrared spectroscopy study. Neuroreport 20, 1344–1350.

Montepare, J.M., Goldstein, S.B., Clausen, A., 1987. The identification of emotions from gait information. J. Nonverbal Behav. 11, 33–42.

Montepare, J.M., Koff, E., Zaitchik, D., Albert, M., 1999. The use of body movements and gestures as cues to emotions in younger and older adults. J. Nonverbal Behav. 23, 133–152.

Nakato, E., Otsuka, Y., Kanazawa, S., Yamaguchi, M.K., Kakigi, R., 2011. Distinct differences in the pattern of hemodynamic response to happy and angry facial expressions in infants: a near-infrared spectroscopic study. NeuroImage 54, 1600–1606.

Niedenthal, P.M., Brauer, M., 2012. Social functionality of human emotion. In: Fiske, S.T., Schacter, D.L., Taylor, S.E. (Eds.), Annu Rev Psychol, Vol 63. Annual Reviews, Palo Alto, pp. 259–285.

Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9, 97–113.

Peelen, M.V., Downing, P.E., 2005. Selectivity for the human body in the fusiform gyrus. J. Neurophysiol. 93, 603–608.

Peelen, M.V., Downing, P.E., 2007. The neural basis of visual body perception. Nat. Rev. Neurosci. 8, 636–648.

Peelen, M.V., Atkinson, A.P., Andersson, F., Vuilleumier, P., 2007. Emotional modulation of body-selective visual areas. Soc. Cogn. Affect. Neurosci. 2, 274–283.

Peelen, M.V., Atkinson, A.P., Vuilleumier, P., 2010. Supramodal representations of perceived emotions in the human brain. J. Neurosci. 30, 10127–10134.

Philip, R.C.M., Whalley, H.C., Stanfield, A.C., Sprengelmeyer, R., Santos, I.M., Young, A.W., Atkinson, A.P., Calder, A.J., Johnstone, E.C., Lawrie, S.M., Hall, J., 2010. Deficits in facial, body movement and vocal emotional processing in autism spectrum disorders. Psychol. Med. 40, 1919–1929.

Pichon, S., De Gelder, B., Grèzes, 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., Grèzes, J., 2009. Two different faces of threat. Comparing the neural systems for recognizing fear and anger in dynamic body expressions. NeuroImage 47, 1873–1883.

Plichta, M.M., Herrmann, M.J., Baehne, C.G., Ehlis, A.C., Richter, M.M., Pauli, P., Fallgatter, A.J., 2006. Event-related functional near-infrared spectroscopy (fNIRS): are the measurements reliable? NeuroImage 31, 116–124.

