

Neural correlates of the first-personperspective

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Human self-consciousness depends on the metarepresentation of mental and bodily states as one's own mental and bodily states. First-person-perspective taking is not sufficient, but necessary for human self-consciousness. To assign a first-person-perspective is to center one's own multimodal experiential space upon one's own body, thus operating in an egocentric reference frame. The brain regions involved in assigning first-personperspective comprise medial prefrontal, medial parietal and lateral temporoparietal cortex. These empirical findings complement recent neurobiologically oriented theories of self-consciousness which focus on the relation between the subject and his/her environment by supplying a neural basis for its key components.

Always a central theme in philosophy, human selfconsciousness has become an increasingly prominent issue in cognitive neuroscience [1]. Self-consciousness can be defined as the ability to become aware of one's own mental and bodily states (e.g. perceptions, attitudes, opinions, intentions to act) as one's own mental and bodily states.

Following a naturalistic view in contemporary philosophy of mind, according to which mental phenomena are based upon neural processes, awareness of one's own mental and bodily states may correlate with particular higher-order brain states, which can then be taken as the neural substrates of self-representation (given adequate operationalizations of such self-reference experiences). With respect to cognitive neuroscience, the question of the self can be reformulated as: which neural ensembles underlie (and may thus be responsible for) the 'subjective' nature of those mental and bodily states that are candidates for self-consciousness?

Representing and integrating such mental and bodily states into one common framework requires the ability to take a first-person-perspective (1PP). Here, the firstperson-perspective refers to the centeredness of one's own multimodal experiential space upon one's own body, thus operating in an egocentric reference frame. As such, 1PP can be considered as a basic constituent of a 'minimal self' which enables us to experience the subjective multimodal experiential space centered upon our own body. In language, the correct assignment of 1PP is reflected by the use of personal pronouns ('T, 'my') [1,2]. Furthermore, 1PP or 'perspectivalness' [3] is a key constituent in our relations with the environment, i.e. spatial cognition, action in space, social interaction and future planning.

Other key features which are constitutive for human self-consciousness comprise the experience of ownership (with respect to perceptions, judgements etc.) [4], agency (with respect to actions, thoughts etc.) [5,6] and the experience of unity forming a long term coherent whole of beliefs and attitudes [7]. The latter are embedded in a preexisting autobiographical context [8,9]. These experiences are necessary, but not necessarily sufficient for the constitution of self-consciousness, which is an integral part of consciousness as a whole.

First-person-perspective in space

1PP in the context of spatial cognition refers to the centeredness of the subjective multidimensional and multimodal experiential space upon one's own body. 1PP can be opposed to the third-person-perspective (3PP), in which mental states are ascribed to someone else. This phenomenal level needs to be distinguished from an underlying representational level, in which different reference frames representing the locations of entities in space can be differentiated (Box 1, Fig. 1).

Several studies have focused on the issue of perspective taking in space. Taking 1PP relies at least in part on temporoparietal processing as suggested by navigational tasks. Maguire *et al.* [10] demonstrated that a right inferior parietal region was activated whenever egocentric calculations were necessary in addition to the processing of allocentric spatial information (mediated via the hippocampus). 'Ego-movement' conditions also involved bilateral medial parietal cortex [10]. These findings have been corroborated by other studies which also showed that the key regions for spatial navigation comprise medial parietal and right inferior parietal cortex, posterior cingulate cortex and the hippocampus [11]. In addition, a simple spatial cognitive task recently performed in our group that was to be solved from either 1PP or 3PP revealed differentially increased neural activity during 1PP (as opposed to 3PP) in the left medial prefrontal and left medial parietal cortex (Box 2).

The relevance of the right parietal cortex for spatial cognition can also be derived from studies on patients with right parietal lesions leading to extinction or spatial neglect [12,13]. Neglect patients with right posterior cortical lesions were studied using a task in which the patients had to point to previously seen targets following a body rotation (in the absence of vision). Patients underestimated the angle of

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Box 1. Reference frames

A **reference frame** can be defined as 'a means of representing the locations of entities in space' [a].

