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Modulation of the Face- and Body-Selective Visual Regions by the Motion and Emotion of Point-Light Face and Body Stimuli

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NOTE: This is a preprint of the article that was accepted for publication. It therefore does not include minor changes made at the 'proofs' stage. Please reference the final version of the article: 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*****(2), 1700-1712. doi: 10.1016/j.neuroimage.2011.08.073**

Abstract

Neural regions selective for facial or bodily form also respond to facial or bodily motion in highly form-degraded point-light displays. Yet it is unknown whether these face-selective and body-selective regions are sensitive to human motion regardless of stimulus type (faces and bodies) or to the specific motion-related cues characteristic of their proprietary stimulus categories. Using fMRI, we show that facial and bodily motion activate selectively those populations of neurons that code for the static structure of faces and bodies. Bodily (vs. facial) motion activated body-selective EBA bilaterally and right but not left FBA, irrespective of whether observers judged the emotion or colour-change in point-light angry, happy and neutral stimuli. Facial (vs. bodily) motion activated face-selective right and left FFA, but only during emotion judgements for right FFA. Moreover, the strength of responses to point-light bodies or faces correlated with voxelwise selectivity for static bodies but not faces, whereas the strength of responses to point-light faces correlated with voxelwise selectivity for static faces but not bodies. Emotional content carried by point-light form-from-motion cues was sufficient to enhance the activity of several regions, including bilateral EBA and right FFA and FBA. However, although the strength of emotional modulation in right and left EBA by point-light body movements was related to the degree of voxelwise selectivity to static bodies but not static faces, there was no evidence that emotional modulation in fusiform cortex occurred in a similarly stimulus category-selective manner. This latter finding strongly constrains the claim that emotionally expressive movements modulate precisely those neuronal populations that code for the viewed stimulus category.

Keywords: Biological motion; extrastriate body area; fusiform face area; point-light display; multivoxel pattern analysis.

Modulation of the Face- and Body-Selective Visual Regions by the Motion and Emotion of Point-Light Face and Body Stimuli

1. Introduction

The human visual system is remarkably sensitive to subtle details in human movements, even in highly impoverished stimuli such as point-light displays, in which static form information is greatly reduced but motion (including form-from-motion) information is preserved. Point-light displays provide not only compelling impressions of moving bodies (Johansson, 1973) and faces (Bassili, 1978), but also a sufficient basis for observers to judge a range of human attributes, such as identity and sex, and their actions and emotions (for a review, see Blake and Shiffrar, 2007). The present study is concerned with how body- and face-selective brain regions process visual cues in point-light displays exhibiting either facial or bodily movements.

Lateral occipital and temporal cortices contain functionally defined regions that respond selectively to faces or to bodies and body parts. These include the fusiform and occipital face areas (FFA and OFAKanwisher et al., 1997; Kanwisher and Yovel, 2006), the extrastriate body area (EBA: Downing et al., 2001) and the fusiform body area (FBA: Peelen and Downing, 2005a; Schwarzlose et al., 2005). These regions are principally defined by their selectivity for static images of bodies or faces, although the EBA, FBA and FFA are also sensitive to motion-related cues in body and face stimuli. For example, relative to scrambled point-light control stimuli, point-light displays of whole-body movements are known to activate EBA (Downing et al., 2001; Michels et al., 2005; Peelen et al., 2006) and fusiform cortex (Grossman and Blake, 2002; Grossman et al., 2004; Santi et al., 2003), with the latter activation most probably reflecting modulation of FBA rather than of FFA (Peelen et al., 2006). Fusiform cortex, including FFA, is also sensitive to facial motion in fully illuminated moving images (Campbell et al., 2001; Fox et al., 2009; Puce et al., 2003; Schultz and Pilz,

2009). However, to the best of our knowledge only one published fMRI study has examined neural responses to point-light displays of facial motion, which reported fusiform activation for point-light body movements but not for point-light facial speech movements (Santi et al., 2003). Yet Santi et al. (2003) did not directly contrast face and body motion or functionally localize the face- and body-selective regions.

Thus, it is unknown whether EBA, FBA and FFA are sensitive to human motion regardless of stimulus type (faces and bodies) or to the specific motion-related cues – particularly form-from-motion cues – characteristic of their proprietary stimulus categories. Our principal aim was therefore to establish whether motion of the face and motion of the body elicit stimulus category-selective activation. Using region-of-interest (ROI) analyses, we directly contrasted responses to point-light face and body movements, which provides a stronger test of selectivity than contrasts against some baseline stimulus condition such as scrambled point-light displays, as performed in previous studies (e.g., Grossman and Blake, 2002; Peelen et al., 2006; Santi et al., 2003).

There is also a region of posterior superior temporal sulcus (STS) that is selective for faces (Haxby et al., 2000; Kanwisher and Yovel, 2006), which we here refer to as the face STS. This region is involved in processing changeable properties of faces related principally to muscle movement, rather than the more invariant properties associated with facial morphology and the configuration of features, the processing of which involves more the FFA (Haxby et al., 2000). A neighbouring and often overlapping region of posterior STS and surrounding gyrus is sensitive to the motion of whole bodies and body parts (Blake and Shiffrar, 2007; Puce and Perrett, 2003), which we here refer to as pSTS. We therefore also explored whether form-from-motion cues in point-light displays are sufficient to elicit category-selective activation of these two regions.

Activation of face-selective cortical regions by point-light faces vs. bodies and

activation of body-selective regions by point-light bodies vs. faces could potentially be driven by differences in the spatial arrangement of the dots in the two types of display, including residual cues to the static form of faces and bodies, rather than by their respective motion-related cues. Our body and face stimuli were also differentiated by the number, size and density of the dots and the overall size of the point-light figures (detailed in the Methods section and the Supplementary Materials), thus providing additional cues as to the stimulus category. Controlling for these differences in image characteristics would substantially reduce the ability of the stimuli to convey the characteristic and intrinsically different movements of faces and bodies. To further elucidate the role specifically of biological motion in eliciting stimulus category-specific neural responses and thus to circumvent these conflicting demands, we asked whether a task manipulation that promotes interpretation of the stimulus dots as moving biological forms produces selectivity over and above that obtained from the stimuli interpreted simply as moving dots. Participants judged either the emotion portrayed in the point-light stimuli, thus promoting attention to the displays as moving faces or bodies, or they judged the colour-change of the dots, thus promoting attention to the displays more as coloured moving dots. To the extent that our manipulation of task set promotes perception of biological forms, we predicted that emotion judgements compared to colour judgements would enhance the activity of face-selective regions when participants viewed point-light faces (vs. bodies), and of body-selective regions when they viewed point-light bodies (vs. faces). These predictions for the effect of task set are based on the findings of previous studies, discussed next.

Several neural regions show enhanced activation to static faces when those faces are attended or task relevant, relative to when they are unattended or task irrelevant, particularly in fusiform cortex (e.g., O'Craven et al., 1999; Reddy et al., 2007; Vuilleumier et al., 2001; Vuilleumier et al., 2004) but also including pSTS (Narumoto et al., 2001; Vuilleumier et al.,

2004). There are also reports of increased activation in fusiform cortex to static faces when participants were explicitly judging their expressed emotion compared to judging their gender (Critchley et al., 2000; though see Winston et al., 2003) or identity (Ganel et al., 2005; though see LaBar et al., 2003). Effects of task or attention have yet to be tested with point-light face stimuli. Safford et al. (2010) showed greater activation of right pSTS when participants were attending to point-light whole-body motion compared to when they were attending to spatially overlapping point-light tool motion. Heberlein and Saxe (2005) directly compared neural responses to viewed point-light displays of body motion as a function of task (emotion vs. personality judgements), yet they did not compare responses in ROIs defined by their selectivity for bodies, faces or biological motion. Although Sinke et al. (2010) also did not functionally localize the body or biological motion-selective regions, they did report that regions corresponding to bilateral EBA, right FBA and bilateral pSTS showed more activation during emotion judgements than colour judgements of fully illuminated movie clips of 2 people interacting with body movements (faces were obscured). Finally, Jastorff and Orban (2009) reported increased activation of right EBA and right FBA when participants performed a 1-back task on point-light displays of whole-body motion, as compared to passive viewing of these displays; posterior regions of STS, as well as neighbouring superior and middle temporal gyri, were also activated by this task set.

To further characterize the selectivity of the face- and body-selective regions to face and body motion, we manipulated the motion of the point-light stimuli with characteristic face and body movements and examined whether these stimulus manipulations modulated neural activity in a stimulus category-selective manner. To this end, we made use of an established finding that the face-selective and body-selective regions show enhanced activation in response to face and body stimuli expressing emotions relative to emotionally neutral versions of these same stimuli (for reviews, see Vuilleumier and Driver, 2007; Vuilleumier and

Pourtois, 2007). Such emotional modulation is thought to prioritize visual processing of emotionally salient events (Vuilleumier, 2005) via feedback from the amygdala (Vuilleumier et al., 2004). To date, the visual stimuli used in studies that have shown emotional modulation of the face-selective and body-selective cortical regions have been either static images of emotional faces or bodies (e.g., Jiang and He, 2006; Pessoa et al., 2002; Van den Stock et al., 2008), or moving images in which the form of the face or body is visible (e.g., Kret et al., 2011; Peelen et al., 2007). The extent to which the *motion* of emotional faces and bodies specifically modulates neural processing, and whether such emotional modulation is stimulus category-selective, remains to be examined. By statistically controlling for differences in perceived kinematics, we focused particularly on form-from-motion cues.

Initial evidence of stimulus category-selective emotional modulation comes from a previous study: Peelen et al. (2007) reported that dynamic emotional body stimuli increased the activity of body-selective EBA and FBA but not face-selective FFA. This finding raises the intriguing possibility that emotion signals from the body might modulate precisely those populations of neurons that code for the viewed stimulus category (see Sugase et al., 1999), instead of reflecting synergies between the perception of facial and bodily expressions (de Gelder et al., 2004), or a global boost to all visual processing in extrastriate visual cortex. That dynamic emotional body stimuli increased the activity of body-selective but not face-selective regions of cortex might, however, reflect a greater sensitivity of body-selective than face-selective cortical regions to emotional modulation per se, rather than category-specific emotional modulation. Evidence of truly category-specific emotional modulation would be provided by modulation both of body-selective (but not face-selective) areas by emotional bodies and of face-selective (but not body-selective) areas by emotional faces. We tested this in the present study.

In the fusiform cortex, BOLD responses to faces and bodies spatially overlap but

nevertheless indicate functionally independent neural populations, as revealed by high spatial resolution fMRI (Schwarzlose et al., 2005) or multi-voxel pattern analysis (Downing et al., 2007; Peelen and Downing, 2005a; Peelen et al., 2006). Thus, in order to confirm that motion-related cues in point-light face and body stimuli specifically drive responses of neuronal populations in fusiform cortex (and other regions of interest) that are selective for faces and bodies, respectively, we performed voxelwise correlation analyses (a form of multi-voxel pattern analysis) as well as standard functional ROI analyses. This allowed us to test whether the strength of motion-related and emotional modulation in our regions of interest by point-light face and body movements was related to the degree of voxelwise selectivity to static faces and bodies.

2. Materials and Methods

2.1 Participants

Seventeen healthy volunteers (9 females) were recruited from university postgraduate student and staff populations. They ranged in age from 21-39 years (mean age = 26.3, SD = 5.8). Three participants were left-handed[1], the remainder right-handed. All participants had normal or corrected-to-normal vision and none had a history of neurological disease or head injury or were currently on medication affecting the central nervous system. All participants provided signed, informed consent. The study was approved by the Durham University's Department of Psychology Ethics Advisory Committee.

