Emotional Complexity and the Neural Representation of Emotion in Motion

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According to theories of emotional complexity, individuals low in emotional complexity encode and represent emotions in visceral or action-oriented terms, whereas individuals high in emotional complexity encode and represent emotions in a differentiated way, using multiple emotion concepts. During functional magnetic resonance imaging, participants viewed valenced animated scenarios of simple ball-like figures attending either to social or spatial aspects of the interactions. Participant's emotional complexity was assessed using the Levels of Emotional Awareness Scale. We found a distributed set of brain regions previously implicated in processing emotion from facial, vocal and bodily cues, in processing social intentions, and in emotional response, were sensitive to emotion conveyed by motion alone. Attention to social meaning amplified the influence of emotion in a subset of these regions. Critically, increased emotional complexity correlated with enhanced processing in a left temporal polar region implicated in detailed semantic knowledge; with a diminished effect of social attention; and with increased differentiation of brain activity between films of differing valence. Decreased emotional complexity was associated with increased activity in regions of pre-motor cortex. Thus, neural coding of emotion in semantic *vs* action systems varies as a function of emotional complexity, helping reconcile puzzling inconsistencies in neuropsychological investigations of emotion recognition.

INTRODUCTION

Our knowledge of others' emotions clearly depends on their perceptible reactions, i.e. facial, vocal and bodily expressions (Darwin, 1872). It is unclear, however, what the fundamental building blocks of emotional expression and perception are. Michotte (1950) asserted that social perception is grounded in the analysis of motion cues (e.g. approach, avoidance, contact intensity). Indeed, 1-year-old infants can attribute emotional valence ($\pm$) to interactions between ball-like figures in simplistic two-dimensional animations, based on simple motion cues, e.g. collision intensity (hard contact–negative, soft contact–positive) (Premack and Premack, 1997). Such cues are used pan-culturally (Rimé *et al.*, 1985).

Neuroscience has implicated several brain structures in emotion recognition, including the amygdala, occipitotemporal neocortex, insula, somatosensory cortex, basal ganglia, ventral premotor cortex, and medial and orbital prefrontal cortex (Heberlein and Adolphs, 2007). Some regions, e.g. the amygdala are activated by minimal emotion cues, and in the absence of attention (Adolphs, 2008), although the extent to which these brain regions are sensitive to the basic motion cues emphasised by Michotte is unclear.

Understanding of emotions is, however, knowledge driven as well as rooted in structure detection: we discern others' emotions via a complex combination of structure-detection skills and relevant knowledge (Baldwin and Baird, 2001; Marshall and Cohen, 1988). That there are potentially large individual differences in emotion knowledge may help account for the puzzling finding that, even when tested using the same emotion-recognition tasks, patients with comparable brain lesions do not always show similar deficits, a finding for which there has been no satisfying explanation (Heberlein and Adolphs, 2007).

Here, we address the influence of a key individual difference, namely, individual differences in propositional knowledge for emotion or emotional complexity (Lindquist and Feldman-Barrett, 2008), as measured by the Levels of Emotional Awareness Scale (LEAS; Lane *et al.*, 1990). According to Lane and colleagues (Lane and Pollerman, 2002), individuals low in emotional complexity encode and represent emotion knowledge in visceral or action-oriented terms, whereas individuals high in emotional complexity encode and represent emotion knowledge in a nuanced and differentiated fashion, using multiple emotion concepts. Increased emotional complexity predicts more normative identification of emotion cues in others and greater empathy (Ciarrochi *et al.*, 2003; Lane *et al.*, 1996, 2000).

In the current study, during functional magnetic resonance imaging (fMRI), participants viewed animated scenarios of simple ball-like figures open to interpretation in terms of emotional attributes. Participants were cued to pay attention to social or spatial aspects of the figures' behaviour. Given that individuals with greater levels of emotional complexity are hypothesised to have more detailed and more differentiated emotion concepts, and to rely less on visceral or action-oriented emotion coding, we predicted that increased emotional complexity would be associated with greater activation in neural regions linked to detailed conceptual knowledge [left temporal poles (TP)] (Rogers et al., 2006), together with reduced activity in brain regions linked to processing visceral/action-oriented components of emotion (hypothalamus, premotor cortex), (Leslie et al., 2004; Thompson and Swanson, 2003) and with greater differentiation between positively vs negatively valenced animations in brain regions coding emotional valence and discrete emotion categories (Murphy et al., 2003; Vytal and Hamman, 2009). In addition, by manipulating attention to social meaning, we could examine the extent to which activity in key neural structures was dependent on attention, and how this interacted with individual differences in emotional complexity.

MATERIALS AND METHODS

During fMRI, participants were asked to watch a series of short animations. Each showed two 'sprites' moving with properties that support varying emotional interpretations (affiliative, antagonistic, neutral social behaviours) in a two-dimensional 'sprite world' (Figure 1). Participants were pre-cued to attend either to the social behaviour that could underlie the movement of the sprites or to the spatial aspects of the same movement. Following the fMRI session, participants completed the LEAS (Lane et al., 1990) (see below for details).
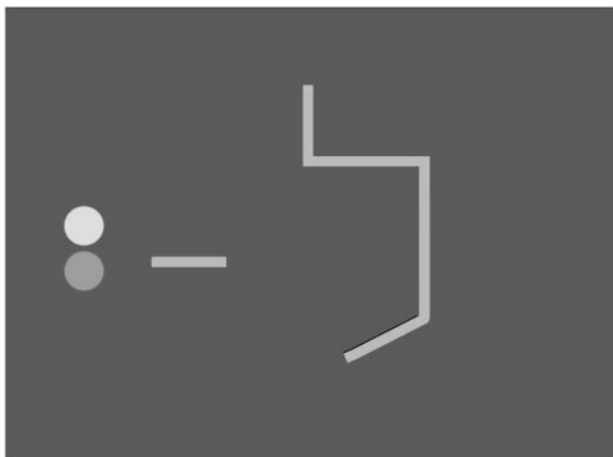

Fig. 1 Schematic of animations.