In an **egocentric reference frame**, constituted by subject-to-object relations (best described in a polar coordinate system), locations are represented related to a personal agent and his physical configuration. Egocentric reference frames can be further subdifferentiated, as they may be defined with respect to the midline of the visual field, the head, the trunk, or the longitudinal axis of the limb involved in the execution of a certain action [b].

An **allocentric reference frame**, sometimes also referred to as 'exocentric' or 'geocentric', is constituted by object-to-object relations (best described in a Cartesian coordinate system). It refers to a framework that is independent from the agent's position [a,c].

Perspective taking: The cognitive operations when perceiving a visual scene from one's own perspective (1PP) differ from taking a view of the same scene from another person's viewpoint, although both tasks are centered on the body of the agent, however, the self or the other. To separate these two levels of descriptions clearly, the perspective-related terms 1PP and 3PP indicate the phenomenal level, whereas the terms egocentric and allocentric reference frames refer to the cognitive or neural level as conceptualized by the onlooking (scientific) observer. The difference between first- and third-person-perspective is that 3PP necessitates a translocation of the egocentric viewpoint.

Alternatively, viewer-, environment-, and object-centered frames of references were suggested, according to which spatial locations are coded with respect to the perceiving subject, its environment or the object, respectively [d].

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rotation which was interpreted as an impaired tracking of changes in egocentric spatial relationships [14]. Other clinical syndromes related to lesions of right posterior parietal cortex are deficits in representing the relative location of objects or other persons with respect to one's own body, also referred to as 'egocentric disorientation' [14,15].

At this point a distinction between perspective taking in space and movement in space is necessary that differentiates between a 'cognitive' representation of perceptions and a 'sensorimotor' representation responsible for visually guided behavior: a subject must not necessarily be aware of a visual information to take this information into account when making a movement [16]. For example, when presenting briefly a dot inside a centered compared to an off-centered frame in the visual field, test persons reported that the dot had moved to the right when the frame has been shifted, but when asked to point to the place where the dot had been, test persons pointed to the correct (i.e. unchanged) location (Roelofs effect [17]). The described phenomenon elicits that cognitive measures can be different from sensorimotor measures and thus

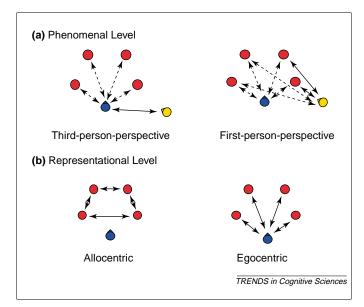


Fig. 1. Illustration of reference frames and first- and third-person-perspectives. (a) Although the cognitive operations differ phenomenally, when perceiving a visual scene from one's own perspective (1PP) or from another person's viewpoint (3PP), both tasks are centered on the body of the agent (self or other). To separate these two levels of descriptions clearly, the perspective-related terms 1PP and 3PP are used to indicate the phenomenal level, whereas the terms egocentric and allocentric reference frames refer to the cognitive or neural level as conceptualized by the onlooking scientific observer (b). The difference between first- and third-person-perspective is that 3PP necessitates a translocation of the egocentric viewpoint.

suggests that these two systems are implemented in at least two differential brain regions corresponding to at least two different representations of space [16].

