Brain activity correlates with emotional perception induced by dynamic avatars

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Abstract

An accurate judgment of the emotional state of others is a prerequisite for successful social interaction and hence survival. Thus, it is not surprising that we are highly skilled at recognizing the emotions of others. Here we aimed to examine the neuronal correlates of emotion recognition from gait. To this end we created highly controlled dynamic body-movement stimuli based on real human motion-capture data (Roether and colleagues 2009). These animated avatars displayed gait in four emotional (happy, angry, fearful, and sad) and speed-matched neutral styles. For each emotional gait and its equivalent neutral gait, avatars were displayed at five morphing levels between the two. Subjects underwent fMRI scanning while classifying the emotions and the emotional intensity levels expressed by the avatars.

Our results revealed robust brain selectivity to emotional compared to neutral gait stimuli in brain regions which are involved in emotion and biological motion processing, such as the extrastriate body area (EBA), fusiform body area (FBA), superior temporal sulcus (STS), and the amygdala (AMG). Brain activity in the amygdala reflected emotional awareness: for visually identical stimuli it showed amplified stronger response when the stimulus was perceived as emotional. Notably, in avatars gradually morphed along an emotional expression axis there was a parametric correlation between amygdala activity and emotional intensity.

This study extends the mapping of emotional decoding in the human brain to the domain of highly controlled dynamic biological motion. Our results highlight an extensive level of brain processing of emotional information related to body language, which relies mostly on body kinematics.

Introduction

There is a large body of literature concerning the neuronal correlates of both emotional processing and biological motion. However, little is known about the neuronal correlates of perception of bodily emotional expression.

So far, a major part of research exploring expression and recognition of emotions has focused on facial expressions (Allison et al., 2000; Ekman et al., 1969; Gobbini and Haxby, 2007; Haxby et al., 2000; Izard, 1971; Puce et al., 2007; Rossion et al., 2003; Vuilleumier and Pourtois, 2007; Winston et al., 2007). However, body language also carries important information about emotional state and inter-individual signaling, which is sometimes more reliable, accessible and action oriented than facial expressions (Aviezer et al., 2012; De Gelder, 2006). A number of studies have begun mapping brain regions showing selective responses to emotional body expressions, employing either static images or dynamic videos. Studies using static images found that emotional compared to neutral body expressions show enhanced activity in the fusiform face area (FFA), the amygdala and the temporal pole (Grezes et al., 2007; Hadjikhani and de Gelder, 2003; Pichon et al., 2008). Studies using naturalistic dynamic videos showed an increased activity in visual body processing areas, such as the extrastriate body area (EBA), and fusiform body area (FBA), as well as the FFA, the temporal parietal junction (TPJ), and the superior temporal sulcus (STS) which is frequently highlighted in biological motion, goal directed action and emotional research (Atkinson et al., 2012; Grezes et al., 2007; Kret et al., 2011; Pichon et al., 2008; Schneider et al., 2014; Sinke et al., 2010). They also showed increased brain activity in regions that are linked to autonomic regulation – such as the hypothalamus, the ventro-medial prefrontal cortex, and the premotor cortex (Grezes et al., 2007; Pichon et al., 2008).

Previous studies have uncovered differential brain processing for static and dynamic bodily stimuli. Thus, fMRI studies which compared directly static and dynamic emotional body gestures showed an exclusive response to dynamic emotional (angry) body gestures, in STS and premotor cortex (Grezes et al., 2007, Pichon et al., 2008), the hypothalamus, the ventro-medial prefrontal cortex, and the temporal pole (Pichon et al., 2008). A behavioral study directly comparing dynamic and static body expressions (Atkinson et al., 2004) revealed that exaggerating body movements enhanced recognition accuracy, and emotional-intensity ratings for movies were higher than for still images. These findings suggest that evaluation of emotional body gestures relies more on movement than on static form information. Also the dynamic aspect may hold important information regarding the emotional intensity of the stimulus.However, a major problem associated with the use of dynamic naturalistic stimuli is the many dimensions of the image kinetics that may vary between different stimuli. One option for dealing with this complex problem is using more minimalistic and controlled stimuli depicting biological motion. Indeed, previous studies have shown that human observers can successfully recognize expressed emotions even in extremely impoverished stimuli such as point- light displays (Alaerts et al., 2011; Atkinson et al., 2004; Clarke et al., 2005; Dittrich et al., 1996; Nackaerts et al., 2012). These findings suggest that essential information of emotional signaling can be derived from minimalistic dynamic displays of the emotional gestures. However, point light displays constitute an extreme abstraction that could affect the emotional experience.

A promising intermediate category, which allows examining dynamic biological motion in a controlled yet more naturalistic manner, is computer-generated avatars. These stimuli offer the advantage of high stimulus control while possessing a much more naturalistic appearance than point-light displays. Indeed Schneider et al. (2013) have used a new set of dynamic avatar stimuli (provided by Roether et al., 2009; Roether et al., 2010) for the first time in a brain imaging study. These faceless avatars were both detailed and highly controlled, expressing a variety of emotional gaits derived from real human movements. In their functional near-infrared spectroscopy (fNIRS) study Schneider et al. (2013), used emotion detection task (identifying the emotion expressed by the avatar), and speed evaluation task as a control (rating the moving speed of each avatar on a 5 point scale). They found enhanced activity to emotional compared to neutral stimuli, in both motion and emotion processing brain regions (in parietal and temporal lobes). Moreover these regions were less responsive when the emotion was not intentionally processed (i.e. during the speed task).

Here we opted to use similar highly controlled stimuli during functional magnetic resonance imaging (fMRI). Using such dynamic avatars enabled us to examine biological motion over several emotions, intensities and speeds, and therefore test a number of hypotheses. First, we hypothesized that body motion has a significant role in emotional recognition. Furthermore, it should engage a wide range of cortical networks, such as visual and emotional brain networks. To this end we measured brain responses to emotional vs. neutral dynamic gaits (experiment 1). Second, we hypothesized that dynamic motion, more than static postures, enhances the emotional selectivity. We examined brain selectivity to static emotional body expressions, by measuring brain responses to emotional vs. neutral static avatars (experiment 2). We further hypothesized that body motion is a reliable indicator not only for identifying distinct emotions, but also for evaluating emotional intensity. Thus we aimed to examine emotional perception from gait (both behaviorally and neuronally) along the emotional intensity axis. To that end we used avatars at several levels of emotional intensities (experiment 3). Finally we hypothesized that the emotion-related brain activations reflect the subjective perception of the observers rather than the objective, physical attributes of the stimuli. In most previous studies, these two aspects were closely linked- rendering it difficult to disentangle them. In the present study, some of the avatar stimuli were emotionally ambiguous- in the sense that the same physical stimuli produced different subjective emotional reports- allowing us to dissociate the physical from the subjective aspects."