Participants

Sixteen healthy right-handed female, native English speaking individuals (mean age = 24 years, s.d. = 4 years) participated. The study was approved by the Cambridgeshire Local Research Ethics Committee and performed in compliance with their guidelines. Written informed consent was obtained from all participants. Individuals with a history of inpatient psychiatric care; neurological disease, or head injury were excluded, as were individuals on medication for anxiety or depression. Following the fMRI session, participants completed the LEAS (Lane et al., 1990) (see below for details). Only female volunteers were scanned as previous work has found considerable sex differences in LEAS scores, with women outperforming men (Barrett et al., 2000; Ciarrochi et al., 2003). We did not control for menstrual cycle phase. In future studies, it will be important to examine both potential menstrual cycle phase effects in women and potential neural sex differences in the effects of LEAS (McRae et al., 2008).

Stimuli

The stimuli consisted of 14-s duration animations, displaying the motion of two sprites—one green circle and one blue circle in a two-dimensional environment (the sprite world), which included some obstacles to motion in a straight line (see Figure 1 and example movies can be viewed at http://www.mrc-cbu.cam.ac.uk/research/emotion/cemhp/tavare-saffant.html). Animations were created using the software package Blender version 2.1 (Blender Foundation, http://www.blender.org). Three categories of animation were constructed, designed to convey the impression of three types of interpersonal situation: (i) Affiliative interactions between the two sprites; (ii) Antagonistic interactions between the two sprites; and (3) Neutral, (non)-interactions between the two sprites.

In the affiliative animations, the two sprites entered from different sides of the sprite-world. They approached each other, and gently touched, suggesting affection, then moved in a mutually coordinated fashion throughout. In the antagonistic animations, the two sprites entered from different sides of the sprite-world and approached each other. They initially maintained a distance from each other, while moving around slowly. In one half of the animations, they then approached each other, making brief, hard contact with each other and retreating rapidly, suggesting physical aggression. In the other half, they never touched, but circled each other in a manner suggestive of hostility. At the end of the sequence, the two sprites left the scene quickly and in different directions. In the emotionally neutral animations, the two sprites entered from different sides of the sprite-world. They moved around, sometimes stopping and changing direction, but never approaching or withdrawing from each other. The sprites then left the scene independently at a gentle pace.

Task

During scanning, each animation (affiliative, antagonistic or neutral) was preceded by a cue word, either 'behavioural' or 'spatial', specifying how they should attend to the scenarios. For the behavioural cue, participants were instructed to identify what type of interaction might be happening between the two sprites (affiliative, antagonistic or neutral). For the spatial cue, participants were instructed to pay attention to various aspects of the motion of the two sprites, such as speed, trajectory, position of entering/exiting the scene, etc. As a manipulation check, following the presentation of each animation, a summary statement appeared describing the contents of the animation, and the participants had to judge (true/false) if the statement could appropriately describe the preceding animation. Examples of behavioural statements include: 'A woman met her partner in an art gallery' (affiliative), 'Street kids were insulting each other' (antagonistic) and 'Two joggers were exercising around a park' (neutral). Examples of spatial statements include: 'The blue circle stayed in the bottom left-hand corner', 'The circles completed a figure of eight movement.' The statement accurately described the content of each animation in 50% of cases. Each animation and each statement was presented only once. The cue word was presented for 1.8 s, the animation for 14 s and the statement for 7.5 s. In addition, a baseline fixation condition was used. In this condition, the cue word 'cross' appeared, followed by a fixation-cross for 14 s, and then a statement saying that the participants should press either the left or right response button. There were 12 examples of each of the animations (affiliative, antagonistic and neutral) in each of the two conditions (behavioural or spatial cue) plus baseline condition. Animations (affiliative, antagonistic and neutral) and task (behavioural or spatial cue) were presented in pseudorandomised, counterbalanced fashion.

Post-task ratings of the animations

Following scanning, participants rated each animation seen during fMRI for valence and emotional intensity using visual analogue scales with lines 11.5-cm long. For valence, the scale ranged from positive (0 cm) through neutral (5.75 cm) to negative (11.5 cm). For intensity ratings, the scale ranged from low (0 cm) to high (11.5 cm). The period of time between the imaging study and the ratings task ranged from 0 days to 6 weeks, depending on the availability of the participant (average ~2 weeks).

Levels of emotional awareness

Emotional Awareness is the ability to recognise and describe emotion in oneself and others. According to Lane and colleagues' Piagetian model (Lane and Pollerman, 2002; Lane and Schwartz, 1987), the development of emotional awareness comprises five stages, ranging from awareness of physical sensations to the capacity to appreciate complexity in the emotional experiences of self and other. The LEAS (Lane *et al.*, 1990) is a written performance measure that asks an individual to describe her anticipated emotions and those of another person in each of 20 short scenarios described in two to four sentences. One scenario is presented per page, followed by two questions, 'How would you feel?' and 'How would the other person feel?' at the top of each page. Participants write their responses on the remainder of each page. They are instructed to use as much or as little of the page as is needed to answer the two questions.