First-person-perspective in action

Experiencing oneself as the agent of an action in the sense of agency contrasts with the experience of another person being the acting cause of a particular action. A systematic investigation on the shift of perspectives in a motor imagery task studied the neural correlates of taking a subjective perspective or the experimentator's perspective during the simulation of an action [18]. On the basis of visual or auditory stimuli, subjects were asked to imagine themselves manipulating an object or to imagine the experimenter manipulating the respective object, thus modeling 1PP and 3PP on a phenomenal level. During 1PP simulation of action, only regions in the left hemisphere were activated, including the inferior parietal lobe, precentral gyrus, superior frontal gyrus, occipito-temporal junction and anterior insula. During 3PP simulation of action, the right hemisphere was activated, namely the inferior parietal cortex, precuneus, posterior cingulate and frontopolar cortex. The left hemisphere dominance in 1PP simulation of action observed in this study contrasts with the right hemisphere dominance in 1PP perspective taking reported above. This discrepancy, however, is likely to reflect the left hemisphere preponderance for action [19] and the right hemisphere dominance for space [20], respectively. In a recently studied navigation task it was shown that attributing an action to someone else was associated with activity in the inferior parietal cortex bilaterally suggesting that hemispheric dominance critically depends on the actual context of the task at hand [21]. Interestingly, increased left temporoparietal activation was also reported in a task in which test persons had to 40

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Box 2. Perspective taking in space

A simple spatial cognitive task to be solved from different perspectives, namely first-person-perspective (1PP) and third-personperspective (3PP), was used in one of our own studies. We systematically varied 1PP and 3PP in a simple 3D-visuospatial task in which a virtual scene consisting of an avatar surrounded by red objects was presented (Fig. I). Subjects were asked to assess the number of red balls as seen from either their own (1PP) or the avatar's perspective (3PP). Both conditions are based on egocentric operations, as the objects have to be located in relation to an agent in both conditions, either the test person or the avatar. In case of 3PP, however, additional use of allocentric operations is necessary to generate egocentric coordinates for the agent. A fMRI study on 11 subjects demonstrated differentially increased neural activity during 1PP (as opposed to 3PP) in the left medial prefrontal cortex and the left medial parietal cortex. By contrast, 3PP was associated with differentially increased neural activity in the region of the superior parietal lobe bilaterally, predominantly on the right side, and right premotor cortex. Areas activated by both conditions comprised a network of occipital and parietal areas bilaterally, including the regions of inferior and superior parietal lobule and the parietooccipital sulcus bilaterally, the inferior frontal gyrus bilaterally, the left medial frontal gyrus, and the left precuneus. The data clearly demonstrate both common and differential brain activations for taking 1PP or 3PP, both operating in egocentric reference frames (Vogeley, K. et al., unpublished).

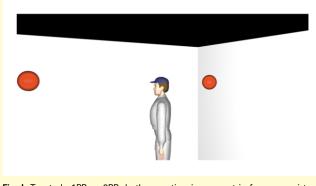


Fig. I. To study 1PP or 3PP, both operating in egocentric frames, a virtual scene with an avatar and red balls in a room was presented to normal volunteers (n = 11) in a functional magnetic resonance imaging (fMRI) experiment. The task for the subjects was to count the objects as seen either from one's own perspective (1PP) or the avatar's perspective (3PP). As not all objects are visible for the avatar, a clear distinction between both instructions can be made on a behavioral level.

make left-right-judgments either in relation to oneself or a human figure opposite to them [22]. Taken together, the data show that medial and lateral parietal cortical areas are involved in perspective taking in the context of intentions to act and performance of action.

Regarding the temporal domain of action, a predictive feed-forward model has been proposed, according to which sensory informations that result from self-generated actions are anticipated and stored in association with the motor plans of these self-generated actions. Efference copy signals and the anticipated sensory consequences of the motor act are then compared with each other [23,24], which determines the source of sensory events [4]. Whereas self-generated actions are usually correctly predictable, as anticipated sensory consequences and efference copy signals are congruent, externally generated actions are not associated with such efference copy signals and therefore cannot be compared and adequately detected as 'self-generated' actions. This suggests that the feed-forward model explains how we are able to reliably distinguish between one's own and others' intentions to act as a specific class of mental states.

