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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.

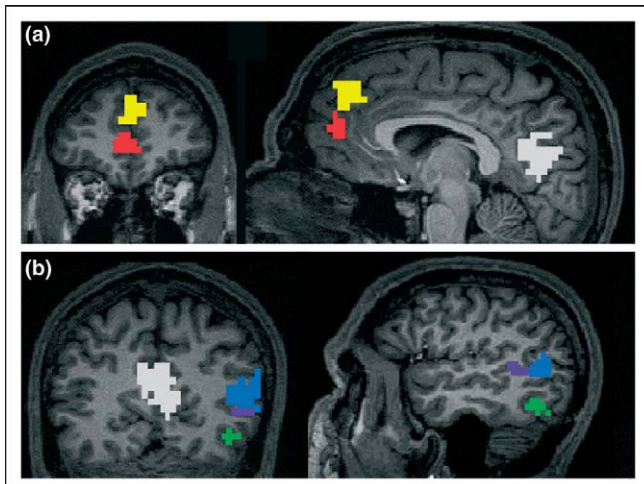
In the brains of healthy human adults, I suggest here that distinct brain regions are implicated in these two uniquely human aspects of social cognition: regions in the temporo-parietal junction (TPJ) and medial prefrontal cortices (MPFC), respectively (Figure 1).

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

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