Scoring is based on specific criteria aimed at determining the degree of specificity in the emotion terms used and the range of emotions described, and the differentiation of self from other. Each of the 20 scenarios receives a score of 0–5, corresponding to the stages of the developmental model underpinning the LEAS. A score of 0 is assigned when non-affective words are used; a score of 1 when words indicating physiological cues are used in the description (e.g. 'I'd feel tired'); a score of 2 when words are used that convey undifferentiated emotion (e.g. 'I'd feel bad') or when the word 'feel' is used to convey an action tendency (e.g. 'I'd feel like punching the wall'); a score of 3 when one word conveying a typical differentiated emotion is used (e.g. angry, happy, etc); a score of 4 when two or more level 3 words are used in a way that conveys greater emotional differentiation than would either word alone. Participants receive a separate score for the 'self' response and for the 'other' response, ranging from 0–4. In addition, a total LEAS score is given to each scenario equal to the higher of the 'self' and 'other' scores. A score of 5 is assigned to the total when 'self' and 'other' each receive a score of 4; thus the maximum LEAS score is 100, with higher total scores indicating greater awareness of emotional complexity in self and other. A computerized LEAS scoring program has recently been developed (Barchard *et al.*, in press).

The LEAS has high inter-rater reliability, internal consistency (e.g. $\alpha = 0.89$, Ciarrochi *et al.*, 2003) and test-retest reliability. It is only weakly correlated with measures of verbal ability. Ramponi *et al.* (2004) found a non-significant correlation ($r = 0.02$) between LEAS scores and the National Adult Reading Test; Lane *et al.* (1995) found a correlation of $r = 0.17$ between LEAS scores and the Shipley Institute of Living Scale Vocabulary Subtest. In a large sample ($n = 869$) of students, a correlation of 0.15 was found between LEAS and Thurstone's Reading Test scores (Romero *et al.*, 2008). Furthermore, sex differences in LEAS are still significant when controlling for verbal ability (Barrett *et al.*, 2000). These data indicate that the LEAS is not just a measure of verbal ability. Nor is LEAS correlated with scores on the affective intensity, manifest anxiety or Beck Depression Scales (Lane and Pollerman, 2002) nor with the big five personality dimensions (Ciarrochi *et al.*, 2003), and there are only low or non-significant correlations between LEAS and the Toronto Alexithymia scale (Ciarrochi *et al.*, 2003; Lane *et al.*, 1998; Lumley *et al.*, 2005; Suslow *et al.*, 2000). Scores on the LEAS are related to the

understanding emotions section of the MSC Emotional Intelligence Test and to the attention to mood scale of the Trait Meta-Mood scale (Lumley *et al.*, 2005), to the perceiving emotions in stories of the Multifactor Emotional Intelligence Scale (MEIS) (Ciarrochi *et al.*, 2003), to the range and differentiation of emotional experience scale (RDEES) (Kang and Shaver, 2004) and have been shown to predict accuracy of facial emotion recognition (Lane *et al.*, 1996, 2000) and self-reported empathy (Ciarrochi *et al.*, 2003).

Two raters scored the LEAS independently. The inter-rater reliability was good (tau-b = 0.893, $N = 100$, $p < 0.01$). On the LEAS, participants' scores ranged from 65 to 90 (mean = 77, s.d. ± 6.7). These scores are similar to published values for young university student populations (Ciarrochi *et al.*, 2003), but somewhat higher than those reported for broader community samples (Barrett *et al.*, 2000).

Image acquisition

Blood oxygenation level-dependent (BOLD) contrast functional images were acquired with echo-planar T2*-weighted (EPI) images using a Medspec (Bruker, Ettlingen, Germany) 3-T MR system with a head coil gradient set. Each image volume consisted of 21 interleaved 4-mm-thick slices (inter-slice gap: 1mm; in-plane resolution: 2.2×2.2 mm; field of view: 20×20 cm; matrix size: 90×90; flip angle: 74°; echo time: 27.5 ms; voxel bandwidth: 143 kHz; repetition time: 1.6 s). Slice acquisition was transverse oblique, angled to avoid the eyeballs, and covered most of the brain. Six hundred and ninety-five volumes were acquired in one continuous run, and the first six volumes were discarded to allow for T1 equilibration.

Image analysis

fMRI data were analysed using statistical parametric mapping software (Wellcome Trust Centre for Neuroimaging, London, UK). Standard pre-processing was conducted, comprising slice timing correction, realignment, undistortion (Cusack *et al.*, 2003) and masked normalisation of each participant's EPI data to the Montreal Neurological Institute (MNI)—International Consortium for Brain Mapping template (Brett *et al.*, 2001). Images were re-sampled into this space with 2 mm isotropic voxels and smoothed with a Gaussian kernel of 8 mm full-width at half-maximum. Condition effects were estimated for each participant at each voxel using boxcar regressors for the 14 s animation period, convolved with a canonical hemodynamic response function (HRF) in a general linear model, with spatial realignment parameters included as regressors to account for residual movement-related variance. A high-pass filter was used to remove low-frequency signal drift, and the data were also low-pass filtered with the canonical HRF. Activation contrasts between conditions were estimated for each participant at each voxel, producing statistical parametric maps.

Random-effects analysis was conducted to analyse data at a group level, with modulations by levels of emotional awareness assessed by simple regression against LEAS scores.