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[1] Excluding the left-handers from our analyses revealed only one result that was substantially different compared to when the left-handers were included, which we note below. See Supplementary Materials for details and further discussion.

2.2 Stimuli

Participants viewed 2s-long digital video clips (25 frames per second) displaying point-light facial or bodily movements (for examples, see online Supplementary Material.). Each of the face and body sets consisted in 6 different versions of each of angry, happy and emotionally neutral movements, each displayed with one of 3 colour-changes (i.e., 54 face + 54 body movie clips in total). Angry and happy movements were chosen for two main reasons. First, the bodily expressions of anger and happiness employed by Peelen et al. (2007), which were drawn from the same larger stimulus set as were the stimuli for the present study, elicited consistently significant emotional modulation in that earlier study. Second, our pilot work indicated that angry and happy point-light movements tended to be more readily identifiable than certain other emotions for both facial and bodily expressions.

The bodily movements were all intended portrayals either of the emotional expressions or non-emotional actions, the latter consisting in 2 examples each of hopping, walking on the spot, and bending to touch toes. These body stimuli were adapted from a larger set originally developed by Atkinson et al. (2004) with subsequent modifications reported in Atkinson et al. (2007) and were converted to point-light displays using in-house programmes implemented in Matlab (see Supplementary Material for details).

The point-light face stimuli were newly created. An initial set of video clips of facial movements was obtained from 13 adults (5 females), each of whom had 50 6mm-diameter white dots glued to their faces. The dots were positioned in a quasi-random arrangement (e.g., Bassili, 1978, 1979; Doi et al., 2008; Pollick et al., 2003), ensuring an approximately equal number of dots in each of the 4 quadrants of the face, defined by imaginary vertical and horizontal lines through the tip of the nose. Such dot placement helps minimize the availability of static form cues, compared to dots placed to highlight the shape of important facial features such as the mouth and eyebrows (e.g., Hill et al., 2003; Rosenblum et al.,

1996). As is the case with the body stimuli, some residual static form cues were nevertheless available in our face stimuli; for the faces, these included the dark regions that are formed by openings of the mouth and eye regions where there were no dots. Both emotional and non-emotional facial movements were filmed. The emotional movements consisted in intended expressions of anger, disgust, fear, happiness, and sadness. The non-emotional facial movements comprised chewing, gurning, and speech. Movements of both lower and upper regions of the face were included in both the emotional and non-emotional subsets. These movie clips were edited so that they were all 2s long, beginning with the face in a relaxed state. These sequences of facial movements were then converted to point-light displays by tracking the positions of each face dot from frame to frame, using the same method as was used for the body stimuli, though with a different in-house motion-tracking programme. The results of 2 pilot studies were used to select the final stimulus set.

As one of the tasks for the participants was to discriminate the colour of the point-light stimuli, approximately 70% of the face and body dots (e.g., 9/13 dots for the bodies) changed colour over the course of the 2s movie clip, while the remaining dots remained white. The luminance of the dots was held constant at 35 cd/m^2, so the colour-change did not alter the high luminance contrast between the dots and the black background. Which dots changed colour varied randomly across stimuli, in an attempt to ensure that accurate performance on the colour task could not be achieved by relying on a particular subset of the stimulus dots across trials, given that accurate emotion judgements from point-light stimuli also require a more global view of the stimulus. For a given stimulus, the selected dots changed colour linearly across movie frames from white to a particular point in CIE colour space. To equate the difficulty of the colour task between the 3 colour categories and with the difficulty of the emotion task, we were able to choose the directions in colour space and the magnitudes of the differences from white that were associated with each colour label. The hue-angles associated

with each colour label, and the trial-to-trial variability in hue-angles that gave the appropriate level of discrimination performance, were set on the basis of pilot work outside the scanner.[2] RGB values for the stimuli used in the main experiment were re-calculated to produce the desired CIE values from the calibrated projection system used in the scanner.

Pilot testing also ensured that the selected stimulus set was equated with respect to emotion classification accuracy across stimulus type (faces vs. bodies) and emotion (angry vs. happy vs. neutral). We did not attempt to balance quantitative aspects of movement in the stimuli across emotions, as has been done in some previous studies (e.g., Peelen et al., 2007; Pichon et al., 2009), because the quantity and quality of motion are important characteristics that help distinguish between both facially and bodily expressed emotions (e.g., Bassili, 1979; Kamachi et al., 2001; Pollick et al., 2003; Wallbott, 1998) and our stimuli were defined principally by motion cues. Instead, to assess and control for differences between conditions in the kinematics of the point-light stimuli and associated differences in perceived emotional intensity, we conducted an additional rating experiment. A new group of participants (8 males, 6 females; aged 25-55 years, mean age = 32) rated the emotional intensity (from 0 = no emotion to 7 = highly emotional) of each point-light movement sequence in the selected stimulus set, as well as scrambled versions of the same point-light displays. In the scrambled displays, the starting location of each dot was independently randomized within the original viewing frame, preserving the individual motions of the dots but disrupting the spatial relations among the dots and thereby eliminating form-from-motion cues (e.g. Grossman and Blake, 1999). The intensity ratings of the scrambled stimuli provided us with a single measure

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[2] CIE (1931) [xyY] coordinates for the white dots were [0.299, 0.3148, 35]; hue angles and distances associated with Red, Green and Blue respectively were 337±99º and 0.034, 112±56º and 0.060, and 207±37º and 0.078 in this (perceptually non-uniform) space.

that captures differences in perceived emotional intensity between stimuli derived from kinematic information. (Obtaining a single measure for use as a parametric regressor in the fMRI analyses was important to avoid problems associated with colinearity, given that different measures of motion in the stimuli were highly correlated.[3]) In effect, by controlling for differences between stimuli on this measure, differences in brain activity across stimulus conditions would be principally due to differences in form-from-motion information. (See Supplementary Materials for the results for the emotion intensity-rating task.)

2.3 Design and Procedure

2.3.1 Main experiment

Participants performed 2 runs (sessions) of the main experiment, in which they judged either the emotion expressed by the bodily or facial movement or the colour to which the majority of the dots changed. Each run consisted in 12 stimulus blocks of variable length (see below), plus 3 fixation periods of 20s, one at the beginning, one in the middle (after stimulus block 6) and one at the end. Task alternated across blocks, with the first task counterbalanced across participants. Each block consisted of only one stimulus type (faces or bodies), with blocks ordered in one of two sequences: ABBAABBAABBA or BAABBAABBAAB. (See Figure 1.) For each participant, the same block sequence was used for each run. Within each block, 3 different versions of each of 3 different emotional expressions were presented (i.e., 1

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[3] Stimulus motion was calculated as the sum of the distance, in pixels, travelled by the dots in each display (a) from one frame to the next across the length of the movie clip, (b) across every two frames and (c) every three frames. These three measures were highly correlated with each other (bodies: all 3 rs > .98, ps < .0001; faces: all 3 rs > .77, ps < .0005) and with the intensity ratings of the scrambled versions of the same stimuli (bodies: all 3 rs > .78, ps < .0005; faces: all 3 rs > .5, ps < .05).

version of each emotion in each of the 3 colour-changes = 9 stimuli per block). Within those constraints, the allocation of stimuli to blocks and the stimulus order within each block were pseudo-randomized across participants.

---------- Insert Figure 1 about here. ----------

The stimuli were presented in a fast event-related fashion, separated by a variable interstimulus interval (ISI) in order to optimize estimation of the event-related BOLD (blood oxygenation level-dependent) response (Dale, 1999). Each ISI consisted of a blank screen, during which participants were required to make their response by pressing one of 3 buttons on a response box, using their right hand. The ISIs were randomly selected from trial to trial from an approximate exponential distribution. In order to optimize the efficiency for estimating the BOLD response for this pseudo-randomized (permuted) fast event-related design, the distribution of the ISIs was selected such that the mean stimulus onset asynchrony was 5s (Henson, 2006); with the stimulus duration being 2s, this resulted in a mean ISI of 3s (range = 1.75-8.0s, SD = 1.68s). As a consequence, the block length varied, from 33.74s to 60.74 (mean = 45.02s, SD = 4.61s). Additional 'null events' were not used, as the primary event-related contrasts of interest were differential effects between stimulus conditions, and not also the effects relative to an interstimulus baseline (Henson, 2006). Each block began with an instruction screen for 3s, indicating which decision (emotion or colour) the participant should make, and which button corresponded to which emotion/colour word (the allocation of answers to buttons was fully counterbalanced across participants). To familiarize the participants with the task, stimuli and response mappings, they were given a practice session prior to being scanned, consisting of 1 run of the main experiment identical to that which they subsequently performed in the scanner (i.e., colour and emotions judgements on all stimuli). This practice session was conducted in a separate laboratory using a monitor calibrated to match the output of the projection system used in the scanner.

2.3.2 Functional localizer runs

Upon completing the main experiment, participants completed 2 runs of a face and body localizer task, as well as 1 run of a biological-motion localizer task. To localize the face- and body-selective areas, we employed a slightly modified version of a standard functional localizer experiment employed in previous work (Downing et al., 2007; Peelen et al., 2007; Peelen and Downing, 2005b). Briefly, this experiment consisted in two runs each of 13 16s blocks consisting of either a fixation period or full-colour images of faces, headless bodies or chairs. Images were presented for 550 ms and participants had to detect the occasional repetition of an image (1-back task). Similarly, to localize biological-motion sensitive pSTS, participants were presented with 19 18s blocks of either fixation-only conditions, point-light whole-bodily movements (marching, walking, running, boxing, and jumping), or scrambled versions of these same movements (e.g., Grossman et al., 2000; Peelen et al., 2006). Each stimulus was presented for 1s and participants again had to detect the repetition of a stimulus.

2.4 Image Acquisition

All scanning was conducted at the Newcastle Magnetic Resonance Centre (UK), on a 3 Tesla Philips Intera Achieva MRI system, fitted with a SENSE 8-channel head coil. Gradient-echo T2*-weighted transverse echo-planar images (EPI) with BOLD contrast were acquired. Each functional volume contained 31 axial slices, with 2.3mm thickness, 1 mm gap, and in-plane resolution of 2.8 × 2.8 mm, acquired parallel to the intercommissural (AC-PC) line in a continuous sequence, with repetition time (TR) = 2020ms, echo time (TE) = 34ms, flip angle = 90°, field of view (FOV) = 210 × 210 mm, and acquired matrix of 76 × 75 voxels (reconstructed with matrix 80 × 80). For each participant, 315 functional volumes (636.3 s) were collected for each of the 2 runs of the main experiment, along with 178 volumes (359.6s) for the biological motion localizer experiment, and 103 volumes (208.1s) for each run of the face and body localizer experiment. An additional 4 ‘dummy’ volumes were

acquired at the beginning of each functional run to allow for signal equilibration. Prior to the functional scans, anatomical T1-weighted images were acquired (TR = 9.6ms, TE = 4.6 ms, slice thickness = 1.2 mm, 150 slices, flip angle = 8°, FOV = 240 × 180 mm, acquired matrix of 208 × 208 voxels, reconstructed with matrix 256 × 256).

2.5 fMRI Data Preprocessing

All image processing and statistical analyses were carried out using SPM5 (Friston et al., 1997; Wellcome Trust Centre for Neuroimaging; see www.fil.ion.ucl.ac.uk/spm) implemented in Matlab. Prior to any statistical analyses, the functional images for the main experiment were spatially realigned to the first volume by rigid-body transformation and resliced to correct for head motion, slice-time corrected for differences in slice acquisition time using the middle slice (15) as reference, and then spatially normalized to the standard Montreal Neurological Institute (MNI) EPI template, using the spatial normalization parameters from the segmentation of the participant's T1-weighted structural image, with a resampled voxel size of 2 mm^3. The same procedure was followed for the functional images from the functional localizer scans, except that no slice-time correction was applied. For ROI and voxelwise correlation analyses, no spatial smoothing was applied. For whole-brain group-average analyses, the single-subject data were spatially smoothed with an isotropic 8 mm full-width at half-maximum (FWHM) Gaussian kernel.