Plichta, M.M., Heinzel, S., Ehlis, A.C., Pauli, P., Fallgatter, A.J., 2007. Model-based analysis of rapid event-related functional near-infrared spectroscopy (NIRS) data: a parametric validation study. NeuroImage 35, 625–634.
Prochnow, D., Hoeing, B., Kleiser, R., Lindenberg, R., Wittsack, H.J., SchÃ¤fer, R., Franz, M., Seitz, R.J., 2013. The neural correlates of affect reading: an fMRI study on faces and gestures. Behav. Brain Res. 237, 270–277.
Reis, D.L., Gray, J.R., 2009. Affect and action control. In: Morsella, E., Bargh, J.A., Gollwitzer, P.M. (Eds.), Oxford Handbook of Human Action. Oxford University Press, Oxford, pp. 277–297.
Ridout, N., Wallis, D.J., Autwal, Y., Sellis, J., 2012. The influence of emotional intensity on facial emotion recognition in disordered eating. Appetite 59, 181–186.
Roether, C.L., Omlor, L., Giese, M.A., 2008. Lateral asymmetry of bodily emotion expression. Curr. Biol. 18, R329–R330.
Roether, C.L., Omlor, L., Christensen, A., Giese, M.A., 2009a. Critical features for the perception of emotion from gait. J. Vis. 9, 1–32.
Roether, C.L., Omlor, L., Giese, M.A., 2009b. Features in the Recognition of Emotions from Dynamic Bodily Expression. In: Mason, G., Ilg, U.J. (Eds.), Dynamics of Visual Motion Processing: Neuronal, Behavioral and Computational Approaches. Springer, New York, Dordrecht, Heidelberg, London, pp. 313–340.
Rotteveel, M., Phaf, R.H., 2004. automatic affective evaluation does not automatically predispose for arm flexion and extension. Emotion 4, 156–172.
Schaefer, K.L., Baumann, J., Rich, B.A., Luckenbaugh, D.A., Zarate Jr., C.A., 2010. Perception of facial emotion in adults with bipolar or unipolar depression and controls. J. Psychiatr. Res. 44, 1229–1235.
Schroeter, M.L., Bucheler, M.M., Muller, K., Uludag, K., Obrig, H., Lohmann, G., Tittgemeyer, M., Villringer, A., von Cramon, D.Y., 2004. Towards a standard analysis for functional near-infrared imaging. NeuroImage 21, 283–290.
Schwarzlose, R.F., Baker, C.I., Kanwisher, N., 2005. Separate face and body selectivity on the fusiform gyrus. J. Neurosci. 25, 11055–11059.
Schweinberger, S.R., Soukup, G.R.d, 1998. Asymmetric relationships among perceptions of facial identity, emotion, and facial speech. J. Exp. Psychol. Hum. Percept. Perform. 24, 1748–1765.
Seidel, E.-M., Habel, U., Kirschner, M., Gur, R.C., Derntl, B., 2010. The impact of facial emotional expressions on behavioral tendencies in women and men. J. Exp. Psychol. Hum. Percept. Perform. 36, 500–507.
Sinke, C.B.A., Sorger, B., Goebel, R., De Gelder, B., 2009. Tease or threat? Judging social interactions from bodily expressions. NeuroImage 49, 1717–1727.
Stins, J., Roelofs, K., Villan, J., Kooijman, K., Hagenaars, M., Beek, P., 2012. Walk to me when I smile, step back when I'm angry: emotional faces modulate whole-body approach-avoidance behaviors. Exp. Brain Res. 212, 603–611.
Telkemeyer, S., Rossi, S., Nierhaus, T., Steinbrink, J., Obrig, H., Wartenburger, I., 2011. Acoustic processing of temporally modulated sounds in infants: evidence from a combined near-infrared spectroscopy and EEG study. Front. Psychol. 2, 1–14.
Tupak, S.V., Dresler, T., Badewien, M., Hahn, T., Ernst, L.H., Herrmann, M.J., Deckert, J., Ehlis, A.-C., Fallgatter, A.J., 2013. Inhibitory transcranial magnetic theta burst stimulation attenuates prefrontal cortex oxygenation. Hum. Brain Mapp. 34, 150–157.
van de Riet, W.A., Grèzes, J., De Gelder, B., 2009. Specific and common brain regions involved in the perception of faces and bodies and the representation of their emotional expressions. Soc. Neurosci. 4, 101–120.
Van den Stock, J., Righart, R., de Gelder, B., 2007. Body expressions influence recognition of emotions in the face and voice. Emotion 7, 487–494.
Van den Stock, J., Tamietto, M., Sorger, B., Pichon, S., Grézes, J., de Gelder, B., 2011. Cortico-subcortical visual, somatosensory, and motor activations for perceiving dynamic whole-body emotional expressions with and without striate cortex (V1). Proc. Natl. Acad. Sci. U. S. A. 108, 16188–16193.
Vuilleumier, P., Pourtois, G., 2007. Distributed and interactive brain mechanisms during emotion face perception: evidence from functional neuroimaging. Neuropsychologia 45, 174–194.
Vuilleumier, P., Armony, J.L., Driver, J., Dolan, R.J., 2001. Effects of attention and emotion on face processing in the human brain: an eventrelated fMRI study. Neuron 30, 829–841.
Weiner, K.S., Grill-Spector, K., 2011. Not one extrastriate body area: using anatomical landmarks, hMT+, and visual field maps to parcellate limb-selective activations in human lateral occipitotemporal cortex. NeuroImage 56, 2183–2199.
Westhoff, C., Troje, N., 2007. Kinematic cues for person identification from biological motion. Percept. Psychophys. 69, 241–253.
Winston, J.S., Henson, R.N.A., Fine-Goulden, M.R., Dolan, R.J., 2004. fMRI-Adaptation reveals dissociable neural representations of identity and expression in face perception. J. Neurophysiol. 92, 1830–1839.