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Cortical midline structures and the self

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For a long time philosophers and psychologists have been intrigued by the question of the self. More recently, this has become a topic of discussion in neuroscience. In this article, we suggest that the processing of self-referential stimuli in cortical midline structures (CMS) is a fundamental component in generating a model of the self. Drawing from neuroimaging studies, we distinguish between representation, monitoring, evaluation and integration of self-referential stimuli. All of these subfunctions are related to distinct regions within the CMS. This relationship between self-referential processing and CMS might provide novel insight into the neural correlates underlying the constitution of the self.

Throughout the history of philosophy and psychology, the question of the self has been one of the most salient problems [1,2]. Recently, this problem has also been discussed in neuroscience [3–9], neurology, and psychiatry [2,10–13]. In particular, neuroimaging studies increasingly address tasks related to the self. A considerable number of PET and fMRI investigations comparing self-referential versus non-self-referential tasks have identified regions located in the midline of the human cerebral cortex (cortical midline structures, CMS; see Box 1). We believe that a fundamental component in generating a model of the self is the processing of self-referential stimuli in CMS (see Figure 1).

Self-referential stimuli are stimuli that are experienced as strongly related to one's own person. They have also been described as 'self-related' or 'self-relevant' [14,15]. Such self-referential stimuli were, for example, investigated by Kelley *et al.* [15] in a trait-adjective judgment task. In this study, participants were asked to judge trait adjectives (for example, 'polite') as to whether they properly described the participants themselves (self-referential), the current US President (other-referential), or a given case (case-referential). It should be noted that the self-relevance of a stimulus is not intrinsic to the stimulus, but rather determined by the individual and the personal context in which it is perceived.

Domains of the self and lateral cortical regions

Although this article focuses on the CMS, several previous studies have associated lateral cortical regions with specific processes related to the self (Figure 1). These processes seem to involve predominantly the right hemisphere [9], in particular the right prefrontal [11,13,16] and parietal cortex. The feeling of being causally involved in an action has been referred to as 'agency'. Agency is related to the right posterior insula and the right inferior parietal cortex [17], but also to CMS such as the anterior cingulate

Box 1. The anatomy of the CMS

The regions referred to as cortical midline structures (CMS) in this article include the orbital and adjacent medial prefrontal cortex (OMPFC), the anterior cingulate (AC; particularly the supragenual part, SAC), the dorsomedial prefrontal cortex (DMPFC) and the posterior cingulate cortex (PC) including the adjacent retrosplenium and precuneus (see Figure 2 in main text). The OMPFC includes the gyrus rectus and the medial half of the orbital gyri, as well as the ventral half of the medial prefrontal surface. The AC covers the anterior part of the cingulate gyrus, which arches around the genu and the body of the corpus callosum. Whereas the ventral section of the AC includes a subgenual and a pregenual part and is anatomically and functionally closely connected to the OMPFC, the dorsal section of the AC is separated from the DMPFC by the cingulate sulcus. The DMPFC covers the dorsal section of the prefrontal cortex, including the middle parts of the superior and medial frontal gyrus. It borders dorsally with the frontal eye field and ventrally with the OMPFC. Finally, the PC covers the posterior part of the cingulate gyrus, where it arches around the body and splenium of the corpus callosum. It borders on the retrosplenial cortex within the callosal sulcus and on the precuneus.

The CMS may be regarded as an anatomical unit for two reasons: (1) these regions maintain strong and reciprocal projections among each other; and (2) they show a similar pattern of connectivity to brain regions outside the CMS [41,60]. These connections include dense links to ventro- and dorsolateral prefrontal cortex, structures in the midbrain and brain stem subserving autonomic functions, and the limbic system, including hippocampus, amygdala and insula.

Lesion studies underline the role of CMS in the processing of self-referential stimuli. Damage to the OMPFC leads to an inability to develop a coherent model of one's own self, with subsequent emotional lability [5,13]. More dorsally located lesions (DMPFC) are associated with planning difficulties and disturbed social interactions, which might reflect inappropriate self-referential judgments. Patients with SAC lesions show deficits in the monitoring of mental states. Besides apathy, lack of initiative, and consecutive akinetic mutism, these patients show aberrant social behavior, which could result from an inability to monitor behavioral and mental states [38].