Materials and methods -

Subjects

Nineteen healthy right handed subjects (ages 28± 4.5, 11 females), participated in the experiments. Most of the subjects participated in more than one experiment (see table 1). Seventeen subjects (10 females) participated in experiment 1, ten subjects (5 females) in experiment 2, and 14 subjects (9 females) in experiment 3. In addition 13 subjects (6 females) participated in an external visual localizer task. Subjects gave a written informed consent and were paid for their participation. All procedures were approved by the local ethics committee.

Stimuli

In order to examine the behavioral and neuronal processing of emotion from natural human gait in a highly controlled manner, three sets of stimuli were created, building on the human motion capture data of emotional gaits from Roether and colleagues (2009). All our stimuli showed uniformly, neutral-gender looking grey avatars walking as on a treadmill whilst expressing the emotions happiness, anger, fear or sadness or walking in a neutral style.

The first set of stimuli contained dynamic animations of individual human gaits recorded using motion capture. For each emotion we chose one individual gait that had previously been rated to be most expressive (Roether et al. 2009). Additionally we included in the stimulus set two neutral gaits, one at the slow speed of fearful and sad walks and one at the fast speed of angry and happy walks (see figure 1a left panel).

A second set of stimuli contained static gait postures taken from the dynamic stimuli in set 1, alternating with blank intervals. Each still frame and blank was presented for 300ms leaving the impression of flashing images instead of a movie sequence. To avoid apparent motion from one static image to the other, the viewpoint always changed between images from left to right and vice versa. Further, the temporal order between static images was randomized. To assist the participants in maintaining fixation during observation of the flashing stimuli, a red fixation square was inserted on every frame (Fig. 1b left panel).

The third stimulus set included animations morphed between neutral and each emotional gait at five morph levels (25%, 50%, 75%, 100% and 125%; Fig. 1c left panel). Animations of gait movements on a continuum from neutral to each of the four emotional expressions were created using motion-morphing based on spatio-temporal correspondences (Giese and Poggio, 2000). As prototypes for the motion-morphing we used for each emotion the three most expressive gaits and three neutral gaits at corresponding walking speeds. Additionally, neutral gaits at four different speeds matching the 100% speeds of each individual emotion were created.

To avoid laterality bias, quick adaptation (repetition suppression effects) or attention drop due to stimulus repetitions and similarities between avatars, all stimuli were animated in two variations: coming from the left and from the right, each turned 20 degrees from the frontal view to maximize the visibility of expressive bodily cues (especially the movements of the elbow and knee joints, the head inclination, and the whole body tilt (Roether et al. 2009).

These highly controlled stimuli allowed the disentangling of the emotional perception from low level features and potential confounds- such as velocity, size, shape, color, gender, clothing as well as high level emotional cues such as facial expressions. Moreover, our modeling methods enabled a systematic change of the transported emotion within the stimuli, in order to investigate the neural response to emotional intensity in a parametric way.

Experimental procedure

Experiment 1 - The neuronal correlates of emotion recognition from dynamic gait (Fig.1a). Four types of emotional dynamic human gaits (happy, angry, fearful and sad), and matched speed neutral gaits were presented for 4 seconds each, in a pseudorandom order, separated by rest periods (8 seconds fixation screen; blank screen with a fixation point). Each stimulus was presented 4 times during the experiment (twice from each direction). Following the presentation of each clip (during fixation), subjects were requested to classify the stimulus as emotional or neutral, using a response box.

Experiment 2 - The neuronal correlates of emotion recognition from static body posture (Fig.1b). Four types of emotional and neutral static postures (single frames taken from the dynamic clips), were presented in pseudorandom order in 6 second blocks, , separated by rest periods (9 seconds - fixation screen). Each still frame and its following blank were presented for 300 milliseconds. Similarly to experiment 1, subjects completed a classification task (emotional/neutral).

Experiment 3 - The effect of emotional load on the neuronal activity (Fig.1c). Since velocity may be a major cue for distinguishing between emotions, the stimuli were separated into two types of runs (scans) based on velocity of the emotionally expressive gait patterns: low velocity runs (fearful and sad) and high velocity runs (happy and angry). Each run included two types of emotional gaits at five different levels of emotional intensity (25%-125%), and neutral gait speeds were matched to the speed of the emotions at 100% intensity. The stimuli were presented in pseudorandom order for 4 seconds each, separated by rest periods (8 seconds - fixation screen). Following each clip (indicated by the fixation cross appearing on the screen) subjects identified the presented emotion (2 alternative forced choices) and rated the emotional intensity of the stimulus on a 1-4 scale, using a response box.

Visual localizer - In order to define category-selective regions within high-order visual cortex, a standard fMRI category-localizer experiment was performed. Similar visual localizers have been used in recently published studies from our lab (Davidesco et al., 2013; Harmelech et al., 2015; Yellin et al., 2015).

Images from five categories (faces, houses, bodies, tools, and textures) were presented in 9 second blocks, each with 9 images of the same category, followed by a 6 second fixation screen. Within blocks, each image was presented for 250 ms, followed by a 750-ms blank screen. Participants performed a 1-back memory task (Harmelech 2015). Body category was represented by images of limbs since they are the most common type of body part images used to localize the EBA (Grill- Spector 2011).

Data acquisition

The data were acquired on a 3 Tesla Trio Magnetom Siemens scanner, at the Weizmann Institute of Science, Rehovot, Israel. Functional images of blood oxygenation level dependent (BOLD) contrast comprising of 35 axial slices were obtained with a T2*-weighted gradient echo planar imaging (EPI) sequence (TR = 2000 or 3000 ms, TE = 30, flip angle = 75º, FOV 240 mm, matrix size 80 × 80, no gap 3 x 3 x 4 mm voxel, ACPC) covering the whole brain. Anatomical images for each subject were acquired in order to incorporate the functional data into the 3D Talairach space (Talairach and Tournoux, 1988) using 3-D T1-weighted images with high resolution (1x1x1 mm voxel, MPRAGE sequence, TR = 2300 ms, TE = 2.98 ms).

Data analysis

Behavioral data. The behavioral data were analyzed using SPSS (IBM SPSS Statistics, New York) and Matlab software (MathWorks, Natick, MA). As behavioral measures we examined the response accuracy for the classification tasks (exp. 1-3), the perceived intensity in the rating task (exp. 3), and the reaction time for all tasks. <u>Experiment 1 and 2:</u> To measure the effect of emotion on the classification accuracy and on reaction time, we first conducted individual repeated-measures ANOVAs for experiment 1 and 2 with the within subject factor of emotion (levels: angry, happy, fearful, sad, neutral fast, neutral slow). In order to compare the differences between the static and the dynamic stimuli we ran an additional repeated measures ANOVA with within-subject factors of emotion (6 levels: angry, happy, fearful, sad, neutral fast, neutral slow) and stimulus presentation (2 levels: dynamic, static) for the classification accuracy and the reaction time individually.

<u>Experiment 3:</u> To investigate the effects of morph weight on correct classification, rating intensity, and the reaction times for both tasks, we conducted four repeated measures ANOVAs with within-subject factors of emotion (4 levels: angry, happy, fearful, sad) and morph weight (5 levels: 25, 50, 75, 100, 125%). Further, to compare the intensity ratings and reaction times (for both tasks) for the neutral speed-matched animations with the corresponding emotional gait stimuli we ran three repeated measures ANOVA with the factors emotion (2 levels: yes, no) and walking speed (4 levels: speed of angry, speed of happy, speed of fearful, speed of sad gait).