A priori regions of interest (ROIs) were determined based on areas activated by emotion, social perception and social cognition. We used small volume correction (SVC) for multiple comparisons applied at $P < 0.05$ (family-wise error) following an initial thresholding at $P < 0.05$ uncorrected. The amygdala, basal ganglia, posterior and anterior cingulate, insula, postcentral gyrus, inferior and medial orbitofrontal cortex (OBFC) and hypothalamus were defined using structural templates derived by automated anatomic labelling (Tzourio-Mazoyer *et al.*, 2002). Spherical ROIs (10 mm radius spheres) were created to sample the lateral fusiform gyrus (FG) (central coordinates −42, −49, −19; 40, −48, −16) and dorsal and ventral medial prefrontal cortex (DMPFC and VMPFC) (−4, 60, 32; 7, 55, 28 and ±2, 48, −12), by computing the average of the reported activation coordinates for these regions across previous imaging studies of animate motion (Castelli *et al.*, 2000, 2002; Martin and Weisberg, 2003; Ohnishi *et al.*, 2004; Schultz *et al.*, 2003). For the superior temporal sulcus (STS) we used the coordinates (±54, −34, 4) taken from Schultz *et al.* (2004). For the TPs we used the coordinates (±44, 14, −27) from Rogers *et al.* (2006). For the premotor cortex we used the coordinates (± 54, 5, 40) from Grèzes *et al.* (2007). For the periacqueductal grey (PAG) we used the coordinates (2, −32, −24) from Bartels and Zeki (2004). In addition, all activations in the vicinity of our ROIs that survived an uncorrected threshold of $P < 0.001$ and a minimum cluster size of five voxels are reported for completeness.

For anatomical labelling purposes, activation coordinates were transformed into the Talairach and Tournoux coordinate system using an automated non-linear transform (Brett *et al.*, 2001) and labelled with reference to the Talairach Demon database (http://www.talairach.org) and the atlas of Talairach and Tournoux (1988). For visualizing activations, group maps are overlaid on the ICBM 152 structural template, an average T_1-weighted image of 152 individuals co-registered to MNI space. Activations are reported using (x, y, z) coordinates in Talairach (not MNI) coordinates.

RESULTS
Film ratings and post-film probe questions

The post-scan visual analogue scale based valence ratings confirmed that the films were rated as intended (affiliative–positive; antagonistic–negative; neutral–neutral) (affiliative mean = 1.3, s.d. = 0.50; antagonistic mean = 9.7, s.d. = 0.60, indifferent mean = 5.8, s.d. = 0.21). With regards to emotional intensity, the antagonistic animations were considered the most intense of the three, followed at some distance by the affiliative animations. The neutral animations were judged to be of low intensity (affiliative mean = 5.2, s.d. = 2.97; antagonistic mean = 8.9, s.d. = 1.00; indifferent mean = 2.7, s.d. = 1.76). All these differences

were significant [affiliative *vs* antagonistic: $t(15) = -7.88$, $P < 0.001$; affiliative *vs* indifferent: $t(15) = 4.13$, $P < 0.001$; antagonistic *vs* indifferent: $t(15) = 16.62$, $P < 0.001$]. LEAS scores were not correlated with intensity or valence ratings.

Participants provided the expected response to 92% of the post-film probe statements and error rates were comparable across the affiliative, antagonistic and neutral films, $\chi^2 = 2.9$, $df = 2$, $P = 0.24$, for the two viewing tasks (behavioural, spatial), $\chi^2 = 0.072$, $df = 1$, $P = 0.79$, and for the two response options (true, false) $\chi^2 = 0.13$, $df = 1$, $P = 0.72$. The high accuracy rates in both conditions show that the manipulation of attention was successful. Error rates were unrelated to LEAS scores.

fMRI data

Cross-participant results. *Main effect of emotion*—For the contrast antagonistic and affiliative *vs* neutral animations, collapsed across task (behavioural *vs* spatial), we found increased activity at a whole brain corrected $P < 0.05$ in the right secondary somatosensory cortex (SII) (with a similar trend in left SII), and at $P < 0.05$ SVC in left and right amygdala, hypothalamus, left and right lateral fusiform gyrus, right inferior orbitofrontal gyrus, right precentral gyrus (with a similar trend in left precentral gyrus), left postcentral gyrus, and left and right STS (Figure 2). There was also trend level activation of the right insula. In addition, at an uncorrected $P < 0.001$ and a cluster extent of five voxels, there was activation in the dorsomedial prefrontal cortex and in the right TP (Table 1).

Effect of emotion: amplification by social attention—For the contrast antagonistic and affiliative *vs* neutral animations, for the behavioural *vs* spatial task, we found increased activity in the anterior cingulate cortex (0, 3, 27, $Z = 3.6$, $P_{svc} = 0.037$) (Figure 3). In addition, at an uncorrected $P < 0.001$ and a cluster extent of five voxels, there was activation in following ROIs: dorsomedial prefrontal cortex (-14, 44, 27, $Z = 3.66$), left insula (-46, -1, 13, $Z = 3.33$), left postcentral gyrus (-48, -23, 38, $Z = 3.58$) and right SII (51, -30, 20, $Z = 3.48$).