2.6 fMRI Model Specification and Estimation

Event-related responses were assessed by setting-up fixed-effects models in which condition-specific effects were modeled separately for each participant. Each run was modeled as a separate session within a single design matrix for each participant. For each session, we specified a linear model with 12 principal conditions of interest, one for each cell of the 2 (task: judge emotion, judge colour) × 2 (stimulus type: bodies, faces) × 3 (emotion: angry, happy, neutral) factorial design. Thus, in total there were 24 conditions of interest (12

for each session). To create event-related regressors for the subsequent general linear model (GLM), these 24 conditions were modeled by convolving delta functions, representing the onset of each event (stimulus duration = 0), with a canonical haemodynamic response function and its temporal and spatial derivatives (Friston et al., 1998). To control for differences between conditions in the kinematics of the stimuli and associated differences in perceived emotional intensity, an additional covariate regressor was added, encoding the mean intensity rating of the scrambled version of each stimulus (as discussed in the Stimuli subsection, above). Additional regressors of no interest were used to model: the instruction screen preceding each block, and, in order to capture residual movement-related artifacts, the 6 realignment parameters. The final two regressors represented the mean (constant) over scans, one for each session. To remove low-frequency drifts from the data, a high-pass filter was applied using a standard cut-off frequency of 128s (0.008 Hz).

Linear contrasts pertaining to the effects of interest were calculated for each participant to produce condition-specific contrast images. As task and stimulus type were blocked, the main effects of these factors were calculated by contrasting the relevant combinations of the event-related regressors.

2.7 Region of Interest Analyses

For each of the two functional localizer experiments, a fixed-effects GLM was used to model condition-specific effects separately for each participant. Each stimulus condition of interest (blocks of faces, bodies or chairs and blocks of biological or scrambled motion stimuli) was specified as a separate regressor for each session. Additional regressors were specified for the fixation blocks, for the 6 realignment parameters determined from initial spatial registration, and for the mean (constant) over scans for each session.

In each participant, we defined 8 functional ROIs from the localizer experiments, using epoch-related designs. Four body-selective regions – right and left EBA and right and

left FBA – were defined by contrasting body responses with chair responses. Face-selective regions in fusiform gyrus – right and left FFA – were defined by contrasting face and chair responses. Using the same contrast, we also delineated a commonly reported face-selective region in right posterior STS (face STS), given this region's involvement in processing changeable properties of faces related principally to muscle movement (Haxby et al., 2000). The biological motion selective right pSTS was defined by contrasting whole-body motion with scrambled whole-body motion. These contrasts were restricted to the appropriate cortical regions: right and left fusiform cortex for the right and left FFA and FBA, the union of middle occipital and middle and inferior temporal cortices in the right and left hemispheres for right and left EBA, and the union of middle and superior temporal cortices in the right hemisphere for right pSTS. These search regions were delineated using the Anatomical Automatic Labeling (AAL) template (Tzourio-Mazoyer et al., 2002), and implemented via the WFU PickAtlas toolbox (Version 2.4: Maldjian et al., 2003). Each ROI was then defined individually for each participant as the set of contiguous voxels that were significantly activated ($p < 0.005$, uncorrected) within a 12 × 12 ×12 mm cube surrounding and including the most significantly activated voxel within the appropriate cortical region. This ROI definition was achieved using the REX toolbox (Susan Whitfield-Gabrieli; http://web.mit.edu/swg/software.htm). The ROIs in right STS were further restricted to clusters lying at least partially in STS, determined by visual inspection of the relevant activation maps overlaid on each individual participant's structural image. In the cases where there was more than one activation cluster for a given ROI, the selected peak was the largest whose coordinates corresponded most closely to previously reported locations (Kanwisher et al., 1997; Peelen and Downing, 2005a). Using these criteria, some of these ROIs could not be identified in a small number of participants, as indicated in Table 1.

---------- Insert Table 1 about here. ----------

Depending on the analysis, the relevant parameter estimates (beta values) or contrast estimates for each condition for each participant were then extracted from the ROIs using the REX toolbox. To test for differences in response magnitude across conditions (task, stimulus type, and emotion) in each ROI, these parameter or contrast estimates were entered into ANOVAs and planned comparison t-tests (one-tailed, Bonferroni-corrected for multiple comparisons). The ANOVAs were initially conducted with imaging run as a factor, but as ROI activations did not show any significant main effects or interactions involving imaging run (all ps $\geq$ .09, except for the main effect of run in left EBA, $F(1, 15) = 4.11$, $p = .06$), this factor was excluded from all subsequent analyses.

2.8 Voxelwise Correlation Analyses

Multivoxel correlation analyses were used to confirm the ROI analyses but also to interpret overlapping functional activations, particularly in the fusiform gyrus, where BOLD responses to faces and bodies spatially overlap but nevertheless indicate functionally independent neural populations (Peelen and Downing, 2005a; Peelen et al., 2006). These analyses were performed in a similar fashion to the voxelwise correlation analyses used in several previous studies (Bedny et al., 2009; Berman et al., 2010; Downing et al., 2007; Peelen et al., 2007; Peelen et al., 2006). To be unbiased with respect to the voxels selected for these correlation analyses, we selected, for each participant and ROI, all voxels in the relevant cortical regions (e.g., right fusiform) within a 12 × 12 × 12 mm cube centred on the peak voxel used to define the functional ROI from the localizer tasks (described above). This was achieved by performing the contrast all point-light stimuli > fixation from the main experiment with the uncorrected p-value set to .999 and selecting the largest single cluster from this contrast within the anatomical region defined by the overlap of the 12mm cube and the relevant anatomical criteria (as specified for the ROI analyses, above). For each of these selected voxels, we then extracted a contrast value for the contrasts of interest. As estimates of

body and face selectivity, contrast values for bodies > chairs and faces > chairs were extracted from the localizer experiments. As estimates of responses to body and face motion from the main experiment, contrast values for point-light bodies > point-light faces and point-light faces > point-light bodies were extracted for each task. Finally, as estimates of emotional modulation from the main experiment, contrast values for angry > neutral and happy > neutral were extracted for each combination of task and stimulus type. Following Bedny et al. (2009), all negative contrast values were set to zero, so as to focus specifically on activity above the baselines for the relevant conditions (i.e., faces or bodies > chairs for face or body selectivity, respectively, and angry or happy > neutral for emotional modulation). To test whether the strength of emotional modulation was correlated with the degree of body and or face selectivity, we then correlated the pattern of emotional modulation with the pattern of body and face selectivity across the set of voxels in the ROI. These correlations were computed for each participant individually and were then Fisher transformed. The resulting mean correlations were entered into ANOVAs and one-sample t-tests, corrected for multiple comparisons using the Bonferroni method.

2.9 Whole-Brain Analyses

Although our principal predictions focused on responses in a priori defined ROIs, which we tested using ROI and voxelwise correlation analyses, for completeness we also report the main findings of the whole-brain analyses in the Supplementary Materials.

3. Results

3.1 Behavioural Results

The responses for one participant were not collected due to a technical error. For the remaining 16 participants, overall classification accuracy was high, at 81% correct for emotion judgments and 80% correct for colour judgments, averaged across task and stimulus type (see Figure 2). A repeated-measures ANOVA was conducted to compare mean

proportion correct classification scores across task (emotion, colour), stimulus type (bodies, faces) and emotion (angry, happy, neutral). Emotion classification accuracy was not significantly different from colour classification accuracy, either overall ($p > .75$) or within each stimulus type (bodies: $p > .2$; faces: $p > .5$). Nonetheless, there was a significant main effect of stimulus type ($F(1, 15) = 24.14$, $p < .0005$), reflecting more accurate classification overall for point-light bodies than for point-light faces. This main effect of stimulus type was modulated by significant interactions with task ($F(1, 15) = 5.75$, $p < .05$) and with emotion ($F(2, 30) = 5.28$, $p < .05$). These 2-way interactions were themselves modulated by a significant 3-way interaction ($F(2, 30) = 4.7$, $p < .05$). To follow-up this significant 3-way interaction, a 2-way ANOVA was conducted for each task separately. For colour judgments, neither of the main effects or the interaction was significant (all ps $> .12$), indicating equivalent colour classification performance across stimulus type and emotion. For emotion judgments, the main effect of emotion was not significant ($p > .2$), but there was a significant main effect of stimulus type ($F(1, 15) = 20.52$, $p < .0005$), which was modified by a significant interaction with emotion ($F(2, 30) = 7.79$, $p < .005$). Simple main effects analyses revealed that emotion classification accuracy did not differ significantly across emotions for the point-light bodies ($p > .4$), but that it did for the point-light faces ($F(2, 30) = 5.5$, $p < .01$). Bonferroni-corrected pairwise comparisons revealed that participants were reliably more accurate in classifying happy and neutral than angry point-light faces (both ps $< .05$).

---------- Insert Figure 2 about here. ----------

3.2 fMRI Results

3.2.1 Category-Selective Activation by Point-Light Displays of Facial and Bodily Motion

We first set out to establish the brain regions activated by point-light body movements and those activated by point-light facial movements, when those stimulus conditions were contrasted with each other, and whether those patterns of activation varied as a function of

task (emotion vs. colour judgement). Given the reasoning and previous findings outlined in the Introduction, we predicted: (1) point-light body movements would activate regions known to be specialized for processing bodily form (EBA and FBA); (2) point-light face movements would activate regions known to be specialized for processing facial form, particularly the right FFA; and (3) Task × Stimulus Type interactions in the body- and face-selective regions, particularly in the right hemisphere, such that emotion judgements would enhance the activation of right FFA to point-light faces vs. bodies, and the activation of right EBA and right FBA to point-light bodies vs. faces, relative to colour judgements on those same stimuli.

3.2.1.1 ROI analyses: Point-light bodies > point-light faces

See Figure 3A. Task × Stimulus Type ANOVAs were conducted separately for each of the 4 body-selective ROIs as well as for biological-motion sensitive right pSTS. There were significantly larger responses in both right and left EBA to point-light bodies relative to point-light faces, irrespective of task (right EBA: $F(1, 16) = 51.53$, $p < .000005$; left EBA: $F(1, 15) = 26.58$, $p < .0005$). There was also significantly greater activation to point-light bodies relative to point-light faces in the right FBA, irrespective of task $F(1, 15) = 23.95$, $p < .0005$). Point-light bodies did not significantly activate left FBA relative to point-light faces, for either task ($F < 1.5$, $p > .25$; planned comparison t-tests: both ps > .2). For right pSTS, there was a non-significant trend for responses to point-light bodies to be greater than responses to point-light faces ($F(1, 14) = 3.34$, $p = .089$). This effect was significant once the 2 left-handed participants with a right pSTS ROI were excluded ($F(1, 12) = 22.36$, $p < .0005$). (Of all our results, this was the only one that was substantially different compared to when the left-handers were included; see Supplementary Materials.) There were no significant Task × Stimulus Type interactions in any of these 5 ROIs (all Fs < 2, all ps > .18). There were significant main effects of task in right EBA ($F(1, 16) = 6.13$, $p < .05$), right FBA ($F(1, 15) = 13.77$, $p < .005$), left FBA ($F(1, 14) = 10.55$, $p < .01$), and right pSTS ($F(1, 14) = 13.54$, $p <$

.005), and a marginally significant effect in left EBA ($F(1, 15) = 4.14$, $p = .06$), in all cases reflecting larger responses for emotion judgements than for colour judgements.

