The neural basis of perceiving emotional bodily expressions in monkeys

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Higher animals invest considerable time and brain resources in monitoring each others' body language. A network of dedicated brain structures is presumably involved in social perception. We hypothesized that functional magnetic resonance imaging may reveal portions of inferior temporal cortex participating in processing social signals. We used contrast agent-enhanced awake monkey functional magnetic resonance imaging to test whether subdivisions of inferior temporal cortex are sensitive to emotional body displays of conspecifics, and whether the degree of activation reflects the social intention expressed. We show that portions of superior temporal sulcus play a central role in processing body images of conspecifics and that these areas are preferentially sensitive to threat signals indicating that threat may be the most salient social signal. *NeuroReport*

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Introduction

Social animals have evolved a whole range of communicative abilities on which their well being and survival in a society hinges. Foremost among the cognitive skills of social species is the ability to monitor each others' behaviour and to adapt continuously to the social signals of others, whether collaborative or competitive [1]. A longstanding assumption in the literature is that there are probably evolutionary-shaped dedicated brain resources devoted to processing social signals, a hypothesis referred to as the 'social brain' for short. Evidence in support of this assumption is intended to apply across widely different social species [2], for whom reliance upon conspecifics is essential for survival.

The hypothesis of a social brain encompassing specialized skills for social perception and cognition has gained wide popularity among neuroscientists over the last decade. Supportive findings are gathered from a wide spectrum of disciplines, ranging from behavioural observations to single cell recordings. Species with a similar social phylogenetic history like human and nonhuman primates may be expected to exhibit important similarities in the neural basis of affective and communicative skills. This assumption is the backbone of much neurobiological emotion research of the last two decades and theoretical models of human emotion processes are partly based on neurobiological findings borrowed from animal research [3]. Yet at present, there is still very little empirical evidence in support of functional similarities between the social brain of human and nonhuman animals.

A complicating factor is that findings from different species have traditionally been obtained using different methods, with single cell recordings as the predominant method in monkey and functional brain imaging in humans. Therefore, an urgent task for a generalized emotion and social brain theory is to bridge the gap between the results obtained in the different species.

Single cell physiology has shown that the superior temporal sulcus provides an exquisitely detailed representation of body posture and face. Recordings from portions of inferior temporal cortex, and in particular regions within the superior temporal sulcus, have shown its involvement in the perception of social signals [4]. These findings leave no doubt about the fact that there are cells capable of describing body postures and that inferior temporal cortex and the superior temporal sulcus can provide the right information to the amygdala. Yet these results do not allow a direct comparison with human functional magnetic resonance imaging (fMRI) data. It is unclear whether representations of bodily postures with different emotional valence are segregated at a millimetre scale that would enable fMRI to pick up voxels with emotion selective properties. These representations may not be clumped according to emotion, and therefore may not show up as selective at the voxel level making it currently difficult to generalize from single cell recordings to data obtained with fMRI. The role of portions of inferior temporal cortex in processing images of neutral faces and bodies is now also shown with functional MRI [5]. But no data are yet

