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Uniquely human social cognition

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Recent data identify distinct components of social cognition associated with five brain regions. In posterior temporal cortex, the extrastriate body area is associated with perceiving the form of other human bodies. A nearby region in the posterior superior temporal sulcus is involved in interpreting the motions of a human body in terms of goals. A distinct region at the temporo-parietal junction supports the uniquely human ability to reason about the contents of mental states. Medial prefrontal cortex is divided into at least two subregions. Ventral medial prefrontal cortex is implicated in emotional empathy, whereas dorsal medial prefrontal cortex is implicated in the uniquely human representation of triadic relations between two minds and an object, supporting shared attention and collaborative goals.

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Introduction: two unique components

Preverbal infants, apes and monkeys share many of the foundational capacities of human social cognition: they recognize conspecifics, monitor others' actions, and engage in contingent interactions. As adults, however, the structure and content of our reasoning about one another vastly surpass these foundations. Among other activities, we can accuse one another (and our selves) of wishful thinking, read and write stream-of-consciousness novels, and organize international scientific conferences. Such complex social behaviours depend on at least two aspects of social cognition that develop throughout childhood.

First, young children and apes selectively attend to faces, bodies and actions, and understand basic mental states such as goals and perceptions [1*]. However, they do not distinguish between the object of a mental state (what a person's mental state is about, the state of affairs to which

the belief or perception refers) and the content (how that state of the affairs is represented, what the person believes or perceives to be true of it). Command of this distinction enables older children to understand how people's mental representations of the world might differ from the way the world really is. As a result, this later-developing, uniquely human component of social cognition is called a 'representational Theory of Mind'.

Second, human infants, apes and monkeys understand two-place, or dyadic relations (such as goals, [1*,2,3**]) between an individual and an object in the world. For example, if a piece of food is hidden, and then an informed experimenter tries (but fails) to reach into one of two containers to get the food for herself, chimpanzees unhesitatingly search in the same container. If the experimenter points to the container to show where the food is, however, chimpanzees search at chance [4**]. That is, adult chimpanzees appear able to represent 'she wants the food' and 'she saw where the food was hidden', but not 'she is showing me where the food is'. By contrast, humans begin to understand and produce such communicative pointing gestures by twelve months [3**]. This second unique component of human social cognition requires representing triadic relations: You, and Me, collaboratively looking at, working on or talking about This.

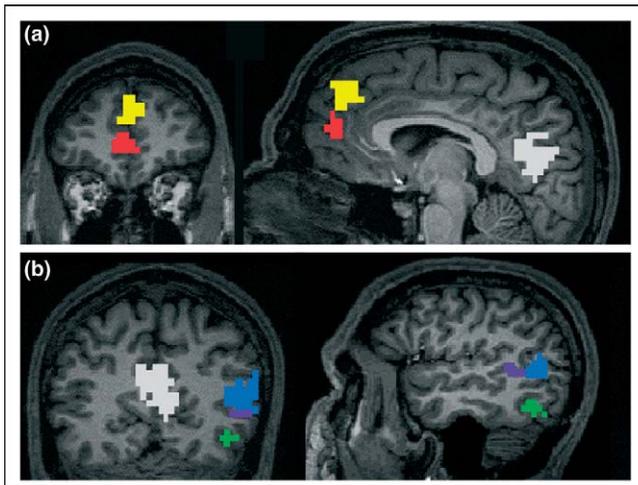
In the brains of healthy human adults, I suggest here that distinct brain regions are implicated in these two uniquely human aspects of social cognition: regions in the temporo-parietal junction (TPJ) and medial prefrontal cortices (MPFC), respectively (Figure 1).

Thoughts and the temporo-parietal junction

The developmental trajectory from attending to human faces and bodies (infants), to understanding goal-directed actions (toddlers), to the uniquely human representational theory of mind (preschoolers), is reflected in the functional profiles of three regions in lateral occipito-temporo-parietal cortex (Figure 1). These are the extrastriate body area for detecting the presence of a body (EBA [5]), the posterior superior temporal sulcus region for understanding action (pSTS-A [1*]) and the temporo-parietal junction area for representing mental states (TPJ-M [6]).

Although only the last of these reflects a uniquely human component of social cognition, many previous authors have often confused the TPJ with its neighbours, obscuring its functional specificity, so I begin with a brief review of these nearby regions.

Figure 1



Brain regions implicated in human social cognition. **(a)** Medial regions. **(b)** Lateral regions. The region selectively recruited when reasoning about others' representation of mental states, the right temporo-parietal junction, is shown in blue. Two nearby but distinct regions are also shown: the posterior right superior temporal sulcus region involved in perceiving intentional action (purple) and the right extrastriate body area (green). In medial prefrontal cortex, two regions are apparent: ventral MPFC associated with attributing emotion (red) and dorsal MPFC, possibly linked to reasoning about triadic relations (yellow). The posterior cingulate region, not discussed in this article but commonly recruited for social cognitive tasks, is shown in white.