Table 1 Main effect of emotional content of animations

| Brain regions	Hemisphere	Talairach coordinates	Cluster size	Z-score	P
P whole brain corrected					
SII	R	57, −34, 18	29	5.51	0.005
P$_{SVC}$ < 0.05					
Amygdala	L	−18, −1, −17	193	4.06	0.002
	R	24, −1, −20	215	3.19	0.026
Hypothalamus	L	−2, −6, −11	97	3.45	0.033
	R	0, −6, −11	132	3.23	*0.058*
Lateral fusiform gyrus	L	−42, −40, −18	144	3.84	0.011
	R	48, −47, −14	162	3.89	0.009
Inferior orbitofrontal gyrus	R	46, 32, −12	474	3.75	0.031
Precentral gyrus	R	50, 0, 46	328	3.85	0.044
Postcentral Gyrus	L	−59, −19, 18	107	4.36	0.01
Superior Temporal Sulcus	L	−53, −30, 13	198	4.3	0.002
	R	55, −39, 4	468	4.64	0.001
Insula	R	50, 0, 0	99	3.5	*0.067*
P$_{unc}$ < 0.001					
Medial frontal gyrus	R	10, 49, 42	7	3.54	<0.001
Temporal pole	R	38, 1, −20	254	3.63	<0.001
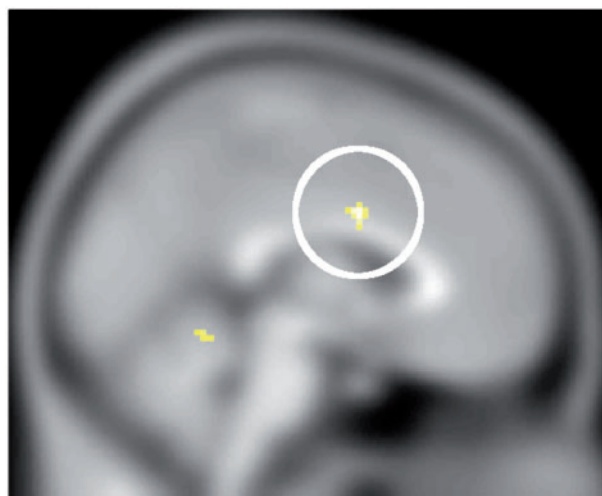
Fig. 3 Dorsal ACC activation for the interaction between emotional content and selective attention.
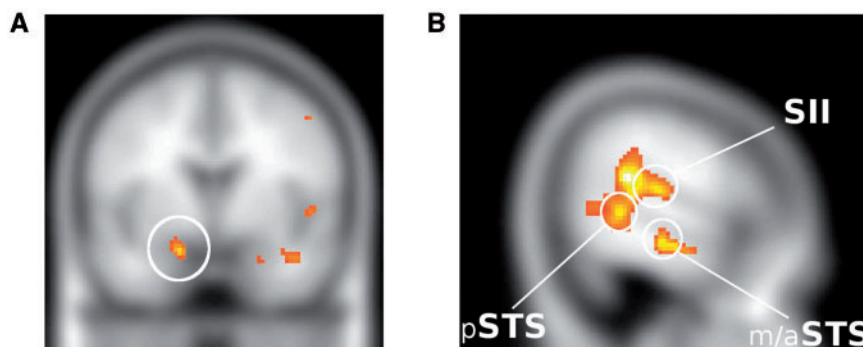

Fig. 2 Main effect of emotional content of animations. (A) Activation in the left amygdala. (B) Activation in the right posterior STS (pSTS), SII and mid/anterior STS extending into temporal pole.

Antagonistic vs affiliative animations—At a whole brain corrected $P < 0.05$, activations were seen in the early visual cortex (-6, -99, 9, $Z = 5.74$; 12, -90, 21, $Z = 5.28$), and at $P < 0.05$ SVC in right STS (51, -29, 2, $Z = 3.82$, $P_{svc} = 0.011$), and right postcentral gyrus (28, -42, 51, $Z = 4.07$, $P_{svc} = 0.024$). At an uncorrected P of < 0.001 and an extent threshold of 5 voxels, there was also activation in left SII (-55, -34, 18, $Z = 3.25$).

Antagonistic vs affiliative animations: Amplification by social attention—For the contrast antagonistic *vs* affiliative animations, for the Behavioural *vs* Spatial task, there was increased activity in the medial orbitofrontal gyrus (12, 32, -12, $Z = 3.75$, $P_{svc} = 0.015$).

Affiliative vs antagonistic animations—There were no areas showing significantly increased activation for the contrast of affiliative *vs* antagonistic animations.

Affiliative vs antagonistic animations: amplification by social attention—The contrast affiliative *vs* antagonistic animations, for the behavioural *vs* spatial task, did however reveal differences in left putamen (-20, 14, 9, $Z = 3.38$, $P_{svc} = 0.051$) and right inferior orbitofrontal gyrus (32, 32, -13, $Z = 3.55$, $P_{svc} = 0.052$).

Correlations with levels of emotional awareness. *Main effect of emotion*—For the main effect of emotion, a positive correlation with increasing LEAS was seen in the left TP (-36, 16, -26, $Z = 3.54$, $P_{svc} = 0.027$) (Figure 4). In addition negative correlations (i.e. increased activation with lower LEAS) were seen at a trend level in the hypothalamus (0, -2, -10, $Z = 3.12$, $P_{svc} = 0.078$) and in the right precentral gyrus (51, 2, 40, $Z = 3.55$, $P_{svc} = 0.027$).

Effect of emotion: amplification by social attention—No significant positive correlations were seen for this contrast. There were significant negative correlations with LEAS for this contrast in the right STS (50, -37, 7, $Z = 3.25$, $P_{svc} = 0.051$), globus pallidus (28, -8, -3, $Z = 2.99$, $P_{svc} = 0.043$) and periaqueductal gray (6, -34, -15, $Z = 2.96$, $P_{svc} = 0.034$), and at an uncorrected $P < 0.001$ and cluster extent five voxels, in the left insula (-40, -6,

12, $Z = 3.32$), postcentral gyrus (54, -18, 44, $Z = 3.74$), left STS (-56, -24, 0, $Z = 3.39$) and left SII (-58, -16, 26, $Z = 3.35$). I.e. with higher levels of emotional awareness, there was a reduced effect of social attention in these regions.