Brain imaging data. fMRI data were analyzed using Brain Voyager QX 2.4 software package (Brain Innovation, Maastricht, The Netherlands), and with complementary in-house software.

Anatomical data. The cortical surface was reconstructed for each subject from the 3D-MP-RAGE scan in a Talairach coordinate system (Talairach and Tournoux, 1988).

Functional data. The first images (2 - in the 1st and 2nd experiments, 7- in the 3rd experiment) of each functional scan were discarded in order to exclude interferences like typical movements at the beginning of the scan. Functional scan preprocessing included 3D motion correction and filtering out of low frequency noise (slow drift), and spatial smoothing using an isotropic Gaussian kernel of 6 mm full-width-half-maximum (FWHM). The functional images were superimposed on 2D anatomic images and incorporated into the 3D data sets through trilinear interpolation. Statistical analysis was based on a general linear model (GLM, Friston et al., 1995) in which all stimuli conditions were defined as predictors, and convolved with the hemodynamic response function (HRF). The first period of each rest epoch was dedicated to a task; therefore the rest condition was defined in the model as the 6 last seconds of the rest periods interspersed between the clips.

Experiment 1 analysis: a GLM analysis was conducted, with two predictors: '(expressed) emotional gait', and '(expressed) neutral gait'. A second GLM analysis was perception-based, with two predictors which were defined per subject according to the individual's emotional ratings: '(perceived as) emotional gait', and '(perceived as) neutral gait'. A third GLM analysis was calculated, defining as a separate predictor the ambiguous cases i.e. slow neutral gait which sometimes were perceived as neutral and other times as emotional (within the same subject). This GLM consisted of five predictors: 'Fast/slow emotional' (expression = perception), 'fast/slow neutral' (expression = perception), and 'slow expressed neutral - perceived as emotional'. In all GLM analyses beta coefficients were calculated for the regressors, and a student's t-test was performed. Multi-subject analysis was based on a random-effect GLM. Multi-subject contrast maps (emotional vs. neutral) were projected on an unfolded, inflated (Fig. 2) or a coronal slice (Fig. 4) Talairach-normalized brain. Significance levels were calculated, taking into account the minimum cluster size and the probability threshold of a false detection of any given cluster. This was accomplished by a Monte Carlo simulation (cluster-level statistical threshold estimator in “Brain Voyager” software). For emotional vs. neutral perception (Fig. 2) a minimum cluster size of 155 voxels was significant. For ambiguous avatar contrast (Fig. 4) the significant minimal cluster size was 123 voxels (same stimulus) and 129 voxels (different stimuli). For the static analysis (Fig. 5) the significant minimal cluster size was 98 voxels (static), and 137 voxels (dynamic). For the emotional parametric map (Fig. 6) a minimum cluster size of 144 voxels was significant.

Finally, a two-way repeated measures ANOVA was calculated, consisting of two within-subjects factors: perceived emotion (emotional/neutral), and speed (fast/slow).
Experiment 2 analysis: A multi-subject, random effects, perception based GLM analysis (identical to experiment 1) was conducted for the static stimuli experiment.
Experiment 3 analysis: a multi-subject, random effect, parametric GLM analysis was conducted, in which each avatar stimulus received a weight according to its emotional intensity (on a 1-5 scale). Thus the emotional load of the avatars was represented in the model as differential amplitude of the BOLD signal. Multi-subject parametrically significant activity maps were projected on an unfolded, inflated and coronal slice Talairach-normalized brain (Fig. 6). Significance levels were calculated, taking into account the minimum cluster size and the probability threshold of a false detection of any given cluster (Monte Carlo corrected).

ROI definition and analysis -
In order to inspect the emotional effect in dynamic as well as static conditions, the most relevant brain areas (according to previous literature) were chosen as regions of interest (ROI).
Five bilateral ROIs were defined independently from the experimental task: the extrastriate body area (EBA), fusiform body area (FBA), fusiform face area (FFA), superior temporal sulcus (STS) and the amygdala. The first four bilateral group-ROIs were defined as the activated voxels located within 30 mm of the multi subject activity center ($p < 0.05$ corrected). Three bilateral ROIs were defined using the visual localizer, and were based on contrasts used in previous published studies - EBA and FBA were defined using the contrast: Body > Texture (Harmelech et al., 2015), FFA was defined using the contrast Faces > Buildings (Davidesco et al., 2013; Kanwisher et al., 1997). STS was defined using the contrast emotional gait vs. neutral gait per subject according to the leave one out criteria (e.g. subject's X individual ROI was defined as the group's function ROI, excluding subject X). The amygdala bilateral group-ROI were defined as follows; a general template anatomy (based on 19 brains anatomy) which was created using Advanced Normalization Tools (ANTs, http://picsl.upenn.edu/software/ants/), was transformed to talairach space (to fit the group's normalized anatomies). The amygdala was manually traced on this template according to an online application (Locator, http://www.thehumanbrain.info/brain/locator.php) of the atlas of the human brain

(Mai et al., 1997). The ROI's averaged beta weight (across voxels) was calculated per subject, for each predictor. Two-tailed paired t-tests (within subjects) were then conducted between emotional and neutral beta weights for dynamic (experiment 1) and static (experiment 2) stimuli. FDR correction for multiple comparison was done according to Benjamini-Hochberg method ($\alpha = 0.05$). For experiment 3, a beta weight was extracted for each morph level. Pearson correlation was calculated between participant's average beta for each morph level (averaged over each ROI) and their emotional intensity. (as plotted in Fig 6.c)

Results

In the present study we conducted three experiments examining various parameters of neuronal emotional processing of dynamic and static avatar images. Figure 1 illustrates the different experiments and the type of images used. Experiment 1 (*dynamic gait*) aimed to distinguish between the neuronal correlates of emotional and neutral body expressions (gait). Experiment 2 (*static posture*) aimed to distinguish between the neuronal correlates of static and dynamic body expressions (gait). Experiment 3 (*morph*) examined the effect of body expression's emotional intensity on brain activity.

Behavioral results:

<u>Experiment 1 and 2:</u> Overall subjects were capable of classifying the emotions, although in both experiments the neutral slow walker was often misinterpreted as sad, resulting in a main effect of emotion (dynamic stimuli: $F(5,80) = 58.93$, $p < 0.001$; static stimuli: $F(5,45) = 6.1$, $p < 0.001$). Further, response times were slower for these neutral slow walker stimuli (dynamic: $F(5,75) = 5.31$, $p < 0.001$; static $F(5,45) = 2.78$, $p < 0.03$).

Comparing both types of stimulus presentation responses for all but neutral slow stimuli were faster and more accurate for dynamic compared to static stimulus presentations, leading to a difference in reaction time depending on the specific emotion (interaction effect of emotion x stimulus presentation $F(5,120) = 3.0$, $p = 0.0136$).