---------- Insert Figure 3 about here. ----------

3.2.1.2 ROI analyses: Point-light faces > point-light bodies

See Figure 3B. A Task × Stimulus Type ANOVA was performed for each of the 3 face-selective ROIs. There was no significant main effect of stimulus type on right FFA activation ($F(1, 15) = 0.31$, $p > .55$), although there was, as predicted, a significant Task × Stimulus Type interaction ($F(1, 15) = 5.08$, $p < .05$), reflecting significantly larger right FFA responses to point-light faces relative to point-light bodies when participants were judging emotion ($F(1, 15) = 4.63$, $p < .05$) but not when they were judging colour ($F(1, 15) = 1.15$, $p = .3$). For left FFA there was a significant main effect of stimulus type ($F(1, 14) = 7.67$, $p < .05$), reflecting greater activation to point-light faces than to point-light bodies irrespective of task, but no significant Task × Stimulus Type interaction ($F < 0.02$, $p > .9$). Point-light faces did not significantly activate right face STS for either task ($F(1, 16) = 3.17$, $p = .094$; planned comparison t-tests: both *p*s > .25). There were significant main effects of task in right FFA ($F(1, 15) = 28.89$, $p < .0001$) and right face STS ($F(1, 16) = 10.79$, $p = .005$), reflecting larger responses for emotion judgements than for colour judgements, but not in left FFA ($F < 2.7$, $p > .12$).

3.2.1.3 Voxelwise correlation analyses

Voxelwise correlation analyses were conducted to confirm the ROI analyses and to counter the possibility that, with respect to the fusiform cortex activation, these findings might be a function of the strong overlap between FFA and FBA (Peelen and Downing, 2005a; Schwarzlose et al., 2005). Five ROIs were selected for these analyses: right and left EBA, the union of FFA and FBA in each hemisphere, and the union of right face STS and right pSTS (the latter because of our finding of considerable overlap between face-selective

and biological motion-selective activity in STS; mean MNI coordinates of activation peaks for right pSTS: 55, -45, 9; right face STS: 51, -52, 13). We computed for each participant for each task and ROI the correlation between responses of selected voxels in the ROI to point-light bodies or point-light faces in the main experiment and body and face selectivity as determined from the localizer experiment. The Fisher-transformed correlation coefficients were first entered into separate ANOVAs for each ROI, to test for differences in correlations as a function of task (emotion, colour), stimulus type (point-light faces, point-light bodies), and selectivity (static faces, static bodies). One-tailed, one-sample t-tests (Bonferroni-corrected) were then used to assess whether the voxelwise correlations between responses to point-light bodies or faces and selectivity for static bodies or faces were statistically greater than zero.

We specifically predicted Stimulus Type × Selectivity interactions in the fusiform ROIs, that is, that responses to point-light bodies would be more strongly correlated with voxelwise selectivity for static bodies than for static faces, whereas responses to point-light faces would be more strongly correlated with voxelwise selectivity for static faces than for static bodies. As there were no significant main effects of task or interactions involving task for any of the ROIs (all Fs < 4.04, ps > .06), the remaining results reported here are those for which the voxelwise contrast values were calculated collapsed over task.

The voxelwise correlation analyses for right and left EBA confirm the results of the ROI analyses reported above and are therefore reported in detail in the Supplementary Materials. In brief: in both right and left EBA, activity elicited by point-light bodies compared to point-light faces was significantly positively correlated with voxelwise selectivity for static bodies (right EBA: $r = .523$, $t(16) = 11.07$, $p < .00000001$; left EBA: $r = .456$, $t(15) = 9.68$, $p < .0000001$), whereas activity elicited by point-light *faces* compared to point-light bodies was significantly *negatively* correlated with voxelwise selectivity for static bodies (right EBA: $r =$

-.156, $t(16) = -7.62$, $p < .000005$; left EBA: $r = -.16$, $t(15) = -5.91$, $p < .00005$).

For the union of FFA and FBA in the right hemisphere, there were significant main effects of stimulus type ($F(1, 14) = 6.72$, $p < .05$) and selectivity ($F(1, 14) = 9.76$, $p < .01$), which were modified by a significant interaction between these two factors ($F(1, 14) = 33.05$, $p = .00005$). Simple main effects analyses revealed significantly larger correlations between activity elicited by point-light bodies and voxelwise selectivity for static bodies than for static faces ($F(1, 14) = 40.51$, $p < .00005$), and, conversely, significantly larger correlations between activity elicited by point-light faces and voxelwise selectivity for static faces than for static bodies ($F(1, 14) = 18.89$, $p < .001$). The patterns of activity elicited by point-light bodies compared to point-light faces was significantly positively correlated with voxelwise selectivity for static bodies ($r = .337$, $t(14) = 6.22$, $p < .00005$) but not faces ($r = .052$, $t(14) = 1.32$, $p > .4$). The patterns of activity elicited by point-light *faces* compared to point-light bodies was significantly positively correlated with voxelwise selectivity for static faces ($r = .143$, $t(14) = 2.53$, $p < .05$) but not static bodies ($r = -.074$, $t(14) = -2.25$, $p > .08$).

For the union of FFA and FBA in the left hemisphere, there was no significant main effect of stimulus type or selectivity (Fs < 2.6, $p > .13$); the interaction between these two factors was nevertheless significant ($F(1, 12) = 25.97$, $p < .0005$). Simple main effects analyses revealed significantly larger correlations between activity elicited by point-light bodies and voxelwise selectivity for static bodies than for static faces ($F(1, 12) = 15.75$, $p < .005$), and, conversely, significantly larger correlations between activity elicited by point-light faces and voxelwise selectivity for static faces than for static bodies ($F(1, 12) = 35.49$, $p < .0001$). The patterns of activity elicited by point-light bodies compared to point-light faces was significantly positively correlated with voxelwise selectivity for static bodies ($r = .221$, $t(12) = 3.09$, $p < .05$) but not faces ($r = -.046$, $t(12) = -1.19$, $p > .5$). The patterns of activity elicited by point-light *faces* compared to point-light bodies was significantly positively

correlated with voxelwise selectivity for static faces (r = .136, $t(12)$ = 2.58, p < .05); there was no significant correlation with selectivity for point-light bodies (r = -.037, t (12) = -0.65, p > .9).

For the union of face-selective and biological motion-selective regions in right pSTS, there were significant main effects of stimulus type ($F(1, 14)$ = 15.67, p < .005) and selectivity ($F(1, 14)$ = 11.42, p < .005), which were modified by a significant interaction between these two factors ($F(1, 14)$ = 19.74, p < .001). Simple main effects analyses revealed significantly larger correlations between activity elicited by point-light bodies and voxelwise selectivity for static bodies than for static faces ($F(1, 14)$ = 18.34, p < .001), and, conversely, significantly larger correlations between activity elicited by point-light faces and voxelwise selectivity for static faces than for static bodies ($F(1, 14)$ = 9.9, p < .01). The patterns of activity elicited by point-light bodies compared to point-light faces was significantly positively correlated with voxelwise selectivity for static bodies (r = .285, $t(14)$ = 5.37, p < .0005) but not faces (r = .043, t (14) = 1.53, p > .29). Activity elicited by point-light faces compared to point-light bodies was not significantly correlated with selectivity for static faces (r = .01, $t(14)$ = 0.4, p > .99) or static bodies (r = -.065, $t(14)$ = -2.08, p > .1).

3.2.2 Category-Selective Emotional Modulation by Point-Light Displays of Facial and Bodily Motion?

We next sought to establish the brain regions activated by emotional (angry or happy) relative to emotionally neutral movements, and whether those patterns of activation varied as a function of stimulus type and task. Our primary aim here was to test further the selectivity of the face- and body-selective regions to face and body motion. We hypothesized that manipulating the motion of the point-light body and face stimuli with characteristic body and face movements would modulate neural activity in a stimulus category selective manner. Specifically, we predicted that emotional relative to neutral bodily motion would increase

activity of body-selective but not face-selective regions (i.e., EBA and FBA but not FFA) and that emotional relative to neutral facial motion would increase activity of face-selective but not body-selective regions.

3.2.2.1 ROI analyses: Emotional modulation of body-selective regions

---------- Insert Figure 4 about here. ----------

Figure 4 summarizes the emotional modulation of the ROIs as a function of the individual stimulus conditions. Contrast estimates for angry > neutral and happy > neutral were entered into Task × Stimulus Type × Emotion ANOVAs, one for each of the 4 body-selective ROIs. These analyses revealed only a significant main effect of stimulus type for right EBA ($F(1, 16) = 13.26$, $p < .005$) and a marginally significant 3-way interaction for left EBA ($F(1, 15) = 4.35$, $p = .054$). All other main effects and interactions were not significant (all ps > .09).

For right EBA, the significant main effect of stimulus type reflected greater emotional modulation by point-light bodies (M = 3.58, SD = 2.01) than by point-light faces (M = 0.23, SD = 2.92). Indeed, there was significant emotional modulation of right EBA by point-light bodies ($t(16) = 7.35$, $p < .000005$) but not by point-light faces ($p > .7$).

For left EBA, the Stimulus Type × Emotion interaction was significant for colour judgements ($F(1, 15) = 6.21$, $p < .05$), but not for emotion judgements ($p > .9$). This interaction reflected reliably greater emotional modulation by point-light bodies than by point-light faces during colour judgements when they expressed anger (bodies: M = 1.51, SD = 1.87; faces: M = -0.76, SD = 3.32; $F(1, 15) = 6.17$, $p < .05$), but not when they expressed happiness (bodies: M = 0.38, SD = 3.51; faces: M = 1.48, SD = 4.53; $F(1, 15) = 0.7$, $p > .4$). The emotional modulation of this ROI was significantly greater than zero, after Bonferroni-correction for 8 comparisons, only for angry point-light bodies during colour judgements

($t(15) = 3.24$, $p < .05$), although there was marginally significant emotional modulation by angry point-light bodies during emotion judgements ($t(15) = 2.72$, $p = .063$).

Neither point-light bodies nor point-light faces elicited significant emotional modulation in right FBA (bodies: $t(15) = 1.58$, $p > .13$; faces: $t(15) = 1.04$, $p > .3$). For left FBA, there was significant emotional modulation by point-light bodies ($t(14) = 2.15$, $p < .05$) and a non-significant trend for emotional modulation by point-light faces ($t(14) = 1.84$, $p = .087$).

3.2.2.2 ROI analyses: Emotional modulation of face-selective regions

Task × Stimulus Type × Emotion ANOVAs were conducted on the angry > neutral and happy > neutral contrast estimates from each of the 3 face-selective ROIs. These analyses revealed only a significant main effect of stimulus type for right face STS ($F(1, 16) = 6.01$, $p < .05$), reflecting reliably greater emotional modulation by point-light bodies (M = 1.83, SD = 3.44) than by point-light faces (M = -0.6, SD = 3.2). All other main effects and interactions were not significant (all ps > .15).

For right FFA, both point-light bodies and point-light faces elicited significant emotional modulation (bodies: $t(15) = 2.19$, $p < .05$; faces: $t(15) = 2.22$, $p < .05$). Neither facial nor bodily point-light emotional expressions modulated the activity of left FFA (both ts < 1.4, ps > .15). There was significant emotional modulation of right face STS by point-light bodies ($t(16) = 2.19$, $p < .05$) but not faces ($p > .4$).