The first step towards reasoning about others' actions is detecting the presence of an intentional actor, usually in the form of a human body (or body part). This function is associated with the EBA, a region in bilateral occipito-temporal cortex that shows a selective response to human bodies and body parts, relative to other familiar objects. Bodies might be defined by a range of static cues [5] or by global dynamics [7]. By contrast, neither verbal stories about a human body [6] nor even a human body that is temporarily occluded [1^{*}] elicit a blood oxygenation level-dependent (BOLD) response in the EBA. The response of right EBA is increased for images of human bodies presented from an allocentric (external), relative to an egocentric, perspective [8,9] consistent with a role in perceiving others.

Second, interpreting the motions of a human body in terms of the person's goals is associated with a nearby but distinct region (usually right-lateralised) in pSTS. This region is recruited during both direct observation of a body movement [10] and indirect observation of the effects of the action [11^{*}]. Importantly for a region implicated in representing goal-directed actions, the response of the pSTS-A reflects the relationship between a movement and its context [1^{*},12–14]. For simple goal-directed actions, the response in right pSTS is increased by a perceived mismatch between action and target [14–16]. For example, the right pSTS response to observed eye movements is increased when a light flashes on one side

of the screen and the character immediately looks in the opposite direction [17]. This gaze-incongruence effect is present in 7–10 year old children [18], but is absent in autistic subjects ([19]; for further evidence of STS abnormalities in autism see [20^{*},21]).

Finally, a region in the temporo-parietal junction, which is adjacent to but distinct from the pSTS region, is specifically associated with the later-developing system for representing the specific (representational) contents of mental states such as beliefs. The TPJ region is very selective; the BOLD response in this region is high when subjects read stories that describe a character's true or false beliefs, but low during stories containing other information about a character, including her appearance, cultural background, or even internal, subjective sensations — such as being tired or achy or hungry — that have no representational content [6,22,23]. The TPJ region is also selectively recruited for determining how the spatial relations between two objects would appear from a character's point of view versus from the subject's own position [24]. Damage to left TPJ causes selective deficits in judging the contents of others' beliefs [25^{**}].

One open question about the TPJ concerns the lateralisation of functional specialisation. Although most studies report bilateral recruitment in the TPJ, some find greater selectivity in the left [24] and others in the right [23]; future investigations of patients with RTPJ damage, or using temporary lesions created by transcranial magnetic stimulation TMS will be particularly informative [26^{*}].

Triadic attention and the medial prefrontal cortices

On the basis of the first functional imaging investigations, many authors speculated that the medial prefrontal cortex (MPFC) was the unique neural substrate of reasoning about representational mental states [27]. Recent research has dramatically changed this picture. No part of the MPFC is specifically recruited for reasoning about representational mental states; instead, subregions of MPFC are implicated in distinct components of social cognition. Ventral MPFC is implicated in emotional perspective taking and sympathy. Dorsal MPFC is implicated in representing shared or collaborative attention and goals; that is, triadic relations between Me, You, and This.

Medial prefrontal cortex: not for representational mental states

Converging results from both neuroimaging and lesion studies are now compelling: the MPFC is neither necessary for nor selectively recruited during reasoning about (the contents of) representational mental states.

First, reasoning about the contents of mental states does not selectively enhance MPFC engagement. Unlike the RTPJ, the response of MPFC is no higher when reading

stories that describe a character's true or false beliefs than when reading stories about the character's appearance, habits or bodily sensations [6,22,23]. Nor is the MPFC recruited during tasks that require taking (or imagining) the visual perspective of another person [24,28].

Second, medial prefrontal regions are recruited during tasks that manipulate the presence of a social or psychological agent or task, but do not require the attribution of any mental state content *per se*. For example, regions of the MPFC (unlike RTPJ) are recruited when subjects consider bare psychological adjectives, such as 'curious' or 'friendly', that apply to minds in general, rather than a specific propositional attitude [29,30,31*].

Finally, lesion studies provide converging evidence that MPFC is not necessary for reasoning about mental states. In one common task, patients are asked to organize the frames of a wordless cartoon into a sequence. For the 'intentional' cartoons, choosing the correct completion requires understanding mental state contents. Nevertheless, six patients with medial frontal lobe epilepsy [32] and one patient with a complete bilateral lesion of MPFC [33*] show no deficit on this task.