No clear difference between dynamic and static stimuli was observed, likely since response accuracy was nearly at ceiling performance for both stimulus presentations.

<u>Experiment 3:</u> As expected the morph weight had a strong influence on correct classification, on intensity rating, and on reaction time. Correct classification of emotions

was increased by the stimulus emotional intensity (main effect of morph weight F(4,52) = 74.74, p <0.001). Reaction times were faster for stimuli with higher morph weights for both the emotion classification (F(4,52) = 7.76, p < 0.001) and the intensity rating (F(4,52) = 3.33, p = 0.017). Neither correct classification percentage nor reaction time differed between individual emotions.

In contrast, for the ratings we observed a main effect of emotion (F(3,39) = 14.91, p < 0.001) in addition to the expected effect of the morph weight (F(4,52) = 431.97, p <0.001) and an interaction effect of emotion x morph level (F(12,156) = 10.9, p <0.001). This was driven by lower emotional intensity ratings for fearful avatars relative to the other emotional stimuli.

The comparison of the emotional gait stimuli with their corresponding speed-matched neutral gait animations revealed the following effects: Responses to emotional stimuli were always faster than those to neutral stimuli in both tasks (classification: main effect of emotion F(1,13) = 23.02, p <0,001; rating: main effect of emotion F(1,13) = 20.04, p = 0.001).

For the ratings we observed a significant effect of emotion (F(1,13) = 120.26, p < 0.001) but also an effect of walking speed (F(3,39) = 26.32, p < 0.001) and an interaction effect of emotion and walking speed (F(3,39) = 10.40, p <0.001). Avatars walking at a high speed (angry) and low speed (sad) were rated at higher intensity levels compared with avatars walking at intermediate speeds (happy and fearful).

Brain imaging results:

In order to inspect whether brain activations were more reflective of subjective perception or the physical aspects of the stimuli, we considered in our analyses two separate measures of dynamic emotions: '*expressed*' and '*perceived*'. *Expressed* emotion (EE) refers to the type of emotion the actors (on whose movements the avatars' motions were built) intended to convey. These emotions were embedded in the objective features of the avatar's movements and kinematics (see methods). The other aspect of this phenomenon is the *perceived* emotion (PE); the emotion subjectively perceived and reported by subjects upon watching the avatar videos.

Experiment 1: We used two different analysis approaches - one was based on the *expressed* emotions, and another based on the *perceived* emotions. These two analyses showed different results regarding the difference between emotional and neutral conditions (sup Fig.1). Both activity maps showed similar enhanced regions (specified below), and a direct comparison between the maps did not show a significant difference between them. Still the subjective-perception based map showed stronger and more significant activations, less deactivation in frontal regions and default mode network (right IPL), and more motor oriented activity (parietal lobule and pre-central sulcus). Considering this trend, in the following experiments the analyses referred to the subjectively perceived emotions model.

Contrasting *perceived* emotional (PE) with *perceived* neutral (PN) gaits highlighted an extensive network of cortical and subcortical regions. Figure 2 depicts these networks on an inflated and unfolded cortex (group map, N = 17, $p < 0.05$). The most prominent regions manifesting preferential activations to PE vs. PN were the amygdala, STS, EBA, FBA and FFA. The visual dorsal (action stream); left superior parietal lobule (SPL), and left inferior parietal sulcus (IPS), as well as the left inferior frontal gyrus (IFG), the right lateral sulcus, and the orbital frontal cortex (OFC).

We independently selected regions of interest (see methods) which are related in the literature to processing of body (EBA, FBA), face (FFA), biological-motion (STS), and emotion (AMG) and compared the PE and PN activity in these regions (Figure2c,d). All ROIs demonstrated a significantly stronger response to PE relative to PN gaits ($p < 0.05$, corrected).

Higher order, category selective, visual areas in both hemispheres showed enhanced positive activation (above the fixation baseline) to the avatars perceived as emotional. Of particular interest was the observation that the FFA showed enhanced activation to these avatars despite the fact that these images did not contain internal face details.

In the Amygdala and left STS the preferential response to emotionally perceived stimuli was characterized by a reduction in BOLD activation compared to the fixation baseline. The preferential nature of emotional response here was expressed as a milder signal reduction in emotional compared to neutrally perceived stimuli.

The preferential activation to emotional avatars could potentially result from low level features of the stimuli rather than emotion per se. A particularly plausible confound is gait speed. To control for this, we conducted a two-factor analysis of variance (for perceived emotion and speed), and the results of the ANOVA showed a significant main effect for emotion in the amygdala and left STS (N = 12 $p < 0.001$, see fig 3). No significant main effect was found for speed nor for interaction between speed and emotion.

The most conclusive demonstration of the link between neuronal activation and subjective emotional perception was provided by emotionally-ambiguous stimuli. In these cases (experienced by 11 out of 17 subjects) the same avatar video was perceived sometimes as emotional and at other times as neutral (by the same subject). Thus, different subjective emotional perceptions were generated for identical visual stimuli. These emotionally-ambiguous avatars allowed us to disentangle the effects of emotional perception from changes associated with the visual images per se. Examining the brain responses of these ambiguous avatars evoked significantly higher activity in the amygdala and parietal lobule when perceived as emotional compared to when perceived as neutral.

Figure 4 depicts the results of this analysis in the amygdale (whole brain analysis, as well as ROI analysis $N = 11$, $p < 0.05$) - the left panel presents a contrast between two different stimuli which were perceived as similar. Indeed the brain reaction was the same for both stimuli. The right panel presents a contrast between the same visual stimuli when perceived as different (emotional vs. neutral). As can be seen, the brain responses were significantly higher for the emotionally perceived condition, and thus corresponded to subjective emotional perception. The magnitude of beta values was similar to that found when contrasting different emotional vs. neutral avatar stimuli.

<u>Experiment 2</u>: A second question we studied was: how critical is the body movement in generating the emotionally-selective brain responses? To answer this question the dynamic videos were replaced by a series of static frames (see methods).

Figure 5 depicts the results of this analysis. Although the percentage of correct detections was similar for dynamic and static stimuli, reaction times were much longer for the static stimuli (fig 5c). Examining brain responses, the static postures revealed a weaker contrast map (PE > PN) compared to the dynamic gait stimuli (fig 5a,b). In contrast to the dynamic stimuli, the static postures did not show significant differential activity between emotional and neutral stimuli, in any of the pre-defined ROIs (two tailed, paired t test, $N = 10$, $p > 0.05$).

<u>Experiment 3</u>: An important question that could be addressed using the computer-generated avatars is whether emotion-related brain regions can provide some quantitative estimate of the intensity of the emotional impact rather than merely a categorical distinction. To address this issue we conducted an experiment in which the level of expressed emotions of the avatars was gradually "morphed" between neutral and high emotional states- including a "hyper emotional condition" in which the parameters representing the emotional state were exaggerated beyond the normal range of parameters (Jastorff et al., 2006; Leopold et al., 2006) (see methods).