3.2.2.3 ROI analyses: Emotional modulation of biological motion-selective pSTS

A Task × Stimulus Type × Emotion ANOVA revealed a significant main effect of stimulus type ($F(1, 14) = 6.67$, $p < .05$), reflecting greater emotional modulation of right pSTS by point-light bodies (M = 1.74, SD = 3.02) than by point-light faces (M = -1.62, SD = 3.28). There was also a significant Stimulus Type × Emotion interaction ($F(1, 14) = 5.29$, $p < .05$), reflecting significantly greater emotional modulation of right pSTS by point-light bodies than

by point-light faces when they expressed anger ($F(1, 14) = 9.2$, $p < .01$; bodies: M = 5.16, SD = 8.0; faces: M = -3.68, SD = 7.95), and a non-significant trend for greater activation when they expressed happiness ($F(1, 14) = 3.13$, $p = .099$; bodies: M = 1.8, SD = 6.31; faces: M = -2.79, SD = 6.38). The other main effects and interactions were not significant (all ps > .24).

Collapsed over task, there was marginally significant emotional modulation of right pSTS by angry point-light body stimuli ($t(14) = 2.5$, $p = .051$) but no emotional modulation by happy point-light body movements ($p > .55$). There was no significant emotional modulation of right pSTS by either angry or happy point-light faces (angry: $t(14) = -1.79$, $p > .18$; happy: $t(14) = -1.69$, $p > .22$).

3.2.2.4 Voxelwise correlation analyses

We next examined the voxelwise degree of emotional responses in the body-selective and face-selective ROIs as a function of body and face selectivity. Emotional effects observed in the ROIs could reflect either a global increase of activity in regions of occipitotemporal cortex or more specific modulation of either body-selective or face-selective neurons (e.g., de Gelder, 2006; Peelen et al., 2007; Sugase et al., 1999). If emotional modulation by body movements is selectively related to body processing and emotional modulation by face movements is selectively related to face processing, we would expect voxels that are more strongly body or face selective (indicating a high percentage of body-selective or face-selective neurons) also to show relatively strong emotional modulation that is specific to the stimulus type for which that ROI is selective. To test this, we computed, for each participant and each ROI that showed emotional modulation at the group level, a set of voxel-by-voxel correlations between emotional effects in the main experiment and selectivity as determined from the localizer experiment. For the ROIs located in the fusiform and STS, we again performed the voxelwise correlations on voxels within the unions of, respectively, FFA and FBA, and face-selective STS and biological-motion selective pSTS. In these ROIs we

therefore examined the correlations with both body selectivity and face selectivity, correcting for 16 comparisons (2 tasks × 2 stimulus types × 2 emotions × 2 forms of selectivity) using the Bonferroni method. For right and left EBA, we examined the correlations with body selectivity only, and therefore corrected for 8 comparisons. A summary of the voxelwise correlation analyses is presented in Table 2.

---------- Insert Table 2 about here. ----------

For right EBA, the correlations between body selectivity and emotional modulation were significantly positive for both angry and happy body movements during both tasks (all rs > .2, all ts > 4.6, all ps < .005). For left EBA, the correlations between body selectivity and emotional modulation were significantly positive for both angry and happy body movements during emotion judgements (both rs > .16, both ts > 3.2, both ps < .05) and only for angry body movements during colour judgements (angry: r = .194, $t(15)$ = 5.45, p < .0005; happy: r = .107, $t(15)$ = 2.6, p = .08). Surprisingly, the degree of emotional modulation of right EBA voxels by point-light angry *face* movements was significantly correlated with voxelwise selectivity for static bodies during emotion judgments (r = .109, $t(16)$ = 2.83, p < .05), although not during colour judgements (r = -.001, $t(16)$ = -0.015, p > .99). This finding ought to be interpreted with caution, however, given the finding from the ROI analyses that angry vs. neutral face movements during emotion judgements did not significantly activate right EBA after correction for multiple comparisons ($t(16)$ = 2.26, p = .153 corrected, p = .019 uncorrected; see Figure 4). By contrast, there were no significant relationships between the degree of emotional modulation of left EBA voxels by face movements and the degree of body selectivity (all rs < .065, all ts < 1.3, all ps > .95).

For right fusiform (the FFA-FBA union), there was no evidence of stimulus-category selective emotional modulation. Emotional modulation of voxels in right fusiform by angry body movements was significantly positively correlated with both body and face selectivity in

this region, irrespective of task (all rs > .12, all ts > 3.4, all ps < .05). Emotional modulation of voxels in right fusiform by happy body movements was significantly positively correlated with only body selectivity during emotion judgements (r = .186, $t(14)$ = 4.33, p < .01; all other ps > .6). Emotional modulation of voxels in right fusiform by face movements was not significantly correlated with either face or body selectivity in either task (all rs < .046, all ts < 1.5, all ps > .99). For left fusiform, there were no significant voxelwise correlations between emotional modulation and body or face selectivity (all rs < .085, all ts < 2.26, all ps > .35).

For right pSTS (the union of face-selective and biological-motion selective ROIs), we also found no evidence of stimulus-category selective emotional modulation. During emotion judgements, there were significant correlations between the voxelwise selectivity to static bodies and emotional modulation by both angry and happy body movements (angry: r = .209, $t(14)$ = 3.99, p < .05; happy: r = .144, $t(14)$ = 3.28, p < .05). However, there were also significant correlations between voxelwise selectivity to static faces and emotional modulation by angry *body* movements during emotion judgements (r = .185, $t(14)$ = 3.33, p < .05) and during colour judgements (r = .112, $t(14)$ = 3.61, p < .05). All other correlations were not significant (all rs < .12, ts < 2.95, ps > .09).

4. Discussion

We used point-light displays to test whether facial- and bodily-motion selectively activate regions of the brain functionally defined by their selectivity for static images of faces and bodies. By statistically controlling for differences in perceived emotional intensity based on kinematics, we focused particularly on the contribution of form-from-motion information. A three-pronged approach was employed.

First, we directly contrasted responses to point-light face and body movements, rather than comparing responses of each stimulus type to scrambled point-light displays, as previous studies have done (e.g., Grossman and Blake, 2002; Peelen et al., 2006; Santi et al., 2003).

Second, to confirm a role specifically for biological motion-related cues in driving stimulus category-selective neural responses, as opposed to simple differences between the point-light face and body stimuli such as the spatial arrangements of the dots, we had participants judge either the emotion portrayed in the stimuli or the colour-change of the dots. If task set influences interpretation of the dots as moving faces or bodies, evidence of the specificity of the face- and body-selective regions to facial and bodily motion, respectively, would be provided by enhanced activation in these regions for their proprietary stimulus types during emotion judgements compared to colour judgements. Third, we manipulated the motion of the point-light stimuli with characteristic face and body movements and examined whether these stimulus manipulations modulated neural activity in a stimulus category-selective manner. Specifically, we tested the extent to which expressed emotions signaled by facial or bodily motion modulate activity in these face- and body-selective regions.

Standard ROI analyses revealed that point-light body movements activated body-selective regions in lateral occipitotemporal cortex (right and left EBA) and fusiform gyrus (right but not left FBA), regardless of whether participants were judging the expressed emotion or the colour-change of the stimulus dots. Point-light face movements activated face-selective FFA bilaterally, although this greater activation to point-light faces than to point-light bodies was evident in the right hemisphere only when participants were explicitly judging the expressed emotion. Voxelwise correlation analyses revealed that, even in bilateral regions of fusiform cortex containing overlapping populations of body-selective and face-selective neurons, the patterns of activity elicited by point-light bodies were positively correlated with voxelwise selectivity for static bodies but not for static faces (which was also the case in right and left EBA), whereas activity elicited by point-light faces was positively correlated with voxelwise selectivity for static faces but not for static bodies. (Task set did not modulate the voxelwise correlations.)

We further demonstrated enhanced activation of several body- and face-selective regions for happy or angry relative to emotionally neutral movements, in some regions depending on task set (i.e., by whether participants were judging emotion or colour). However, we found only a limited degree of stimulus category selective emotional modulation. Specifically, emotional body movements enhanced right and left EBA activity but emotional face movements did not. In both these ROIs, voxels that were more strongly body selective were also more strongly modulated by the emotional expressions displayed by body movements, regardless of task. In left EBA, voxelwise selectivity for static bodies was unrelated to the degree of emotional modulation by face movements, but in right EBA, voxels that were more strongly body selective were also more strongly modulated by angry *face* movements during emotion (but not colour) judgments. While emotional face and particularly body movements modulated activity in fusiform gyrus and emotional body movements modulated activity in right posterior STS, there was no evidence that emotional modulation in these regions occurred in a stimulus category-selective manner.

4.1 Category-Selective Activation by Point-Light Displays of Facial and Bodily Motion

Our findings of substantially greater activation of bilateral EBA to point-light bodies compared to point-light faces are consistent with previous reports of activation for whole-body point-light displays in posterior inferior temporal sulcus/middle temporal gyrus (Michels et al., 2005; Peuskens et al., 2005; Saygin et al., 2004), including functionally localized bilateral EBA (Downing et al., 2001; Jastorff and Orban, 2009; Peelen et al., 2006). Indeed, given that those previous studies contrasted whole-body point-light with scrambled point-light displays, our results extend their findings to show that point-light whole-body movements activate bilateral EBA even when contrasted with point-light face movements. Furthermore, we found that fusiform gyrus activation to point-light body movements, particularly in the right hemisphere, reflects engagement of body-selective FBA but not face-selective FFA.

This result is consistent with Peelen et al.'s (2006) finding that the selectivity of fusiform activation to point-light body motion correlated on a voxelwise basis with the selectivity of this region to static bodies but not with its selectivity to static faces. Together these results indicate that the face-selective regions of fusiform gyrus play no functional role in the perception of whole-*body* movement, contrary to Grossman et al.'s (2004) suggestion.

Contrary to our initial predictions, the EBA and FBA activation to point-light bodies vs. point-light faces was not enhanced during emotion judgements relative to colour judgements; the strong activation of these body-selective regions by point-light bodies was equivalent across tasks. One explanation for this finding is that the *motion-related* cues in our point-light body stimuli are, relative to the motion-related cues in our point-light faces, sufficiently compelling to strongly activate these body-selective regions irrespective of whether observers are attending to the stimuli as arrays of moving dots as to when they are attending to them as bodies or faces. Alternatively, the equivalent responses across tasks in EBA and FBA might be driven by the *spatial* arrangement of the dots in the two types of display, including residual cues to the static form of faces and bodies. Further research is required to tease apart these alternative explanations.

On the basis of their own and earlier findings, Peelen et al. (2006) suggested that EBA and FBA responses to point-light body motion reflect the operation of processes that extract body form per se, rather than processes that extract patterns of changing body posture from these stimuli. Yet, a more recent study by Jastorff and Orban (2009) provides evidence that EBA and FBA integrate bodily motion and form cues, and that EBA has a greater role in processing bodily motion (specifically, kinematics) whereas FBA as a greater role in processing body form (specifically, the configuration of the body and its parts). Insofar as EBA and FBA process motion or form cues, or both, our results demonstrate the specificity of these processes for bodily over facial motion and form. Nonetheless, given that we controlled

for differences in neural activation resulting from differences in the perceived emotional intensity of our stimuli derived from their kinematics, we can infer that the category-selective activation of EBA and FBA by point-light body stimuli in the present study is driven at least in part by form-from-motion cues.