Antagonistic vs affiliative animations—For the contrast of the antagonistic animations with the affiliative animations, increased LEAS led to increased activity in the left globus pallidus/hypothalamus (-14, -2, -2, $Z = 3.63$, $P_{svc} = 0.008$) and at a trend level in the left anterior cingulate (-12, 43, 2, $Z = 3.23$). This latter finding is consistent with McRae *et al.* (2008) who found that LEAS scores in women (but not men) were positively correlated with activity in the anterior cingulate to high, but not low, arousal emotional images.

Antagonistic vs affiliative animations: amplification by social attention—No significant correlations were seen for this contrast.

Affiliative vs antagonistic animations—For the contrast of the affiliative animations with the antagonistic animations, increased LEAS was correlated with increased activity in the insula bilaterally (-36, -1, -13, $Z = 3.95$, $P_{svc} = 0.019$; 48, 2, 2, $Z = 3.68$, $P_{svc} = 0.041$), and the periaqueductal gray (8, -36, -20, $Z = 3.33$, $P_{svc} = 0.045$). In addition, at an uncorrected $P < 0.001$ and a cluster extent of five voxels, this contrast was associated with activation in the globus pallidus (24, -16, -4, $Z = 3.49$). Notably, the pallidal correlation for affiliative animations and LEAS fell relatively more posterior to the correlation with antagonistic animations (Figure 5). An analogous anterior–posterior division in the pallidum has been observed in the rat brain (Smith and Berridge, 2005; see Discussion section). At this same threshold positive correlations were also seen in the cingulate gyrus (-2, 25, 30, $Z = 3.44$) and posterior cingulate (2, -41, 4, $Z = 3.44$).

Affiliative vs antagonistic animations: amplification by social attention—Attention to social meaning correlated positively with LEAS in the contrast of the affiliative *vs*
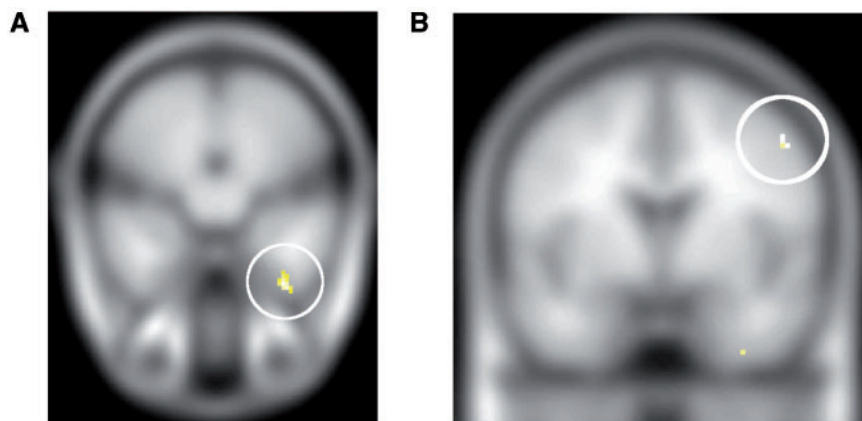

Fig. 4 Increased levels of emotional awareness are associated with increased left temporal polar activation (**A**), and decreased levels of emotional awareness are associated with increased right premotor activation (**B**) whilst viewing emotional relative to neutral animations.
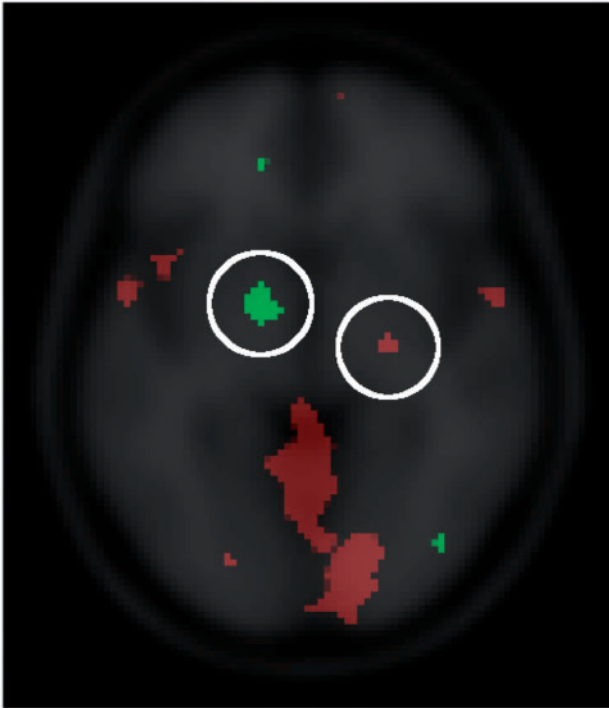
Fig. 5 In red, the correlation of LEAS with the contrast affiliative *vs* antagonistic animations (social and spatial tasks). In green, the correlation of LEAS with the contrast antagonistic *vs* affiliative animations (social and spatial tasks). Highlighted with the white circles are the left and right pallidum, respectively.

antagonistic animations in the periaqueductal gray (0, −34, −17, $Z = 3.01$, $P_{svc} = 0.031$).

DISCUSSION

With the goal of locating the neural structures involved in processing emotion from motion dynamics, and how these were influenced by selective attention and levels of emotional awareness, healthy volunteers viewed animations of affiliative, antagonistic and neutral interactions. Our findings suggest that neural representation of emotion is critically dependent on individual differences in emotional complexity.