Fig. 1
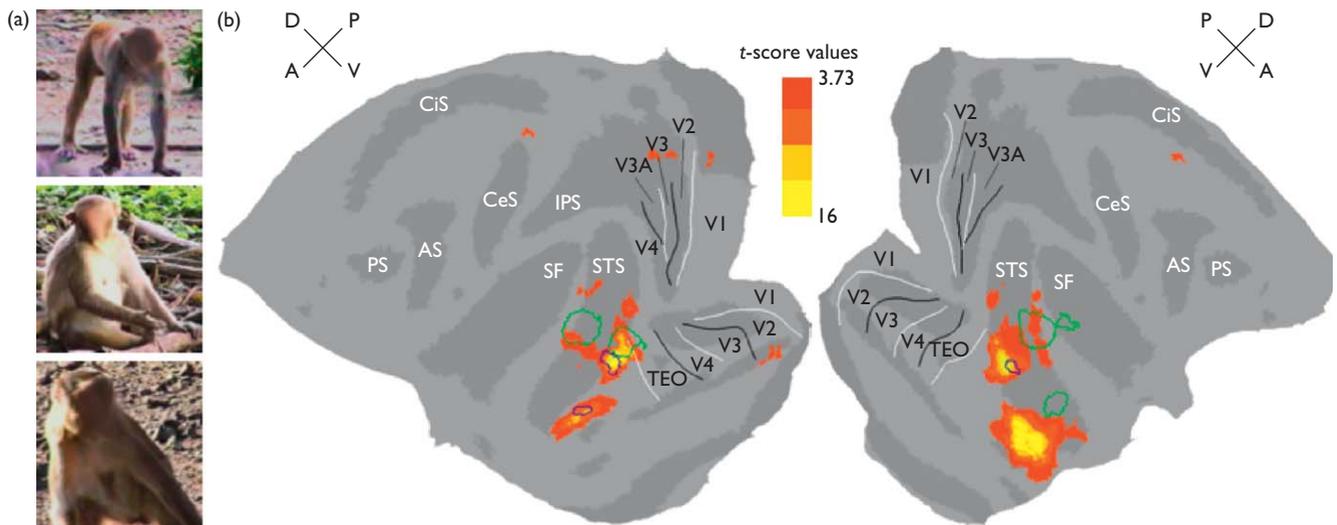
Superior temporal sulcus response to emotional body displays in one monkey. (a) Examples of emotional body stimuli (top to bottom – anger, neutral, fear). (b) Flat maps of left and right hemispheres, respectively. Yellow-orange scale represents (bodies minus scrambled; $P < 0.0001$, uncorrected), blue outline represents (conjunction of bodies minus scramble and threat minus neutral; $P < 0.01$, uncorrected) and the green outline represents (faces minus places; $P < 0.0001$, uncorrected). A, anterior; D, dorsal; P, posterior; V, ventral.

available on whether inferotemporal cortex is also sensitive to the emotional meaning of bodies like, for example threat [6].

An interesting question is therefore whether inferior temporal cortex plays a significant role in processing images of bodily expression of anger and fear as shown in recent imaging studies in humans [7]. To probe the neural correlates of viewing emotional body signal processing in monkeys, we turned to contrast agent-enhanced awake monkey fMRI [8]. Specifically, we tested whether visual cortical areas and in particular inferior temporal cortex may be selectively sensitive to viewing bodies of conspecifics and whether this sensitivity varies as function of the emotion and social intention (threat or fear) expressed. Fixating macaques ($N=2$) were scanned while presented with images of monkey bodies with neutral, fear and threat expressions, as well as their scrambled controls. Importantly, we masked the faces to isolate the functional effects of emotional body expressions from those of facial expressions (Fig. 1a).

Methods
Animals
Two male rhesus monkeys (5–6 kg, 5–7 years of age) were scanned. All animal care and experimental procedures conformed to Massachusetts General Hospital-Subcommittee on Research Animals protocol (2003N000338) and National Institutes of Health guidelines. The details of the surgical procedures, training of monkeys, image acquisition, eye monitoring and statistical analysis of monkey scans have been described earlier [8]. The

monkeys sat in a sphinx position in a plastic monkey chair directly facing the screen. During training, they were required to maintain fixation within a $2 \times 2°$ window centred on a red dot ($0.35 \times 0.35°$) in the middle of the screen. Eye position was monitored at 120 Hz using a corneal reflection system (Iscan, Burlington, Massachusetts, USA). The monkeys were rewarded (water) for fixating to the small red dot within the fixation window for long periods, while stimuli were projected in the background. Before each scanning session, a contrast agent, monocrystalline iron oxide nanoparticle, was injected into the femoral/saphenous vein (4–11 mg/kg).

Visual stimuli
Body stimuli
Rhesus macaques were filmed in a natural setting on Cayo Santiago, Puerto Rico. Still images were obtained from these video films showing free-ranging animals engaged in social interactions with conspecifics. Images of fear and aggression were chosen that best represented the stereotypical expression of these emotions in the monkeys. The faces were later digitally erased so as to leave only the body postures in the final stimuli. The fear postures included monkeys cringing and leaning away, whereas the aggressive ones most often had stiff forelegs and bodies with an approach expressing posture. Videotapes were digitized with 'Dazzle Moviestar' software Version 4.22 (Mediaware Solutions Pty Ltd., Fremont, USA) and stills of body postures displaying a fearful, aggressive or neutral pose were created. Each frame chosen for a fear or aggression still was selected at the maximal point of expressiveness, defined as the

maximum difference from the neutral, nonexpressive pose by two judges familiar with the animals and natural environment in which they were filmed. Neutral images included solitary animals engaged in calm eating or involved in behaviour with relaxed postures. Mosaic-scrambled control stimuli were made for each body stimulus. Average stimulus size was 280×250 pixels and stimuli were presented at a distance of 54 cm corresponding to a visual angle of $8.75 \times 7.8°$.