Compared to point-light bodies, point-light faces activated face-selective left FFA and right FFA, but in the latter case only when participants were explicitly judging the expressed emotion; right FFA activity did not differentiate between point-light face and body movements when participants were judging the colour-change of the stimulus dots. These findings are consistent with a role specifically for facial motion-related cues in driving right FFA activation to point-light face vs. body stimuli, rather than (or perhaps in addition to) differences in the spatial arrangement of the dots in the two types of display, including residual cues to static facial form. It is possible that the effect of task set on right FFA activation to point-light faces vs. bodies is a function mostly of top-down influences, viz., simply attending to or thinking about the point-light face stimuli *as* faces might increase right FFA activity relative to attending to or thinking about the point-light body stimuli as bodies. Consistent with this account are the results of a study showing that when observers expected to see faces (rather than houses), there was an increase in the baseline activity of FFA (measured at the time point halfway between the onset of a word cue and the subsequent stimulus) and enhanced stimulus-evoked selectivity for faces vs. houses (Puri et al., 2009). The *level* of expectation has also been shown to influence the selectivity for faces vs. houses. Egner at al. (2010) found that FFA activity did not differentiate between faces and houses when presentation of a face stimulus was strongly predicted by a preceding symbolic cue. Given that stimulus type was blocked in our study, we can consider our participants as operating under conditions of high expectation, in which case the observed selectivity for point-light faces vs. point-light bodies in right FFA is more likely to reflect enhanced

processing of facial motion cues resulting from the task instructions that encouraged attention to facial vs. bodily motion than to expectation effects alone.

4.2: Category-selective emotional modulation by the motion of faces and bodies

As a further test of the selectivity of the face- and body-selective regions to face and body motion, we contrasted emotional with emotionally neutral face and body movements. Our reasoning was that manipulating the stimuli with stimulus category-specific movements should modulate neural activity in a stimulus category-selective manner. Emotionally expressive movements were chosen in view of previous findings that the face-selective and body-selective regions show enhanced activation in response to fully illuminated static and dynamic face and body stimuli expressing emotions relative to emotionally neutral versions of these same stimuli (reviewed by Vuilleumier and Driver, 2007; Vuilleumier and Pourtois, 2007). As noted above, however, our findings of selective activation of body-selective and face-selective regions by point-light body and face movements do not extend to emotional modulation of those regions.

Thus, our findings suggest an asymmetry in emotional modulation of neural responses by body and face motion in body- and face-selective regions. This asymmetry constrains the claim that expressive movements modulate neuronal populations that code for the viewed stimulus category (Peelen et al., 2007). The emotional modulation of left EBA was clearly category-selective, as revealed by both the ROI and voxelwise correlation analyses. For right EBA, however, the case for category-selective emotion modulation was less clear: the ROI analyses revealed a small degree of emotional modulation by angry point-light faces, though this effect did not survive correction for multiple comparisons, and the voxelwise correlation analyses revealed that the enhanced activity elicited by angry relative to neutral point-light faces was positively correlated with voxelwise selectivity to static bodies. Moreover, although the emotional content of face and particularly body movements enhanced right FFA and left

FBA activity, there was no evidence that emotional modulation in these regions occurred in a stimulus category-selective manner. Further research is required to test whether these findings extend to emotional expressions other than of anger and happiness and to fully illuminated displays of face and body stimuli, in which the static form is visible.

Although the emotional content of our point-light face stimuli modulated the activity of several brain regions, this emotional modulation was not correlated with the patterns of face-selectivity across voxels, and was correlated with the patterns of body-selectivity only for angry face movements during emotion judgements. Thus, whatever specific visual processes are enhanced by the emotional content of facial motion, and particularly of form-from-motion, they do not appear to be processes specific to the extraction of static facial (or bodily) form. Alternatively, it could be argued that the failure to find a relationship between the emotional modulation elicited by point-light faces and face-selectivity (and, in some cases, body-selectivity) across voxels is due to a relative lack of the capacity of the point-light face stimuli to elicit emotional modulation, compared to the point-light body stimuli. It is true that the emotional expressions represented in our point-light face stimuli were significantly less recognizable and contained less overall dot motion than the expressions represented in our point-light body stimuli. Moreover, participants were less accurate in classifying the emotions, particularly anger, in the point-light faces than in the point-light bodies. Yet it was precisely these less recognizable angry facial expressions that elicited activity (relative to neutral face movements) that was correlated across voxels with body selectivity in right EBA. Furthermore, we did our best to statistically control for differences in the quantity of motion and emotional expressiveness between the face and body stimuli (and between emotions within each stimulus category) by effectively equating the perceived emotional intensity derived from kinematic cues. It is possible that point-light body stimuli contain stronger or more compelling form-from-motion cues than point-light face stimuli, but if so that is more a

function of fundamental biomechanical differences between bodies and faces than of inadequate control over the motion characteristics of our stimuli. A task for future research will be to investigate more directly the relationship between the expressiveness of emotional face and body movements and the extent to which they elicit emotional modulation (cf. the work by Surguladze et al., 2003 with static facial expressions).

4.3 Conclusion

We have demonstrated that bodily and facial motion represented in point-light displays activate precisely those populations of neurons that code for the viewed stimulus category. However, our results provide only limited support for the hypothesis that *emotions* signaled by motion-related cues alone can modulate precisely those populations of neurons that code for the viewed stimulus category. Although emotional relative to emotionally neutral face and body movements activated face- and body-selective regions, this emotional modulation was not category-selective.

References

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., Tunstall, M.L., Dittrich, W.H., 2007. Evidence for distinct contributions of form and motion information to the recognition of emotions from body gestures. Cognition 104, 59-72.

Bassili, J.N., 1978. Facial motion in the perception of faces and of emotional expression. Journal of Experimental Psychology: Human Perception and Performance 4, 373-379.

Bassili, J.N., 1979. Emotion recognition: the role of facial movement and the relative importance of upper and lower areas of the face. Journal of Personality and Social Psychology 37, 2049-2058.

Bedny, M., Pascual-Leone, A., Saxe, R.R., 2009. Growing up blind does not change the neural bases of Theory of Mind. Proceedings of the National Academy of Sciences 106, 11312-11317.

Berman, M.G., Park, J., Gonzalez, R., Polk, T.A., Gehrke, A., Knaffla, S., Jonides, J., 2010. Evaluating functional localizers: The case of the FFA. Neuroimage 50, 56-71.

Blake, R., Shiffrar, M., 2007. Perception of human motion. Annual Review of Psychology 58, 47-73.

Campbell, R., MacSweeney, M., Surguladze, S., Calvert, G., McGuire, P., Suckling, J., Brammer, M.J., David, A.S., 2001. Cortical substrates for the perception of face actions: an fMRI study of the specificity of activation for seen speech and for meaningless lower-face acts (gurning). Cognitive Brain Research 12, 233-243.

Critchley, H., Daly, E., Phillips, M., Brammer, M., Bullmore, E., Williams, S., Van Amelsvoort, T., Robertson, D., David, A., Murphy, D., 2000. Explicit and implicit neural mechanisms for processing of social information from facial expressions: a functional magnetic resonance imaging study. Human Brain Mapping 9, 93-105.

Dale, A.M., 1999. Optimal experimental design for event-related fMRI. Human Brain Mapping 8, 109-114.

de Gelder, B., 2006. Towards the neurobiology of emotional body language. Nature Reviews Neuroscience 7, 242-249.

de Gelder, B., Snyder, J., Greve, D., Gerard, G., Hadjikhani, N., 2004. Fear fosters flight: a mechanism for fear contagion when perceiving emotion expressed by a whole body. Proceedings of the National Academy of Sciences 101, 16701-16706.

Doi, H., Kato, A., Hashimoto, A., Masataka, N., 2008. Role of biological-motion information in recognition of facial expressions by young children. Perception 37, 1399-1411.

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.

Downing, P.E., Wiggett, A.J., Peelen, M.V., 2007. Functional magnetic resonance imaging investigation of overlapping lateral occipitotemporal activations using multi-voxel pattern analysis. The Journal of Neuroscience 27, 226-233.

Fox, C.J., Iaria, G., Barton, J.J.S., 2009. Defining the face processing network: Optimization of the functional localizer in fMRI. Human Brain Mapping 30, 1637-1651.

Friston, K.J., Ashburner, J.T., Kiebel, S., Nichols, T.E., Penny, W.D. (Eds.), 1997. Statistical Parametric Mapping: The analysis of functional brain images Academic Press/Elsevier, Amsterdam.

Friston, K.J., Fletcher, P., Josephs, O., Holmes, A., Rugg, M.D., Turner, R., 1998. Event-related fMRI: Characterizing differential responses. Neuroimage 7, 30-40.

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.

Grossman, E.D., Blake, R., 1999. Perception of coherent motion, biological motion and form-from-motion under dim-light conditions. Vision Research 39, 3721-3727.

Grossman, E.D., Blake, R., 2002. Brain areas active during visual perception of biological motion. Neuron 35, 1167-1175.

Grossman, E.D., Blake, R., Kim, C.Y., 2004. Learning to see biological motion: brain activity parallels behavior. Journal of Cognitive Neuroscience 16, 1669-1679.

Grossman, E.D., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., Blake, R., 2000. Brain areas involved in perception of biological motion. Journal of Cognitive Neuroscience 12, 711-720.

Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2000. The distributed human neural system for face perception. Trends in Cognitive Sciences 4, 223-233.

Heberlein, A.S., Saxe, R.R., 2005. Dissociation between emotion and personality judgments: Convergent evidence from functional neuroimaging. Neuroimage 28, 770-777.

Henson, R.N.A., 2006. Efficient experimental design for fMRI. In: Friston, K., Ashburner, J., Kiebel, S., Nichols, T., Penny, W. (Eds.), Statistical Parametric Mapping: The analysis of functional brain images. Elsevier, London, pp. 193-210.

Hill, H., Jinno, Y., Johnston, A., 2003. Comparing solid-body with point-light animations. Perception 32, 561-566.

Jastorff, J., Orban, G.A., 2009. Human functional magnetic resonance imaging reveals separation and integration of shape and motion cues in biological motion processing. The Journal of Neuroscience 29, 7315-7329.

Jiang, Y., He, S., 2006. Cortical responses to invisible faces: Dissociating subsystems for facial-information processing. Current Biology 16, 2023-2029.

Johansson, G., 1973. Visual perception of biological motion and a model for its analysis. Perception and Psychophysics 14, 201-211.

Kamachi, M., Bruce, V., Mukaida, S., Gyoba, J., Yoshikawa, S., Akamatsu, S., 2001. Dynamic properties influence the perception of facial expressions. Perception 30, 875-887.

Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. The Journal of Neuroscience 17, 4302-4311.

Kanwisher, N., Yovel, G., 2006. The fusiform face area: a cortical region specialized for the perception of faces. Philosophical Transactions of the Royal Society B: Biological Sciences 361, 2109-2128.

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

LaBar, K.S., Crupain, M.J., Voyvodic, J.T., McCarthy, G., 2003. Dynamic perception of facial affect and identity in the human brain. Cerebral Cortex 13, 1023-1033.

Maldjian, J.A., Laurienti, P.J., Kraft, R.A., Burdette, J.H., 2003. An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. Neuroimage 19, 1233-1239.

Michels, L., Lappe, M., Vaina, L.M., 2005. Visual areas involved in the perception of human movement from dynamic form analysis. Neuroreport 16, 1037-1041.

Narumoto, J., Okada, T., Sadato, N., Fukui, K., Yonekura, Y., 2001. Attention to emotion modulates fMRI activity in human right superior temporal sulcus. Cognitive Brain Research 12, 225-231.

O'Craven, K.M., Downing, P.E., Kanwisher, N., 1999. fMRI evidence for objects as the units of attentional selection. Nature 401, 584-587.