Brain regions sensitive to emotion (antagonistic and affiliative *vs* neutral interactions)

According to Michotte (1950) the detection of emotion is grounded in the analysis of motion cues, e.g. approach, avoidance, contact intensity. Consistent with this, we found that participants could extract not just emotional valence (±) and arousal, but complex social meanings from our simple animations. Regardless of task, viewing emotional animations, relative to neutral animations, resulted in activation across a distributed set of neural structures implicated in processing emotions and social intentions from facial, vocal and bodily expressions, and in the representation of one's own emotions (amygdala, lateral FG, posterior STS, SII, OBFC, premotor cortex, TP,

hypothalamus, insula and DMPFC) (Frith and Frith, 2003; Heberlein and Adolphs, 2007; Kober *et al.*, 2008; Heberlein and Atkinson, 2009). Our results refine previous findings that lesions encompassing, but not restricted to, amygdala (Heberlein and Adolphs, 2004) and somatosensory cortices (Heberlein *et al.*, 2003) result in a diminished use of affective and social words to describe the original Heider and Simmel animation.

Interaction between social attention and emotion

The influence of attention on the neural processing of emotion cues is a key issue (Adolphs, 2008). Our attentional manipulation was realised by directly cueing participants to pay attention to social or spatial attributes of the sprites' motion. Attention to social meaning resulted in increased activity in the dorsal ACC, together with SII, insula and DMPFC. Previous studies have shown heightened activity in these regions when attending to facial expression: dACC (Vuilleumier *et al.*, 2001), which might supervise 'top–down' attentional allocation to salient emotional and social stimuli (Peers and Lawrence, 2009); SII and insula (Winston *et al.*, 2003), lesions to which impair explicit emotion recognition (Adolphs *et al.*, 2000, 2002; Heberlein *et al.*, 2004; Pitcher *et al.*, 2008), and which are involved in processing the somatic and visceral aspects of self and others emotions (Damasio *et al.*, 2000; Heberlein and Adolphs, 2007); and DMPFC, which is involved in processing the affective meanings which generate emotions by the cognitive route (Teasdale *et al.*, 1999; Ochsner *et al.*, 2009), and mental state attribution or theory of mind more generally (Amodio and Frith 2006; Frith and Frith, 2003; Moriguchi *et al.*, 2006; van Overwalle, 2009).

Brain regions sensitive to social interaction type (antagonistic *vs* affiliative)

When compared with the affiliative animations, antagonistic ones activated bilateral early visual cortex (BA 17–19), right pSTS and right postcentral gyrus. This is consistent with previous studies of dynamic facial and bodily expression processing (Grosbras and Paus, 2006; Grèzes *et al.*, 2007; Kilts *et al.*, 2003; Pelphrey *et al.*, 2007; Sato *et al.*, 2004). These activations might have been due to differences between the animations in motion content (the circles of the antagonistic animations moved consistently more and at a faster pace), or in emotional valence or arousal (in the post-scanning behavioural ratings the antagonistic animations were considered to be more emotionally intense). Early visual areas, pSTS and premotor cortex are all sensitive to biological motion (Casile *et al.*, 2009; Jastorff and Orban, 2009; Pelphrey *et al.*, 2003), as well as emotional valence and arousal (Lane *et al.*, 1999; Sugurladze *et al.*, 2003). The relative contributions of kinematics and arousal may be impossible to differentiate, as, consistent with Michotte's (1950) proposals, there is a very direct relationship between the kinematic properties (e.g. velocity) of biological motion

stimuli and perceiver's ratings of arousal (Aronoff, 2006; Chouchourelou *et al.*, 2006; Ikeda and Watanabe, 2009; Pavlova *et al.*, 2005; Pollick *et al.*, 2001; Roether *et al.*, 2009). We found no increase in amygdala activity for antagonistic relative to affiliative films. This contrasts with some studies (Carter and Pelphrey, 2008; Sinke *et al.*, 2010), but is consistent with lesion work (Heberlein and Adolphs, 2004) and likely relates to the complexity of the affiliative interactions or the lack of imminent threat to the viewer in our antagonistic interactions (which were viewed 'from above') (Sinke *et al.*, 2010).

Interaction between social attention and social interaction type

Under social attention, we observed differential activations of the OBFC, with the antagonistic animations activating medial OBFC and the affiliative animations activating an inferior and more lateral OBFC region. This finding is consistent with a recent study which reported that words with increasing negative valence were associated with increased activity in medial OBFC/subgenual cingulate, whereas increasing positive valence was associated with increased activity in lateral OBFC (Lewis *et al.*, 2006). It is unlikely, however, that these differences simply reflect differences in emotional valence ($\pm$) between the films, since Kringelbach and Rolls (2004) have shown in a meta-analysis that medial and lateral OFC are both capable of coding rewarding (i.e. positive valence) and punishing (i.e. negative valence) information. Rather, the differences in OBFC may relate to some more specific aspect of the type of social interaction (antagonistic *vs* affiliative) and its implications for the viewer. For example, Mobbs *et al.* (2007) found that medial OBFC/subgenual cingulate was specifically activated by remote, rather than imminent threats; whereas Nitschke *et al.* (2004) found that lateral OBFC was activated when mothers viewed their own infants (i.e. a specifically affiliative condition) and Sollberger *et al.* (2009) found that alterations in warm, affiliative personality traits, but not other interpersonal traits, were correlated with structural changes in lateral orbitofrontal cortex in individuals with neurodegenerative diseases. The specific nature of emotion coding in medial *vs* lateral OBFC, which form distinct neural networks (Price, 2007) is an important topic for future investigation.