Face localizer
As part of an independent study data from a face localizer were available from scanning sessions that included the same two animals that were scanned for the body expression study reported here. The stimuli consisted of coloured face and place stimuli presented on a black background. Different sizes of stimuli (ranging between 3 and 20°) were used and the activity map is based on the combined activation of all face stimuli versus place stimuli. The face stimuli were extracted from group photos where multiple equal-sized faces were adjacent to each other. The place images were pictures of familiar indoor scenes for the monkey. Size of the place and face stimuli were matched and spatial frequency distribution was virtually identical.

Data acquisition
Monkeys were scanned in a Siemens Allegra 3T scanner (Siemens Medical Systems, Erlangen, Germany) and a single-loop radial transmit–receive surface coil (11 cm diameter). Contrast agent-enhanced fMRI was used [8]. Each functional time series consisted of gradient-echo echoplanar images (repetition time 3 s; echo time 24 ms; field angle 90°, $1.25 \times 1.25 \times 1.25 \text{ mm}^3$ voxels, 45 slices – covering the whole brain except for the anterior pole of frontal cortex). In the face-localizer tests, we acquired four to five times 20–25 functional runs in the individual monkeys. A block design was used with 24 s long epochs, and 15 epochs/run to measure fMRI activations specific to emotional body expressions. The monkeys performed a passive, central fixation task during each run as described below. In a typical block design (14 blocks/run, 30 s/block), the presentation order of the conditions was randomized with different orders in different time series. In an additional scan session, high-resolution three-dimensional T1-weighted images (magnetization prepared rapid gradient echo, $0.35 \times 0.35 \times 0.35 \text{ mm}^3$) were obtained while the monkey was anaesthetized using ketamine/xylazine (intramuscularly). A voxel-based analysis was performed using SPM99 (Wellcome Trust Centre for Neuroimaging, UCL, UK), following previously described procedures to fit a general linear model [8]. The t-score maps from both monkeys were thresholded and overlaid on a template derived from T1-weighed anatomical images, which were reconstructed with FreeSurfer and FS-FAST software (*http://surfer.nmr.mgh. harvard.edu/*) [9,10]. Flattened cortical representations were created with Caret (*http://brainmap.wustl.edu/caret*) [11,12]. Activity profiles were sampled using custom extensions to SPM99.

Results
fMRI responses to bodies as compared with their phase scrambled counterparts activated several areas in the inferotemporal cortex, centred on the superior temporal sulcus (see orange-yellow t-score maps in Fig. 1b). These results are in agreement with earlier studies in both monkey [13] and human [14] showing a degree of category selectivity in portions of inferior temporal cortex to images of bodies. Most interestingly, a subset of those body-sensitive voxels showed increased fMRI signals for the threat images (two patches in the left and one in the right hemisphere) compared with other emotional expressions (see Fig. 1b, blue outlines). No such pattern is associated with expressions of fear, testifying to the critical significance of social threat conveyed by the body language of conspecifics.

Discussion
Our goal was to make a beginning with investigating the neurofunctional basis of social-affective communication from whole body images in monkeys. The present results establish that superior temporal sulcus neurons are sensitive for emotional expressions, that they are clustered rather than being distributed and that these clusters are not too small to be detected by fMRI.