Peelen, M.V., Atkinson, A.P., Andersson, F., Vuilleumier, P., 2007. Emotional modulation of body-selective visual areas. Social Cognitive and Affective Neuroscience 2, 274-283.

Peelen, M.V., Downing, P.E., 2005a. Selectivity for the human body in the fusiform gyrus. Journal of Neurophysiology 93, 603-608.

Peelen, M.V., Downing, P.E., 2005b. Within-subject reproducibility of category-specific visual activation with functional MRI. Human Brain Mapping 25, 402-408.

Peelen, M.V., Wiggett, A.J., Downing, P.E., 2006. Patterns of fMRI activity dissociate overlapping functional brain areas that respond to biological motion. Neuron 49, 815-822.

Pessoa, L., McKenna, M., Gutierrez, E., Ungerleider, L.G., 2002. Neural processing of emotional faces requires attention. Proceedings of the National Academy of Sciences 99, 11458-11463.

Peuskens, H., Vanrie, J., Verfaillie, K., Orban, G.A., 2005. Specificity of regions processing biological motion. European Journal of Neuroscience 21, 2864-2875.

Pichon, S., de Gelder, B., Grézes, J., 2009. Two different faces of threat. Comparing the neural systems for recognizing fear and anger in dynamic body expressions. Neuroimage 47, 1873-1883.

Pollick, F.E., Hill, H., Calder, A., Paterson, H., 2003. Recognising facial expression from spatially and temporally modified movements. Perception 32, 813-826.

Puce, A., Perrett, D., 2003. Electrophysiology and brain imaging of biological motion. Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences 358, 435-445.

Puce, A., Syngeniotis, A., Thompson, J.C., Abbott, D.F., Wheaton, K.J., Castiello, U., 2003. The human temporal lobe integrates facial form and motion: evidence from fMRI and ERP studies. Neuroimage 19, 861-869.

Puri, A.M., Wojciulik, E., Ranganath, C., 2009. Category expectation modulates baseline and stimulus-evoked activity in human inferotemporal cortex. Brain Research 1301, 89-99.

Reddy, L., Moradi, F., Koch, C., 2007. Top-down biases win against focal attention in the fusiform face area. Neuroimage 38, 730-739.

Rosenblum, L.D., Johnson, J.A., Saldana, H.M., 1996. Point-light facial displays enhance comprehension of speech in noise. Journal of Speech and Hearing Research 39, 1159-1170.

Safford, A.S., Hussey, E.A., Parasuraman, R., Thompson, J.C., 2010. Object-based attentional modulation of biological motion processing: Spatiotemporal dynamics using functional magnetic resonance imaging and electroencephalography. The Journal of Neuroscience 30, 9064-9073.

Santi, A., Servos, P., Vatikiotis-Bateson, E., Kuratate, T., Munhall, K., 2003. Perceiving biological motion: Dissociating visible speech from walking. Journal of Cognitive Neuroscience 15, 800-809.

Saygin, A.P., Wilson, S.M., Hagler, D.J., Bates, E., Sereno, M.I., 2004. Point-light biological motion perception activates human premotor cortex. Journal of Neuroscience 24, 6181-6188.

Schultz, J., Pilz, K., 2009. Natural facial motion enhances cortical responses to faces. Experimental Brain Research 194, 465-475.

Schwarzlose, R.F., Baker, C.I., Kanwisher, N., 2005. Separate face and body selectivity on the fusiform gyrus. Journal of Neuroscience 25, 11055-11059.

Sinke, C.B.A., Sorger, B., Goebel, R., de Gelder, B., 2010. Tease or threat? Judging social interactions from bodily expressions. Neuroimage 49, 1717-1727.

Sugase, Y., Yamane, S., Ueno, S., Kawano, K., 1999. Global and fine information coded by single neurons in the temporal visual cortex. Nature 400, 869-873.

Surguladze, S.A., Brammer, M.J., Young, A.W., Andrew, C., Travis, M.J., Williams, S.C., Phillips, M.L., 2003. A preferential increase in the extrastriate response to signals of danger. Neuroimage 19, 1317-1328.

Van den Stock, J., van de Riet, W.A.C., Righart, R., de Gelder, B., 2008. Neural correlates of perceiving emotional faces and bodies in developmental prosopagnosia: An event-related fMRI-study. PLoS One 3, e3195.

Vuilleumier, P., 2005. How brains beware: neural mechanisms of emotional attention. Trends in Cognitive Sciences 9, 585-594.

Vuilleumier, P., Armony, J.L., Driver, J., Dolan, R.J., 2001. Effects of attention and emotion on face processing in the human brain: an event-related fMRI study. Neuron 30, 829-841.

Vuilleumier, P., Driver, J., 2007. Modulation of visual processing by attention and emotion: windows on causal interactions between human brain regions. Philosophical Transactions of the Royal Society B: Biological Sciences 362, 837-855.

Vuilleumier, P., Pourtois, G., 2007. Distributed and interactive brain mechanisms during emotion face perception: Evidence from functional neuroimaging. Neuropsychologia 45, 174-194.

Vuilleumier, P., Richardson, M.P., Armony, J.L., Driver, J., Dolan, R.J., 2004. Distant influences of amygdala lesion on visual cortical activation during emotional face processing. Nature Neuroscience 7, 1271-1278.

Wallbott, H.G., 1998. Bodily expression of emotion. European Journal of Social Psychology 28, 879-896.

Winston, J.S., O'Doherty, J., Dolan, R.J., 2003. Common and distinct neural responses during direct and incidental processing of multiple facial emotions. Neuroimage 20, 84-97.

Funding

This work was supported by the Science Faculty of Durham University (UK).

Acknowledgements

The authors are grateful to Craig Douglas and Chris Saunter for their help in developing the point-light stimuli, to Marius Peelen for the static face, body and chair images, to Michael Firbank for fMRI technical assistance, to Louise Morris and Carol Smith for assistance with fMRI data collection, to Cristiana Cavina-Pratesi and Lauri Nummenmaa for initial advice, and to two anonymous reviewers for their helpful comments. *Conflicts of interest:* None declared.

Table 1

Mean coordinates (and SDs) for each ROI

	MNI coordinates			
ROI	**x**	**y**	**z**	**N**
Right EBA	50	-69	1	17
	(5)	(6)	(7)	
Left EBA	-48	-76	4	16
	(5)	(6)	(6)	
Right FBA	39	-51	-20	16
	(3)	(6)	(3)	
Left FBA	-38	-49	-20	15
	(4)	(5)	(3)	
Right FFA	39	-53	-20	16
	(3)	(8)	(4)	
Left FFA	-31	-52	-19	15
	(3)	(8)	(5)	
Right face STS	51	-52	13	17
	(8)	(12)	(6)	
Right pSTS	55	-45	9	15
	(6)	(7)	(5)	
Right amygdala	24	0	-17	13
	(4)	(2)	(3)	
Left amygdala	-22	2	-17	12
	(4)	(2)	(3)	

Note: N = number of participants for whom the particular ROI was identified (out of 17).

Table 2

Summary statistics for analyses examining voxelwise correlations between emotional modulation and body or face selectivity in key regions of interest for each task

		Right EBA		Left EBA		Right Fusiform[1]		Left Fusiform[1]		Right STS[2]	
		r	*t*	*r*	*t*	*r*	*t*	*r*	*t*	*r*	*t*
Emotion Judgement											
Correlation with body selectivity	***Bodies***										
	Angry	**0.262**	**7.15**[f]	**0.12**	**3.12**[a]	**0.158**	**3.31**[a]	0.058	1.38	**0.169**	**4.33**[b]
	Happy	**0.231**	**6.55**[e]	**0.138**	**3.19**[a]	**0.195**	**4.3**[b]	0.038	1.29	0.11	3.1[¶]
	Faces										
	Angry	0.062	1.67	-0.016	-0.37	0.035	0.97	0.053	1.1	0.109	2.81
	Happy	0.027	0.65	0.01	0.24	0.01	0.43	0.018	0.5	0.017	0.52
Correlation with face selectivity	***Bodies***										
	Angry	-	-	-	-	**0.154**	**3.65**[a]	0.065	1.81	**0.148**	**3.35**[a]
	Happy	-	-	-	-	0.092	2.11	-0.014	-0.44	0.095	2.39
	Faces										
	Angry	-	-	-	-	0.013	0.4	0.042	1.06	0.045	1.74
	Happy	-	-	-	-	0.007	0.26	0.041	0.83	0.011	0.31
Colour Judgement											
Correlation with body selectivity	***Bodies***										
	Angry	**0.266**	**9.57**[g]	**0.163**	**5.06**[c]	**0.108**	**3.54**[a]	0.104	1.99	0.085	2.28
	Happy	**0.181**	**4.67**[d]	0.066	1.83	0.003	0.13	0.058	1.42	0.063	1.46
	Faces										
	Angry	-0.04	-1.33	-0.024	-0.65	0.022	0.65	-0.005	-0.15	-0.006	-0.29
	Happy	0.035	0.89	0.035	0.8	0.034	0.9	-0.027	-0.69	0.042	1.7
Correlation with face selectivity	***Bodies***										
	Angry	-	-	-	-	**0.118**	**3.45**[a]	0.071	2.1	0.09	3.0[¶]
	Happy	-	-	-	-	0.000	0.01	-0.022	-0.58	0.055	1.73
	Faces										
	Angry	-	-	-	-	0.04	1.18	-0.02	-1.03	-0.006	-0.01
	Happy	-	-	-	-	0.029	0.76	0.021	0.65	-0.004	0.001

Note: *r* = Pearson correlation coefficient (mean across participants); *t* = t-statistic. [1]The union of face-selective FFA and body-selective FBA. [2]The union of face-selective pSTS and

biological-motion selective pSTS. Statistically significant results (after Bonferonni correction for 8 or 16 comparisons) are highlighted in bold: $^{a}p < .05$, $^{b}p < .01$, $^{c}p < .001$, $^{d}p < .0005$, $^{e}p < .00005$, $^{f}p < .000001$, $^{g}p < .0000005$. Non-significant trends at $p < .1$ are denoted with ¶.

Figure Captions

Figure 1. Schematic overview of the stimulus block and trial structure in the main experiment. At the beginning of a block, participants were presented an instruction screen for 3000ms, which specified whether they were to judge the expressed emotion or the colour-change in the subsequent stimuli, as well as the mapping between emotion or colour words and the 3 response buttons. Nine 2000ms movie clips of either point-light face movements or point-light body movements were presented in each block. Each clip was separated by a variable interstimulus interval (a blank screen) during which participants made their button-press response.

Figure 2. Mean proportion correct classification accuracy for the main experiment as a function of task, stimulus type, and emotion (collapsed over the 3 stimulus colour-changes). Error bars represent standard error of the mean (SEM) across the 16 participants from whom data was collected. *$p < .05$.

Figure 3. Mean activation (parameter estimates) as a function of task (emotion and colour judgements) and stimulus type (point-light bodies and faces) in (A) each body-selective ROI, and (B) each face-selective ROI. Note that, whereas right and left EBA and FBA were defined by selectivity for static images of bodies (vs. chairs), right pSTS was defined by selectivity for whole-body motion in point-light displays (vs. scrambled versions of these point-light stimuli). Error bars represent standard error of the mean (SEM) across participants (Ns for the individual ROIs are detailed in Table 1). *$p < .05$, **$p < .0005$, ***$p < .000005$. Note that, when the data for the 2 left-handed participants with a right pSTS ROI were excluded, this ROI showed a significantly greater response ($p < .005$) to point-light bodies than to point-light faces irrespective of task (the main effect illustrated here, for the data from both the left- and right-handers, is only marginally significant, $p = .089$); see Supplementary Materials for details.