Ventral medial prefrontal cortex: emotional versus cognitive empathy

Although MPFC is not selectively involved in reasoning about mental state contents, subregions of MPFC do appear to support distinct components of human social cognition (Figure 1). One such component is emotional empathy; recent evidence points to a neural substrate of emotional empathy in ventral MPFC.

Studies of neuropsychological patients suggest a double dissociation between 'cognitive empathy' (that is, Theory of Mind) and 'emotional empathy' [34**] (that is, the cognitive and neural processes that produce a congruent emotion in the observer in response to others' directly perceived emotional displays or to descriptions of others' emotion-laden experiences). Blair [34**] argues that autism is characterised primarily by deficits of 'cognitive empathy', leaving emotional empathy relatively intact. Psychopathy and antisocial behaviour, by contrast, are related to diminished emotional empathy but not to impaired Theory of Mind. A similar dissociation is observed following pure autonomic failure [35].

Mounting evidence suggests that the distinct neural substrate of emotional empathy is a region in ventral MPFC. Two recent studies using functional magnetic resonance imaging (fMRI) explicitly compare cognitive and emotional empathy. Vollm *et al.* [36] compare reasoning about a protagonist's thoughts versus feelings in non-verbal cartoons; Hynes *et al.* [37] investigate a similar contrast using verbal stories. Both report selective activation in vMPFC [38].

Converging evidence comes from investigations of a wide range of patient populations. For example, lesions of ventral medial prefrontal cortex (vMPFC) are associated with abnormally low self-rating on an emotional empathy scale, but relatively normal self-rated cognitive empathy [39]. Degeneration of vMPFC in frontal-variant Frontotemporal Dementia produces a rapid and selective drop in empathetic concern, as rated by spouses and long-term carers [40*]. Conversely, high-resolution voxel-based morphometry in the brains of twenty one autistic children reveals normal vMPFC [21], which is consistent with the dissociation between impaired Theory of Mind and relatively intact emotional empathy in autism.

Dorsal medial prefrontal cortex: triadic attention and collaboration

The components of human social cognition considered so far are distinguished by the kind of internal state attributed to another person (e.g. goals versus thoughts versus emotions), but all of these attributions share a simple structure. In each case, the observer represents the two-place, or dyadic, mental relation between a person and an object or state of affairs (e.g. 'he is afraid of that bear', 'she knows that it is raining'). Much of the power of human social cognition, however, depends on our ability to form representations of mental states with a three-place, or triadic structure: You, Me and This. Drawing together the extensive comparative studies conducted in human children, ape and monkey species [3**], Tomasello *et al.* argue that the propensity for triadic relations — sharing attention to an object, collaborating on a shared goal — is a crucial unique component of human social cognition (see also [41]).

One intriguing possibility is that the neural substrate of understanding triadic social relations is in dorsal MPFC. This hypothesis brings coherence to a range of apparently disparate observations from tasks not explicitly manipulating triadic attention, but recruiting components of triadic attention. Similar regions of dMPFC are implicated in monitoring others' actions [11*,42], sensations [43] and personalities [44], in monitoring one's own social responses [45] and characteristics [29], and in judgments that combine both self and other [31*].

In two studies, a character established shared (dyadic) attention (i.e. You and Me, but no object identified) with the subject, either by turning to look directly at the subject as if in preparation for communication [46,47] or by calling the subject's first name [46]. Shared attention often forms the invitation to, or basis for, triadic attention. Both studies report selective recruitment of the same region of dMPFC.

Only one study to date has directly investigated the neural correlate of triadic attention involving the subject. Williams *et al.* [20*] report selective recruitment of dMPFC when the subject and a visible avatar (an

animated character resembling a person) both look together at the same moving object, relative to when the character's gaze and the subject's attention are incongruent. There is also convergent evidence from the neural representation of triadic attention that does not include the self. A region of dMPFC is recruited selectively when subjects reason about two cartoon characters engaged jointly in a collaborative, triadic action with each other, relative to cartoons depicting two characters separately pursuing private intentions [48*].

In addition, the proposed role of dMPFC in triadic attention sheds new light on the well-established finding of selective dMPFC recruitment when subjects play a simple game against a human versus against a computer opponent [49]. Subjects probably experience greater triadic engagement during the game when playing against a person, an opponent capable of sharing attention.

Conclusions

An explosion of new neuroscientific evidence suggests that distinct components of social cognition are associated with at least five brain regions, three in posterior temporal cortex and two in medial prefrontal cortex. Each of these components deserves further investigation, especially the proposed link between dMPFC and representation of triadic relations. In addition, space constraints have prevented the discussion of other implicated regions, including medial parietal cortex and the amygdala. Detailed investigations of each of these regions, informed by advances in social and comparative psychology, will be crucial in the ongoing investigation of the uniquely human 'social brain'.

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