Subjects were able to accurately assess the level of the avatars' emotional expression, indicated by the high correlation between the emotional expression level (1-5) of the stimuli and subjects' ratings ($R^2 = 0.996$). This linear effect remained also in the extreme case of 125% emotional load, and there was no ceiling effect. However we did not find corresponding neuronal evidence for differential activation between 125% and 100% morph levels.

Examining brain responses that correlated with the gradient of emotional levels expressed by the avatars revealed a significant correlation in the amygdala ROI (Fig.6c Pearson correlation $r = 0.89$, $p < 0.05$). As can be seen in Figure 6, the amygdala and left rostral inferior parietal lobule (IPL) showed the strongest parametric connection between brain activity and emotional intensity derived from dynamic body movements (whole brain parametric GLM analysis, $N = 14$, Montecarlo corrected $p < 0.01$).

Discussion:

Neuronal networks showing selective gait-driven emotional responses

We present here a novel paradigm to assess human brain processing while observing emotional body movements, made by avatars. Preferential emotion-related responses were expressed mainly in visual, emotion, and motion-related brain networks;Enhanced activity in response to emotional gait was shown in the extrastriate body area (EBA), and fusiform body area (FBA) - high order visual areas related to body representation, and the decoding of emotion from body movements (Downing et al., 2007; Peelen et al., 2007; Peelen and Downing, 2007; Taylor et al., 2007). An interesting result was the enhanced activation of the fusiform face area (FFA), which is strongly related to face processing, in response to emotional bodily movements despite the lack of facial features. This finding has been previously reported (Hadjikhani and de Gelder, 2003; Kret et al., 2011), suggesting face completion effects when processing human bodily expression even when detailed facial information is missing.

Activity in the visual dorsal (action) stream, and motor cortex was also stronger for emotional compared to neutral stimuli (particularly emphasized when comparing perceived vs. expressed conditions); left superior parietal lobule (SPL), left inferior parietal sulcus (IPS), have both been linked to preparation for action (Chao and Martin, 2000; Corbetta and Shulman, 2002; Goodale and Milner, 1992; Goodale et al., 1991;

Grill-Spector and Malach, 2004; Mishkin et al., 1983; Shmuelof and Zohary, 2005; Shulman et al., 1997; Ungerleider and Haxby, 1994).In a previous study (Goldberg et al., 2014) we showed that natural, emotional stimuli with narrated context enhanced activation of the dorsal visual stream, as a possible expression of mental preparation for action (even during passive viewing). De Gelder et al have also shown that emotional body gestures activate the premotor brain regions (De Gelder et al., 2004; Grezes et al., 2007; Pichon et al., 2008). The recruitment of action related brain regions in the present study may be another evidence for the emotion-action link.

Recognizing and evaluating emotional state of others is a fundamental feature of human communication. Indeed, preferential emotion related responses were evident also in social-cognition related regions, which are involved in recognizing and evaluating the emotional state of others; The superior temporal sulcus (STS) has been linked to social cognition and biological motion processing (Allison et al., 2000). Orbito frontal cortex (OFC) is important for social mentalizing and self-reflection (Frith 2006). Right inferior frontal gyrus (IFG) is part of the mirror neuron system which function in understanding other's behavior and emotion (Rizzolatti and Craighero, 2004). Only few previous studies in the field of bodily emotional expression have shown frontal activations (Grezes et al., 2007; Pichon et al., 2008), and even fewer found IFG involvement (Sinke et al 2010). These studies used, among others, dynamic stimuli of humans or even two interacting humans (Sinke et al 2010).

Some previous studies (De Gelder et al., 2004; Grezes et al., 2007; Pichon et al., 2008; Sinke et al., 2010) have demonstrated emotion-selective enhancement of the amygdala, which is strongly linked to emotional processing (Adolphs et al., 1994; Davis and Whalen, 2001; Grezes et al., 2007; Morris et al., 1998a; Morris et al., 1998b; Pichon et al., 2008; Sinke et al., 2010; Whalen et al., 1998). In the present study the amygdala showed the most robust and consistent sensitivity to emotional stimuli, both in distinguishing between emotional and neutral gaits (experiments 1 and 2), and in evaluating the emotional intensity of the gait (experiment 3).

Amygdala and emotional perception

We showed that in a concrete emotional context (emotion detection task), amygdala activity was correlated with the perceived emotional reports. The perception-based analyses (taking the subject's experience as a parameter), showed significant and more selective emotional responses, compared to expression-based analyses (taking the avatar's physical attributes as a parameter). The amygdala's preference for subjectively perceived emotions rather than objective emotional expression was demonstrated most directly in the case of "emotionally ambiguous" avatars, in which subjects' perception alternated between emotional and neutral categories for the same avatar stimulus (Fig. 4). The amygdala was the only ROI which showed significant neuronal selectivity for these purely subjective alterations.

Previous studies have reported an unconscious, automatic processing of emotion in the brain, especially in the amygdala (Fried et al., 1997; Morris et al., 1998b; Öhman, 2002; Vuilleumier et al., 2001; Whalen et al., 1998; Winkielman et al., 2005). Such non-conscious detection of emotional stimuli points to an objective subliminal element in the amygdala's emotional responses. However other studies have reported that target supraliminal perception is essential and coupled with amygdala's responses to fearful faces (Pessoa et al., 2006; Pessoa et al., 2002; Pessoa et al., 2005). Our findings extend the range of emotional processes carried by the amygdala in the supraliminal, reportable domain.

Parametric relation between amygdala's activity and emotional perception

The whole brain analysis revealed a significant parametric modulation of brain activity levels by subjects' ratings of emotional intensity in several regions. These effects were most evident in the amygdala and left rostral IPL. Amygdala activity has long been associated with emotional processing (Adolphs et al., 1994; Davis and Whalen, 2001; Morris et al., 1998a; Morris et al., 1998b; Whalen et al., 1998), and IPL is part of the mirror neuron system (MNS) in human and non human primates. The MNS is a network characterized by common selectivity for both action execution and action observation. This neurophysiological mechanism is considered important in understanding action of others, and in action imitation (Rizzolatti and Craighero, 2004). The use of both dichotomous (emotional/neutral) and parametric analytic approaches allowed us to explore different aspects of the emotional processing, and several brain mechanisms. We found that the amygdala has a role in both qualitative categorization (i.e. distinguishing between emotional to neutral content), as well as more quantitative aspects of emotional evaluation along a continuous scale. This result is compatible with the relevance detector theory suggesting that the amygdala has an important role of evaluating relevant events (relevance detector theory - Sander et al., 2003).

Interestingly, the amygdala's BOLD response showed a consistent reduction below the resting baseline, with the preferential emotional response manifested as a milder reduction in BOLD activation compared to the neutral stimuli.