First-person-perspective in social interaction

Closely related to the ability to assign and maintain a selfperspective is the meta-representational capacity to attribute opinions, perceptions or attitudes to others, often referred to as 'theory of mind' (ToM) or 'mindreading' [25,26]. This is an essential social skill which can be assessed in paradigms, in which mental states of another person are to be modeled. Several functional imaging studies have successfully delineated brain regions involved in 'reading other minds' [27-32]. These studies have repeatedly demonstrated increased neural activity associated with ToM conditions in the anterior cingulate cortex (for reviews, see [33-36]). We were able to replicate these findings and to demonstrate additional differential brain activation when the test persons themselves were involved as an agent in the particular story. The capacity for taking 1PP in such ToM contexts showed differential activation in the medial aspects of the superior parietal lobe and the right temporo-parietal junction [37]. Interestingly, the latter region is also critically involved in the detection of biological motion in general [38], especially in experiences of something moving that is approaching the own body [39]. However, the functional role of the region of the temporoparietal region is certainly not restricted to egocentric cognitive operations, as the right temporo-parietal junction is also activated in 'classical' theory of mind tasks that do not differentiate between firstand third-person-perspective [31,33,34].

The fact, that differential brain loci in different brain lobes are activated associated with the attribution of 1PP relative to 'mind-reading' of others, suggests that these components are implemented in different brain modules and thus constitute distinct psychological processes. Interestingly, 1PP specific activations were induced in this case by a language task, namely the use of personal pronouns of the first person singular, which may be taken as evidence that spatial as well as language-driven tasks all refer to the same mental construct that integrates data about the dynamic organization of one's own body and its relation to that of other bodies or physical objects [40].

First-person-perspective and body representation

Taking a first-person-perspective is a key component of human self-consciousness that also requires the ability to refer to our body schema representation in the brain. It has been hypothesized, that 1PP creates a literally spatial model of one's own body, upon which the experiential space is centered [40]. This conjecture is in good accordance with reports on increased neural activity of right inferior parietal cortex involving visuo-spatial attention not only in navigation tasks [10] but also the assessment of the subjective mid-sagittal plane [41,42]. Also concerned with the centeredness on one's own body-axis are studies operating in an egocentric reference frame (Box 2).

Another important source of information of bodily states is the reference to a gravitational vertical as upright orientation. There is evidence for the hypothesis that vestibular information is used by the posterior parietal cortex for the perception of self-motion [43]. In line with that evidence, a significant interaction of allocentric line bisection judgments and galvanic vestibular stimulation generating a distortion of the egocentric frame of reference was observed to be associated with increased neural activity in right inferior parietal cortex [44]. All these studies provide evidence for the crucial involvement of the predominantly right parietal cortex in the computation of egocentric reference frames.

The relevance of right parietal cortex for correct assignment of 1PP can also be inferred from neuropsychological studies of brain damaged patients who are unaware of or even deny some of the very deficits that impair their performance in every day life. This condition is called 'anosognosia' [45] and is commonly found in association with personal and peripersonal neglect [12,13].

From a conceptual point of view, Damasio worked out in his 'somatic marker hypothesis', that the representation of a body image probably involves activation of right parietal cortex and prefrontal cortex, especially in its ventromedial parts. The theoretical account behind these empirical data are that there is 'a simple linkage... between the disposition for a certain aspect of a situation..., and the disposition for the type of emotion that in past experience has been associated with the situation'. (Ref. [46], p. 1415). In other words, this suggests that 'emotional traces' of past experiences trigger our actual decisions based upon experiences similar to the actual experience. This linkage thus subserves the evaluation of actual situations on the basis of former emotional reactions to similar situations in the past. This effectively leads to a constrainment of the 'space of decision-making'.