Correlations with LEAS

LEAS and brain regions responsive to emotional content. Lane and Schwartz (1987) proposed that a person's ability to recognise and describe emotion in oneself and others, called emotional awareness or complexity, undergoes a five-stage structural development. A fundamental tenet of this model is that individual differences in emotional awareness reflect variations in the degree and differentiation of the 'schema' used to process emotional information. The first two stages of development are 'action-oriented' emotion processing stages, namely bodily

sensations and actions tendencies. The three remaining stages, single emotions, blends of emotion and combinations of blends, are associated with more highly differentiated emotional knowledge (for self and others) (Lane, 2000, 2008; Lane and Pollermann, 2002), that is with a propositional (e.g. conceptual) knowledge of emotion (Lindquist and Barrett, 2008). In our study, for the main effect of emotion (i.e. independent of attentional set), LEAS scores correlated positively with activity in the left TP, and negatively with activity in the hypothalamus and the right precentral gyrus. Left TP activity has been associated with detailed emotional perspective taking (Derntl *et al.*, 2010; Ruby and Decety, 2004), in narrative and story processing (Maguire *et al.*, 1999) and more generally with the level of specificity of retrieved semantic knowledge (Grabowski *et al.*, 2001; Rogers *et al.*, 2006), as part of a semantic 'hub' (Patterson *et al.*, 2007). Burnett *et al.* (2009) found that left TP activity when processing social emotions increased from adolescence to adulthood, consistent with the increasing refinement of emotion categories during development (Widen and Russell, 2008). Thus, consistent with LEAS theory, increasing emotional complexity is linked with increased neural coding of emotion in the semantic system.

Conversely, lower emotional complexity was associated with increased activity in the hypothalamus, a visceromotor structure (Thompson and Swanson, 2003) and premotor cortex [($Z = 40$), falling within ventral premotor cortex (Tomassini *et al.*, 2007)]. The latter region has been identified as a key node in a putative human 'mirror neuron system' (Morin and Grèzes, 2008), implicated in goal-directed action observation (Rizzolatti and Craighero, 2004) and activated in previous studies of the perception and production of emotional actions (Grèzes *et al.*, 2007; Grosbras and Paus, 2006; Henenlotter *et al.*, 2005; Leslie *et al.*, 2004; van der Gaag *et al.*, 2007; Warren *et al.*, 2006; Zaki *et al.*, 2009). The negative correlation with LEAS suggests, again consistent with Lane's model of emotional awareness, that low LEAS is associated with a greater tendency to encode emotional information in an action-oriented and visceral fashion. These findings place critical constraints on 'motor' theories of empathy (Gallese *et al.*, 2004; Pfeifer *et al.*, 2008; Montgomery *et al.*, 2009).

LEAS, social attention and social interaction type. Higher LEAS scores did not predict greater activity in any region during the social *vs* spatial attention condition. Rather, we found a negative correlation between LEAS score and amplification of activity as a function of social attention in several cortical (STS, insula, SII) and subcortical (globus pallidus, periacqueductal gray) regions. That is, the attentional amplification of emotional content, in STS and insula, was attenuated in individuals with increasing emotional complexity, presumably because heightened emotional complexity is associated with a greater default tendency to attend to emotional and social information, thus reducing the impact of instructed attentional set (Ciarrochi *et al.*,

2003, 2005). The finding that LEAS score positively correlated with activity in regions linked to detailed semantic processing (left TPs) regardless of task, is also consistent with this suggestion. Ongoing work is examining the extent to which individual differences in emotional complexity influences patterns of brain activity during explicit retrieval of detailed emotional knowledge.

Increased emotional differentiation as indexed by increased LEAS score, was accompanied by an increased neural differentiation between the positive and negative animations within the pallidum, where activation to antagonistic animations showed a positive correlation with LEAS in the anterior pallidum, whereas activation to affiliative animations showed a positive correlation with LEAS in the posterior pallidum. Smith and Berridge (2005) found evidence for an anterior–posterior 'hedonic gradient' in the rat pallidum reflecting increased 'liking' of foods. Our findings suggest increased differentiation between emotions of different valence with increasing LEAS in regions coding basic 'building blocks' of emotional valence. This accords with the hierarchical organisation of levels of emotional awareness theory, in which functioning at each level adds to and modifies the functioning of previous levels (Lane, 2000, 2008). The greater differences seen between affiliative and antagonistic animations with increasing LEAS score in regions implicated in processing affiliative signals (the insula) (Henenlotter *et al.*, 2005) and basic affiliative behaviours (PAG) (Bartels and Zeki, 2004; Lonstein and Stern, 1997), are also consistent with Lane's theory. Increased LEAS scores are associated with heightened interpersonal closeness (Lumley *et al.*, 2005).

In conclusion, simple motion cues alone communicate rich information about emotional interactions and trigger widespread activity across a range of structures implicated in processing emotion and social information. Regions including dACC were modulated by selective attention to social meaning. Critically, individual differences in emotional complexity profoundly influenced the neural coding of such cues, and the influence of attention, as predicted by Lane's model of Levels of Emotional Awareness (Lane 2000; Lane *et al.*, 1990). Increased levels of emotional awareness predicted increased semantic neural emotion coding, whereas decreased levels of emotional awareness predicted visceral and action-oriented coding. If extended and confirmed, results of this type could do much to clarify why the effects on emotion processing of lesions to specific regions are subject to individual variation. Indeed, future fMRI studies in this domain would benefit from including measures of individual differences in emotional complexity on a more routine basis.

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