Such a profile is reminiscent of a "Default" or "Intrinsic" – i.e. self-oriented -system response (Fox and Raichle, 2007; Golland et al., 2007; Gusnard and Raichle, 2001). Thus, it is possible that the emotional effect may be superimposed on a more fundamental inhibitory effect resulting from the visually engaging- "extrinsic" - i.e. world-oriented -nature of the moving avatars. In other words, the visually-engaging avatar stimuli may have caused a general suppressive effect of the amygdala, but when adding the positive activation effect of the emotional avatars- the net result was a milder suppression of the signals below baseline for the emotional avatars.

Another recent study (Sinke et al., 2010), found a similar pattern of responses (lower de-activation) in the amygdala, to certain types of emotional signaling between two people in a dynamic social interaction paradigm (short videos).

Emotion, motion and speed

A central goal for the use of highly controlled avatars in this study was to disentangle as much as possible the emotional content from other low level features, especially motion and speed. Experiment 2 in which we examined emotion perception from static body postures, revealed the important role of kinematics for assessing the emotional impact of the avatars. The importance of biological motion kinematics in emotion perception and communication has been previously indicated by a number of studies (De Gelder, 2006, 2009; Tamietto and De Gelder, 2010). In their studies Grezes, Pichon and de Gelder used both dynamic and static body gestures in a 2 by 2 factorial design (emotion and motion), enabling a direct comparison between static and dynamic categories. The stimuli were neutral and angry whole body images of actors, and the task was an oddball target detection (emotional context is implicit). In this present study we also used both dynamic and static stimuli of the same images, but in 2 separate experiments. The paradigm was also different - one avatar presented 4 different emotions in 5 different intensities, and the task was emotion detection and rating (explicit emotional context). These studies aforementioned (Grezes et al., 2007; Pichon et al., 2008)., demonstrated that some networks (e.g. STS) showed significant preference for emotional content only when the stimuli were dynamic These findings are compatible with the current study in which all examined ROIs (including STS) showed significant preference for emotional content only when using dynamic avatars. This effect was diminished (in all ROIs) when using static postures of the same avatars (despite the fact that subjects were still able to classify the groups correctly, albeit much more slowly. See, Fig.5).

On the other hand, more recent research using transcranial magnetic stimulation over the right posterior STS revealed a differential role of this region in the perception of threatening compared to neutral stimuli even for static postures (Candidi et al., 2011) and stimulation of this area specifically increased the dominance of fearful body postures over houses in a binocular rivalry paradigm (Candidi et al., 2015).

In contrast to these results we did not observe such a clear involvement of the STS in the perception of static postures. A possible explanation for the discrepancy may be due to different levels of implied motion in the static stimuli used by the two studies. The differential activity of static and dynamic stimuli whilst similar recognition rates, as well as the parametric dependence of the activations described above, argue against a possibility that amygdala activation was driven by task difficulty or stimulus processing times. Notably, reaction times were significantly longer for the static stimuli, yet the activation was significantly lower.

A further advantage of the presented approach is the ability to disentangle the impact of speed from the emotional aspects. An ANOVA with emotion and speed as factors (see Fig.3) revealed a main effect in emotion-relevant regions (left STS, and amygdala) only for the emotion factor, and null results for speed or interaction factors.

Along the same line, a recent study (Schneider et al., 2014) using similar computer generated dynamic avatars showed that during an emotion task, subjects were most successful in recognizing the fearful and sad emotions, while in a speed task subjects were most successful in differentiating the sad from happy avatars. These results are compatible with the notion that speed detection and emotion detection are different, independent tasks (Barliya et al., 2013).

It should be noted that the avatar stimuli used in the present study were an abstracted emotional representations. Clearly- the emotional experience elicited by computer generated avatars, particularly in an fMRI setting, is different from real life experience. Nevertheless, as our study reveals, the dynamic avatars were very effective in eliciting consistent emotional evaluations and activity in the relevant brain areas. This further underscores that high sensitivity of emotion-related networks in the human brain.

Conclusion:

Using dynamic computer-generated avatars we were able to show that emotion perception from body movements engages a wide range of brain networks- visual, social and emotional-related. The highly controlled avatar stimuli allowed us to demonstrate a parametric modulation of amygdala activity with emotional intensity, and to disentangle effects of speed and motion from emotional processing of body motion. Notably, we were able to uncover a subjective component to these amygdala responses by demonstrating differential activation linked to changes of subjective perception, generated under identical physical stimulus conditions.

We suggest that these results provide a neuronal demonstration for the potential gap in human communication between expressed and perceived emotions. They highlight the role of the amygdala in generation of emotional percepts.

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Figures captions:

Figure .1. Experimental design .(a) Experiment 1 (Exp1). Left side- 6 types of dynamic gait stimuli; low velocity emotions (fearful and sad), high velocity emotions (angry and happy), and neutral gaits (speed-matched to low/high velocity emotions). Right side- the experimental protocol: stimuli were presented for 4 seconds, separated by 8 seconds rest fixation periods. Task- during rest, subjects were required to classify the stimulus as *Emotional* or *Neutral*.(b) Experiment 2 (Exp2). Left side- static posture stimuli; single frames taken from the dynamic stimuli, presented for 300 ms, with spacing of 300ms fixation screen. Right side- the experimental protocol: stimuli were presented for 6 second in a block design, separated by 9 seconds rest fixation periods. Task- subjects were required to classify the stimulus as *Emotional* or *Neutral*. (c) Experiment 3 (Exp3). Left side- morph levels stimuli- each emotion was presented by dynamic gait stimuli in 5 levels of emotional load (25% to125% from the original dynamic gait stimuli (panel a)), and neutral gaits speed-matched to the 100% of each emotion. Right side- the experimental protocol: In separated scans for high /low velocity emotions, stimuli were presented for 4 seconds, separated by 8 seconds rest fixation periods. Task- during rest subjects were required to identify the specific emotion and to rate the emotional intensity (1-4 scale), of previous stimulus.

Figure .2. Comparison of Emotion and Neutral-related cortical activations. Emotional vs. neutral multi subjects activity map (N = 17, corrected $p<0.05$) is presented on an inflated cortex, in a medial view (a), lateral view (b) and unfolded cortex (c). Color scale indicates t values. Yellow- orange scale represents regions which were more activated while perceiving emotional content from gait compared to neutral gait (blue-green scale).Colored ROIs' contours are overlaid on the activation map (c): Extrastriate body area (EBA) and fusiform body area (FBA) in magenta, fusiform face area (FFA) in dark blue, and superior temporal sulcus (STS) in light blue. Parahippocampal place area (PPA), lateral occipital sulcus (LO), inferior parietal sulcus (IPS), superior parietal lobule (SPL), inferior frontal gyrus (IFG), orbito frontal cortex (OFC). (d) ROI analysis- Twotailed, within subjects paired t-test between ROI activities (beta value) of Emotional gaits (red), compared to Neutral gaits (green), N = 16, Bonferroni corrected for multiple comparisons, $\alpha = 0.05$, $*p <0.05$, error bars indicate the groups' standard error (SE).

Figure .3. Two-factor analysis of variance (for emotion and speed). ANOVA map (per voxel) is presented on a coronal slice, Y = -6 (left side) and unfolded cortex (right side) Yellow- orange scale represents regions which their activity was attributed to the ANOVA factor: (a) emotion, (b) speed, (c) emotion*speed interaction. (N = 12 $p <0.001$). Amygdale anatomic ROI is marked by purple contours.