Figure 4. Emotional modulation of functional ROIs. The graphs show the mean contrast estimate for each emotional expression (angry, happy), relative to emotionally neutral movements, at each ROI as a function of task (colour judgement, emotion judgement) and stimulus type (point-light bodies, point-light faces). Error bars represent standard error of the mean (SEM) across participants. Statistically significant differences between conditions (from F-tests) and statistically significant emotional modulations, i.e., angry or happy > neutral (from one-sample t-tests) are reported in the main text.

Figure 1

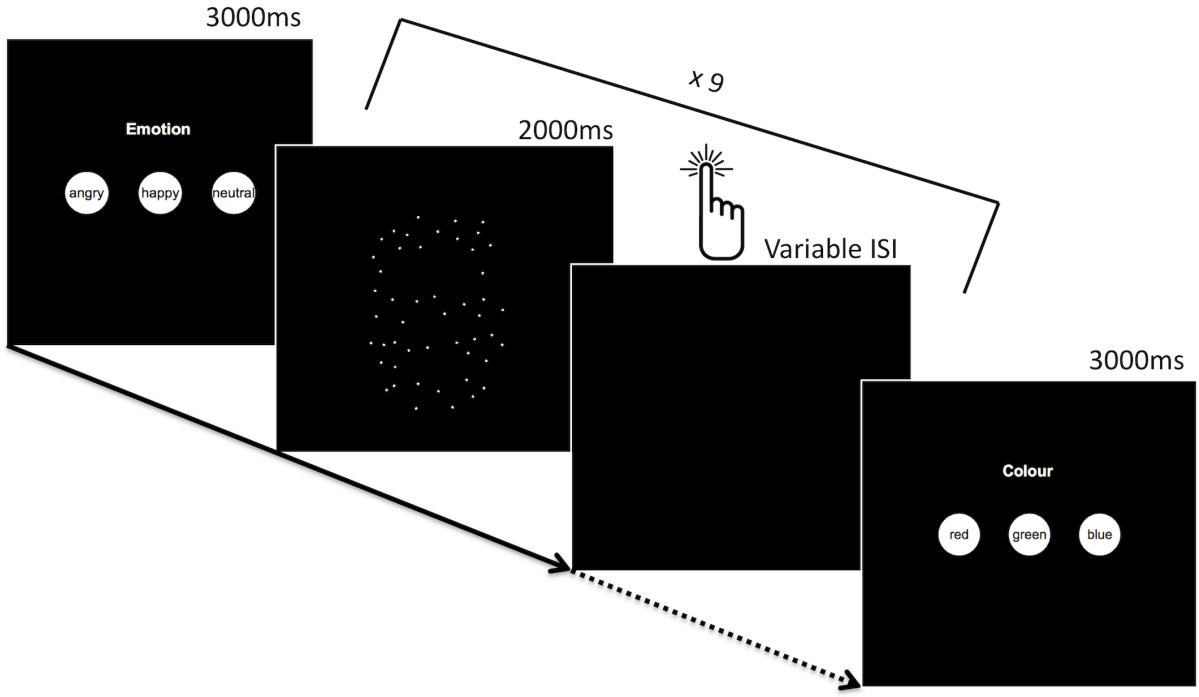

3000ms
Emotion
angry
happy
neutral
x 9
2000ms
Variable ISI
3000ms
Colour
red
green
blue

Figure 2

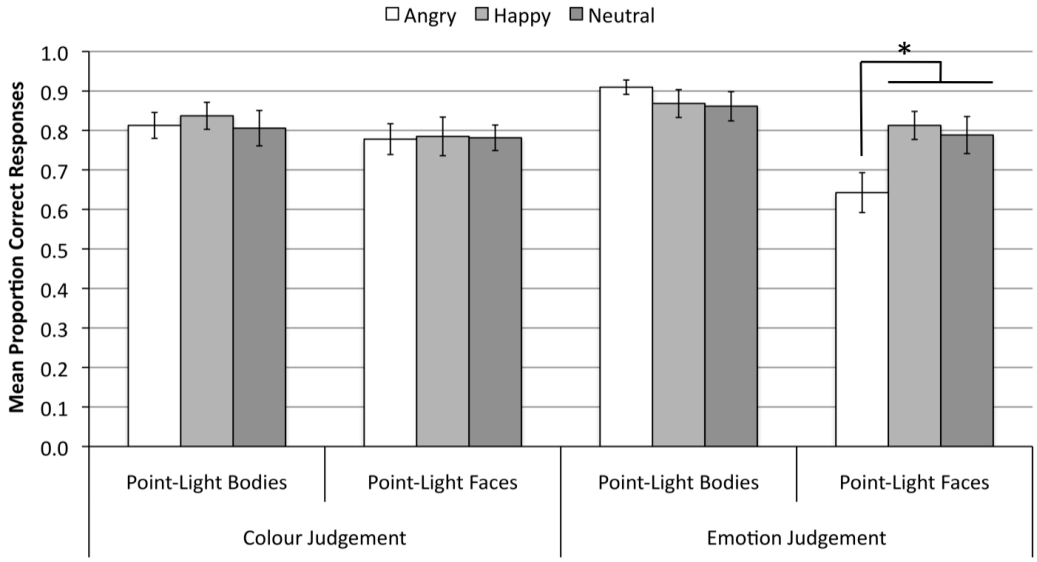
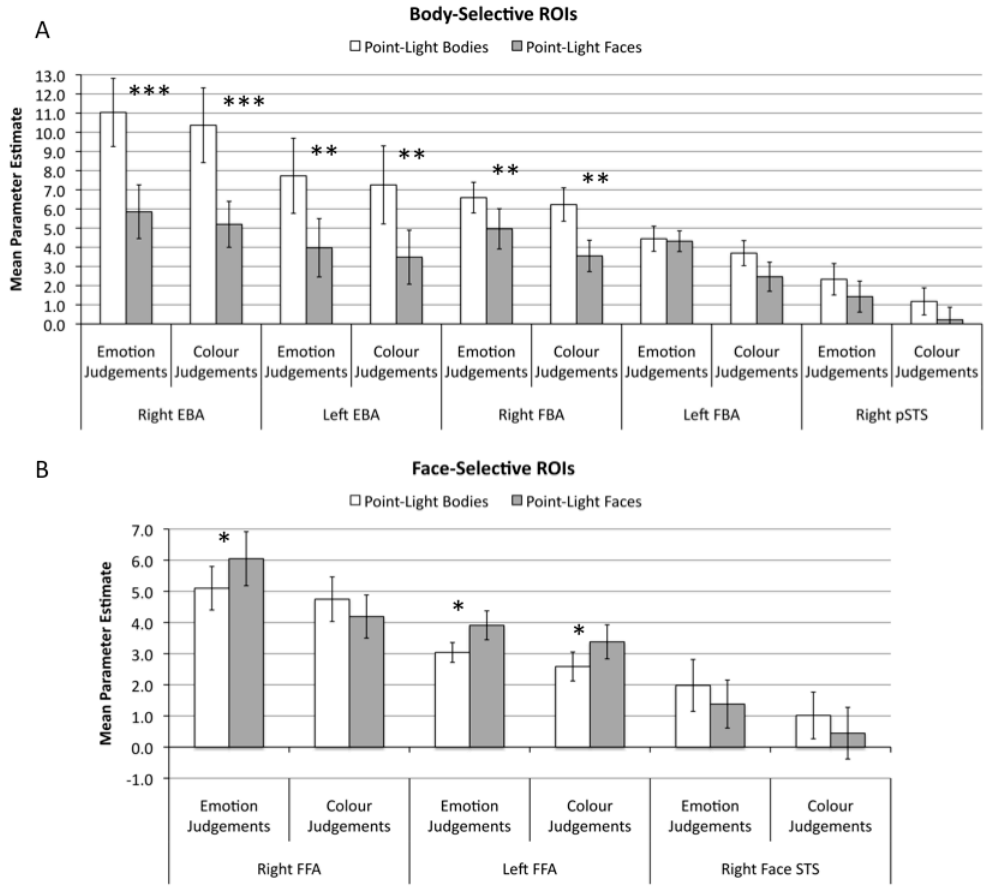

Angry
Happy
Neutral
Mean Proportion Correct Responses
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
*
Point-Light Bodies
Point-Light Faces
Point-Light Bodies
Point-Light Faces
Colour Judgement
Emotion Judgement

Figure 3


A
Body-Selective ROIs
Point-Light Bodies
Point-Light Faces
Mean Parameter Estimate
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12.0
11.0
10.0
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
***
***
**
**
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**
Emotion Judgements
Colour Judgements
Right EBA
Left EBA
Right FBA
Left FBA
Right pSTS
B
Face-Selective ROIs
Point-Light Bodies
Point-Light Faces
Mean Parameter Estimate
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
-1.0
*
*
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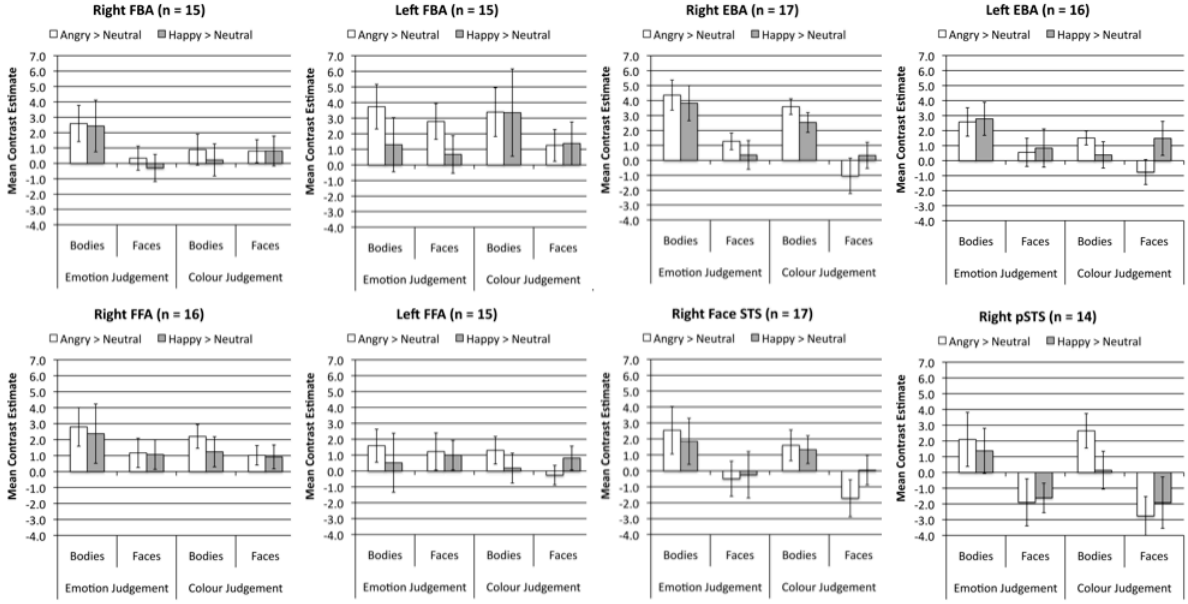
Emotion Judgements
Colour Judgements
Right FFA
Left FFA
Right Face STS

Figure 4


Right FBA (n = 15)
Left FBA (n = 15)
Right EBA (n = 17)
Left EBA (n = 16)
Right FFA (n = 16)
Left FFA (n = 15)
Right Face STS (n = 17)
Right pSTS (n = 14)
Angry > Neutral
Happy > Neutral
Mean Contrast Estimate
Bodies
Faces
Emotion Judgement
Colour Judgement