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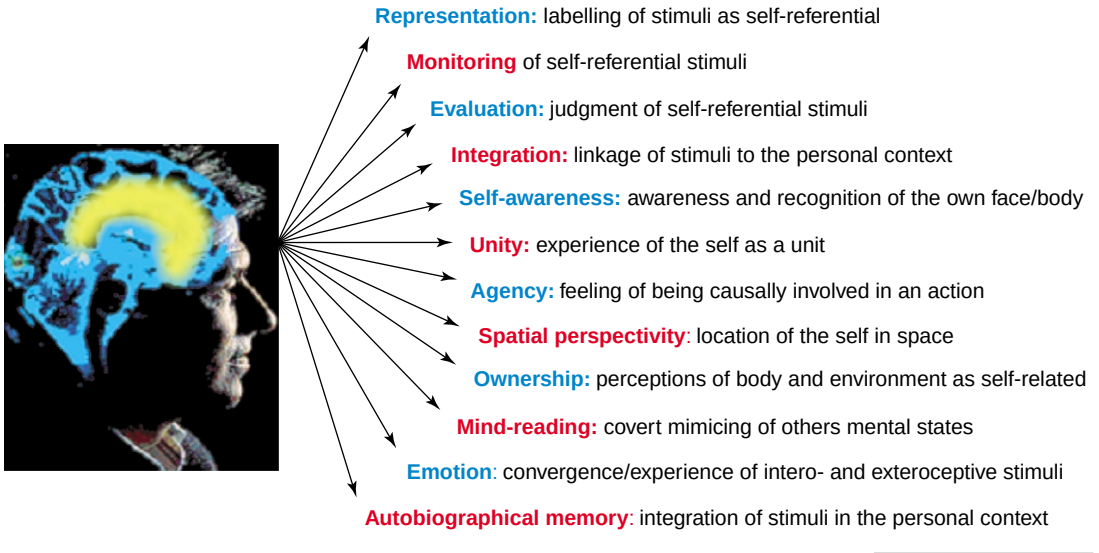

Figure 1. Domains of the self. Many processes associated with the self have been associated with cortical midline structures.

and the medial prefrontal cortex [18]. By contrast, the inferior parietal cortex, insula and somatosensory cortex in the left hemisphere were activated during the simulation of one's own actions [19].

Another process related to the self is called 'ownership'. This concerns the experience that one's own body and environment are perceived as personal and closely related to one's own self. Neural correlates of ownership of one's body, as reflected in the body image, are assumed to involve the right parietal cortex but also the ventromedial prefrontal cortex [5]. The right parietal cortex is also implicated in spatial perspectivity and location of the self in space [7]. Accordingly, lesions in the right parietal and right temporo-parietal cortex lead to spatial body disturbances like anosognosia (denial and unawareness of a paralyzed limb) [20] or asomatognosia (misidentification and denial of ownership of a limb) [21].

A final domain to be mentioned concerns the recognition of one's own face. The findings are controversial so far. Some studies emphasize the role of the right hemisphere, in particular the right ventrolateral prefrontal cortex [22,23], whereas other reports suggest predominance of the left hemisphere [24]. A few studies also observed involvement of both hemispheres (right insula; left prefrontal and superior temporal cortex) as well as CMS (anterior cingulate) [25,26].

Domains of the self and CMS

A remarkable variety of domains and cortical regions have been associated with the processing of the self. The constitution of the self might result from some kind of integration of these distinct domains. What is the thread linking the diverse processes related to the self? We argue that this is what Damasio [3,5] calls the 'core self'. Damasio relates the 'core self' to the continuous conjunction of intero- and exteroceptive stimuli leading to the experience of the self as a unit. Anatomically the 'core self' is associated with the orbitofrontal and ventromedial prefrontal cortex. We suggest that this concept might be analyzed in further detail. What is the 'core'? We believe that this is the processing of self-referential stimuli, and the cortical midline structures seem to be crucial for this.