Figure .4. Ambiguous avatar analysis. Multi study activity map (N = 10, corrected $p < 0.05$) presented on a coronal slice (Y = -4), color scale indicates t values. Yellow- orange scale represents regions which were more activated while perceiving emotional content from gait compared to neutral gait (blue-green scale). (a) Left side: contrast map between two different stimuli *Emotional* >*Neutral* which were perceived both as *Emotional*. Right side: contrast map between the same physical stimulus, which was perceived as emotionally different. E (emotional), N (neutral). (b) Amygdala ROI analysis- Two tailed, within subjects paired t-test between amygdala's activities (beta value) of *Emotional* gait (red), compared to *Neutral* gaits (green). Left side t(10)= 0.22 p = 0.829, Right side t(10)= 2.54 p=0.029.

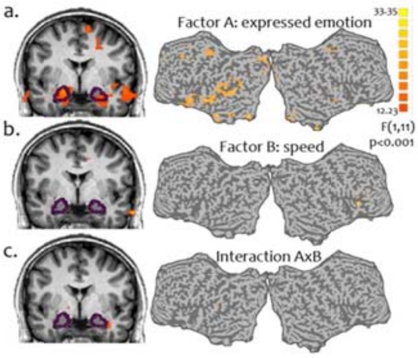
Figure .5. Dynamic vs. static stimuli (a) Behavioral performance during dynamic (red) and static (blue) stimuli: upper row- correct detection (for each emotion and neutral categories), lower row: reaction time. (b) *Emotional>Neutral* (E>N) contrast maps using dynamic gait stimuli (upper row) and using static postures stimuli (bottom row). Multi study activity maps (N =10, corrected p<0.05) are presented on an unfolded cortex, color scale indicates t values. Yellow- orange scale represents regions which were more activated while perceiving emotional content from gait compared to neutral gait (blue-green scale). Colored ROIs' contours are overlaid on both activation maps: extrastriate body area (EBA) and fusiform body area (FBA) in magenta, fusiform face area (FFA) in dark blue, and superior temporal sulcus (STS) in light blue. Parahippocampal place area (PPA), lateral occipital sulcus (LO), inferior parietal sulcus (IPS), superior parietal lobule (SPL), inferior frontal gyrus (IFG), orbito frontal cortex (OFC). (c) The same contrast maps from coronal view (Y = -6), amygdala anatomic ROI is marked by purple contours.

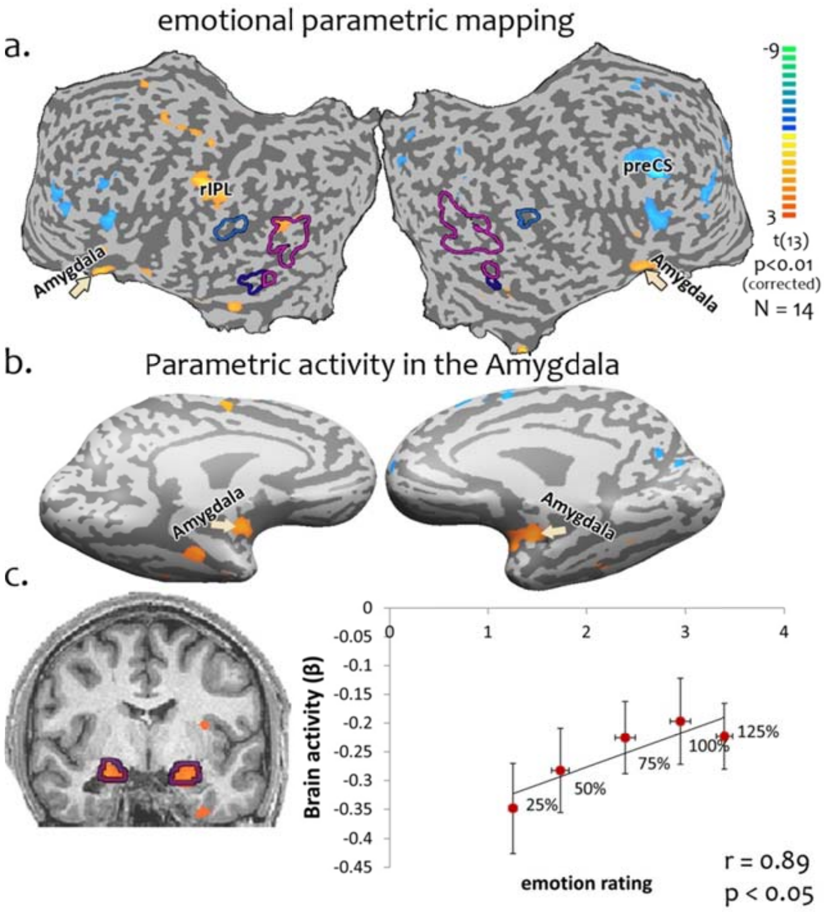
Figure .6. Emotional arousal parametric mapping. Cortical activity maps of multi subjects (N = 14 , corrected p < 0.01), random effect, parametric GLM analysis, presented on (a) unfolded cortex, (b) inflated medial view, and (c left side) coronal view (Y = -6). Color scale indicates t values. Yellow-orange scale represents regions which showed positive parametric relation with subjects' emotional ratings. Blue-green scale represents regions which showed negative parametric relation with emotional ratings. Anatomic definition of bilateral Amygdala is marked by purple contours. (c right side) Amygdala activity (averaged beta values) as a function of emotion ratings (group averaged, N = 14). Red dots represent the five morph levels, the linear trend-line is demonstrated in black. Pearson correlation r = 0.89, p < 0.05.

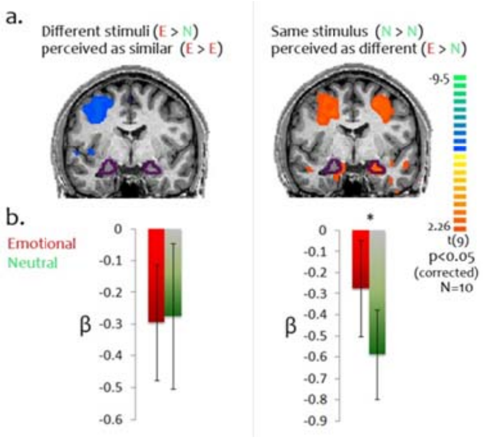
Supplementary Figure .1. Comparison of cortical activations for expressed and perceived Emotions. *Emotional vs. neutral* multi study activity maps (N = 17, corrected p<0.05) are presented on an unfolded cortices. Color scale indicates t values. Yellow- orange scale represents regions which were more activated by emotional content from gait compared to neutral gait (blue-green scale). (a) Expressed emotions (EE) compared to expressed neutral (EN). (b) Perceived emotions (PE) compared to perceived neutral (PN). (c) Emotion compared to neutral (E > N) The borders of the activation map in panel b (perceived emotion > perceived neutral, blue contours) superimposed on the activation map of panel a (expressed emotions > expressed neutral). Extrastriate body area (EBA) and fusiform body area (FBA), fusiform face area (FFA), and superior temporal sulcus (STS), parahippocampal place area (PPA), lateral occipital sulcus (LO), inferior parietal sulcus (IPS), superior parietal lobule (SPL), inferior frontal gyrus (IFG), orbito frontal cortex (OFC). Right hemisphere (RH), Left hemisphere (LH).