Self and world

To understand how an individual successfully behaves in its environmental context, one needs a conceptualization of the 'self' in the context of its environment. This relation, constituted by the relation of the subject with the surrounding objects was conceptualized as the 'core self' by Damasio (Ref. [47], p. 16), who postulated that the core self is based on transient relations, which need re-instantiation from moment to moment, which in turn constantly refer to the 'proto self' representing bodily states. Medial cortical regions are hypothetically recruited if such a state of 'core self' is instantiated (Ref. [47], p. 169-172), a prediction which is in accord with medial cortical activation sites during the take of 1PP (Ref. [47], p. 106, p. 264) (Fig. 2). Alternatively, the activation of medial cortical sites could also reflect so-called 'competitive relational mind states' which have been suggested to underlie memorial components of contentful consciousness [48].

Empirical evidence for the recruitment of medial cortical activation sites during experiences of self-reference is provided by the concept of a so-called 'default mode of the brain' put forward recently [49,50] (see also Box 3). According to these authors, resting states correlate with a certain cortical activation pattern in the anterior and posterior cingulate and medial parietal cortex. The authors hypothesize that if a cognitive activity requires higher processing demands, neural activation is then 'shifted' towards the neuronal network recruited by the specific task; medial frontal and medial parietal regions then tend to decrease their activity [50]. Similarly, a posterior cingulate

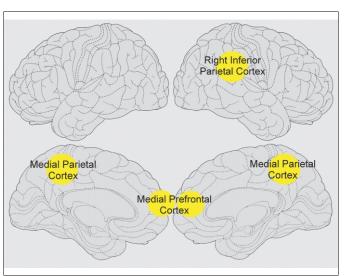


Fig. 2. Regions of activation during first-person-perspective tasks. Medial cortical regions, that comprise anterior medial prefrontal, medial parietal and posterior cingulate cortex, are hypothetically recruited if such a state of 'core self' is instantiated. The right inferior parietal cortex is the implementation site of the body representation, which most probably is involved in the computation of the egocentric reference frame.

activation during situations in which subjects were not engaged in a focused cognitive task was described [51]. This ongoing purely associative mentation would then be suspended when the subject becomes engaged in an experimental task requiring specific cognitive activities. In the same sense, it was argued that the precuneus supports the inspection of internal images [52]. However, thus far the attribution of states of self to this resting state remains speculative, as we don't have any behavioral or introspective data that provide evidence for the presence of such a 'state of self' (e.g. by asking subjects at random moments about any self-referential experience during such resting conditions).

Conclusions

In conclusion, building up relationships between oneself and objects in the outer world constitutes an important basis for the core self which is re-instantiated from moment to moment and which is the necessary component for the socalled autobiographical self, that integrates particular states of the core self over one's personal life history [47]. The specific subjective perspectivalness in the first-personaccount is realized by the integration of both the subject and the world model as the two main constituents of the internal

Box 3. Questions for future research

- Do spatial (e.g. navigational) and language-based (e.g. narrative) tasks refer to the same abstract body representation?
- How can we further elucidate both the subjective experience and the specific neural mechanisms underlying the default mode of the brain?
- To what extent is the body representation involved in the 'default mode of the brain', that is found in resting states?
- What is the nature of and what are the neural processes underlying anosognosia? What is its specific relation to brain damage in general and to neglect in particular?
- How does this model of first-person-perspective relate to psychopathological syndromes which can be reduced to a disturbance of self-other-discrimination and to the underlying pathophysiological disturbances of brain processes?

representation framework. It has been postulated that these basic properties are integrated in a so-called 'self model' as an episodically active complex neural activation pattern in the human brain, possibly based on an innate and 'hard-wired' model [53–56]. This self model could then plausibly serve as a continuous source of a specific kind of milieu information on the own body and organism, which is activated whenever conscious experiences including properties of ownership, perspectivity and unity occur. As such, 1PP is constitutive and a necessary pre-requisite for human self-consciousness. Evidence from functional imaging, neuropsychology and lesion data imply medial cortical structures (comprising anterior medial prefrontal, medial parietal and posterior cingulate cortex) and inferior lateral parietal cortex as the basic neural mechanisms involved in 1PP.

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