Three aspects of these results are important. The first issue concerns the relation between the currently observed activity and monkey or human studies in the literature. Monkey studies have reported cells in the anterior part of the monkey superior temporal sulcus that respond selectively to body actions and body postures [15]. Recently, it has been shown in normal individuals that perceiving human bodies or body parts activates an area in extrastriate cortex, labelled extrastriate body area [14]. The present body-sensitive area seems to be different from the neutral body selective described in fMRI human studies. The human body-sensitive area lies anterior to Brodmann area 18 with little overlap between both. The extrastriate body area can be divided in an anterior and posterior part [16]. In contrast, currently available fMRI studies point to an area consisting of portions of the anterior superior temporal sulcus as the most important for viewing images of monkey body parts. Single unit recordings from anterior superior temporal sulcus in the monkey, in contrast, show its responsiveness to biological motion [17]. Accordingly, it was found that the body part-selective region in macaque anterior superior temporal sulcus was adjacent or even partially overlapping to face-selective activations in two monkeys [18], suggesting a more continuous representation of bodies in the anterior superior temporal sulcus. In

line with this, human brain imaging results showed sensitivity to body motion in superior temporal sulcus [19] including its activation to still images with implicit movement [7]. Clearly, future studies need to address correspondences between the putative neural basis of human and monkey body perception and the role of emotional body movements.

The next issue concerns the novel finding of specialization within this area for emotional bodies in monkey. The role of human superior temporal sulcus in the perception of expressive body images was reported in recent human fMRI studies [20]. Human superior temporal sulcus is relevant for processing the affective component of faces and figures prominently in distributed models of face processing [21]. The present findings are consistent with the results in monkey physiology that neurons in superior temporal sulcus code the emotional expression of faces, whereas neurons responsive to identity are primarily found in the inferior temporal gyrus [22]. One may speculate, in line with the emotion-specific activation we observe, that the face-sensitive patches (green outlines in Fig. 1b) do not overlap with the subset of body-related voxels that are specifically sensitive to the threat expression (blue outlines). But as our study was not designed to compare facial and bodily expressions, no firm conclusions can be reached at this stage. At present, there are no studies available that compare systematically facial to bodily expressions in monkeys and our goal was not to provide such a full-fledged comparison which would need to use monkey faces versus bodies as done in human observers [23]. But at present, conclusions concerning human and monkey category representations remain difficult because no study so far has systematically compared neutral versus emotional as well as body versus face images. The indication of segregation suggested by the present data may thus be because of the fact that human faces were used in the face-localizer test and it may or may not reflect a distributed representation with partly overlapping face and body-sensitive areas. Future studies need to address the issue of category-specific representation in inferior temporal cortex with the caveat that a simple comparison of faces and bodies is likely to be confounded by major differences in low level visual differences but also by perceptual and functional ones (e.g. presence of eyes in the face and not in the body) and by the presence of action information in the body but not in the face.

Finally, our results show that the strongest fMRI responses in these body-sensitive areas are obtained by threatening body postures. The expression-sensitive voxels we see here represent a subset of two larger body-sensitive areas. This clearly indicates that the threat signals are more salient than fear signals. Interestingly, as predicted, our current monkey data are in agreement with the role of human superior temporal sulcus for processing bodily signals of threat [19] and with the role of superior

temporal sulcus as gateway to amygdala. This selectivity for angry body postures suggests that anger, at least anger expressed in the body posture, may be more salient and more socially relevant than neutral or fear expressions. As a matter of fact, anger also functions as a fear signal, but in contrasts to fear expressions, which signal the presence of a cause for fear for the social agent one is observing, anger expressions present that cause directly. Human studies increasingly report that anger signals trigger activation that is as least as strong as observed for fear.

One may argue that the enhanced activations for threatening body expressions do not reflect an emotion-specific effect *per se*, but are caused by increased attention to threatening body postures relative to neutral or fearful ones. Yet the emotion-based and attention-based explanation should not be viewed as mutually exclusive. It is well known that stimulus salience modulates the deployment of attentional resources and that stimulus salience influences processing at different levels of the visual system, even including the striate cortex [24]. For example, the attention deficit of patients suffering from hemineglect because of parietal lesion is considerably reduced by presentation of bodily emotion expressions [25]. Such attentional modulation underscores the intimate link between stimulus properties and deployment of attentional resources.

Conclusion
Social threat is the most salient communicative signal processed by the superior temporal sulcus, more so than is a fearful body expression. Our study underscores the importance of using realistic whole body images for studying emotional communication in nonhuman and human primates and as such it is an important step towards building a bridge between what is currently known about the social brain from single cell recordings in monkeys and lesion studies and brain imaging in humans.

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