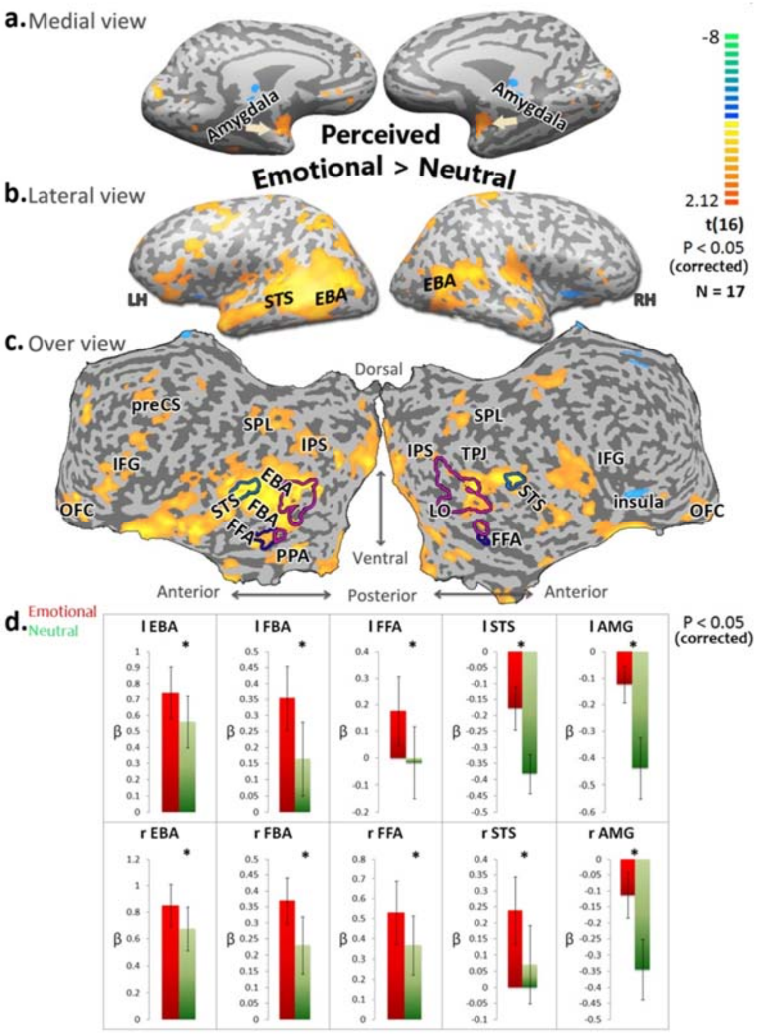
Table caption

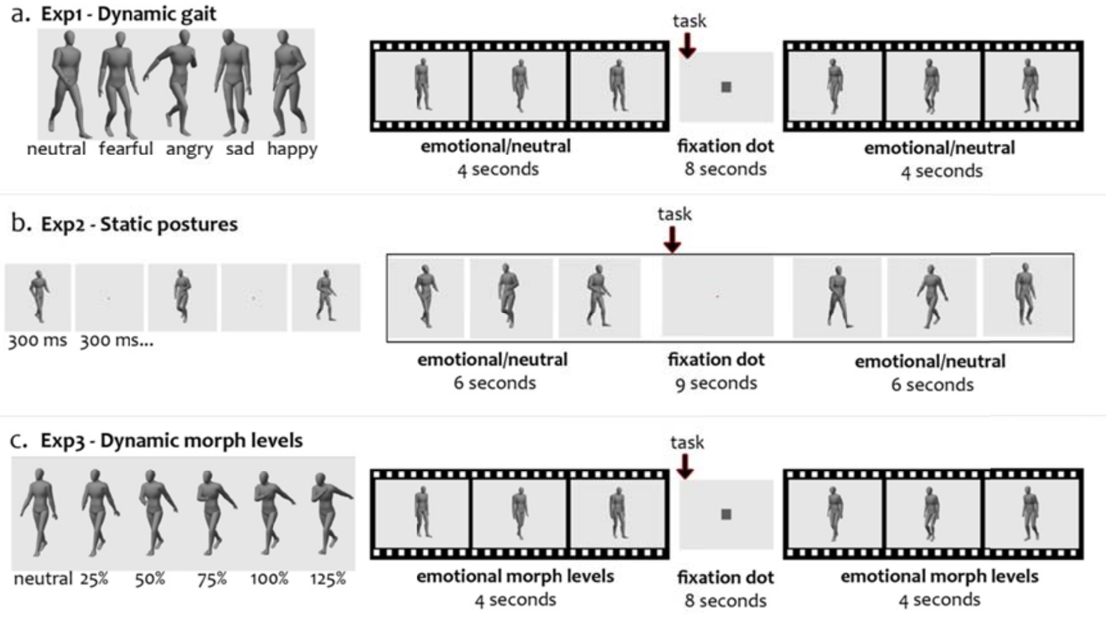
Table 1. Overview of subjects' participation. Overall 19 subjects took part in our experiment.






a.
Different stimuli (E > N)
perceived as similar (E > E)
Same stimulus (N > N)
perceived as different (E > N)
-9.5
2.26
t(9)
p<0.05
(corrected)
N=10
b.
Emotional
Neutral
β
0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
-0.7
-0.8
-0.9
*


a. Medial view
Amygdala
Amygdala
Perceived
Emotional > Neutral
b. Lateral view
LH
STS
EBA
EBA
RH
-8
2.12
t(16)
P < 0.05
(corrected)
N = 17
c. Over view
Dorsal
preCS
SPL
IPS
IFG
OFC
EBA
STS
FBA
FFA
PPA
Ventral
SPL
IPS
TPJ
IFG
LO
STS
FFA
insula
OFC
Anterior
Posterior
Anterior
d. Emotional
Neutral
l EBA
l FBA
l FFA
l STS
l AMG
P < 0.05
(corrected)
r EBA
r FBA
r FFA
r STS
r AMG
β
*


a. Exp1 - Dynamic gait
neutral
fearful
angry
sad
happy
task
emotional/neutral
4 seconds
fixation dot
8 seconds
emotional/neutral
4 seconds
b. Exp2 - Static postures
300 ms
300 ms...
task
emotional/neutral
6 seconds
fixation dot
9 seconds
emotional/neutral
6 seconds
c. Exp3 - Dynamic morph levels
neutral
25%
50%
75%
100%
125%
task
emotional morph levels
4 seconds
fixation dot
8 seconds
emotional morph levels
4 seconds