As we will explicate in detail below, a considerable amount of data exist that suggest a role for the CMS in the processing of self-referential stimuli. Given these data, why have the CMS drawn relatively little attention so far? This might be because of psychophysiological features specific to the CMS. Physiologically, the CMS show a high level of neural activity in so-called resting states (for example, during the presentation of a fixation cross) [27,28]. During transient cognitive tasks (whether self-related or not) CMS are predominantly deactivated, whereas other brain regions (for example, lateral cortical areas) show activation. Consequently, signal changes in CMS tend to be passed over in favor of activations detected in lateral cortical regions. Psychologically, we suggest the continuous high neural activity is related to the ongoing processing of self-relevant stimuli which might correspond to the 'core self'. This ongoing process tends to be superseded and psychologically masked during transient cognitive tasks even if a task refers to the self. Thus, whereas transient self-related cognitive processes mainly involve lateral cortical regions, the continuous processing of self-referential stimuli seems to be related to the CMS.

Empirical findings: the processing of self-referential stimuli in the CMS

In the following, we review the current evidence in support of a link between CMS and the processing of self-referential stimuli. We distinguish between representation, monitoring, evaluation and integration of self-referential stimuli. We relate these psychological processes to specific regions within the CMS (Figure 2). Specifically, the orbitomedial prefrontal cortex (OMPFC) seems to account for the continuous representation of self-referential stimuli. Once represented in the OMPFC, self-referential stimuli appear to be monitored in the supragenual anterior cingulate cortex (SAC) and evaluated

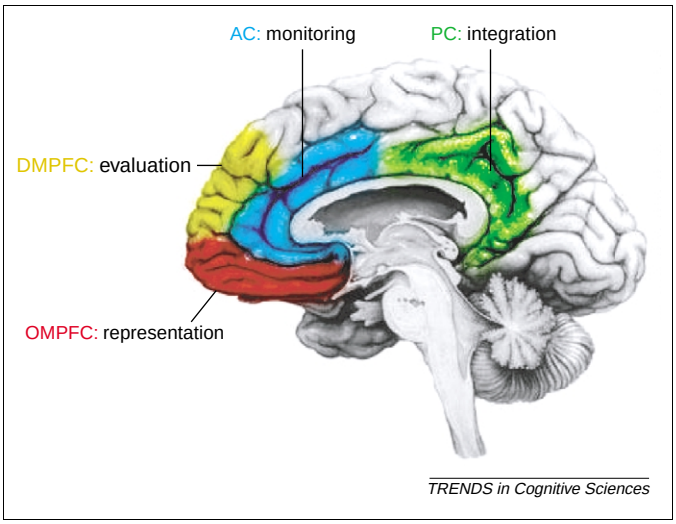

Figure 2. Processing of self-referential stimuli in the cortical midline structures (CMS). Orbitomedial prefrontal cortex (OMPFC; ventromedial part of BA10; medial parts of BA11 and 12), dorsolateral prefrontal cortex (DMPFC; medial part of BA9 and dorsomedial part of BA10), anterior cingulate cortex, particularly the supragenual region (AC; dorsal parts of BA24 and 32), posterior cingulate cortex (PC; BA23 and 31) including the adjacent retrosplenial cortex (BA29 and 30). The four subprocesses of self-referential processing associated with each region are shown.

in the dorsomedial prefrontal cortex (DMPFC). These functions might be complemented by the integration of these stimuli in the emotional and autobiographical context of one's own person. This latter function is related to the posterior cingulate cortex (PC).

Because the CMS are relatively old brain structures (in phylogenesis), which are not limited to humans, it seems reasonable to assume that animals also show self-referential processing in the CMS. Despite the principal problem of transferring animal data to humans, animal studies of medial prefrontal cortex seem to underline human imaging results. Lesions in the medial prefrontal cortex of the rat were shown to elicit impaired coding of egocentric versus allocentric spatial information [29] and reduced working memory performance for egocentric responses [30].

Orbitomedial prefrontal cortex and representation

The generation of a model of self-referential (as opposed to non-self-referential) stimuli in the brain is here referred to as representation. Neuroimaging studies implicate the OMPFC in the representation of self-referential stimuli. For example, Kelley *et al.* [15] used the above mentioned trait-adjective judgment task in an fMRI study. They demonstrated that the OMPFC (and the DMPFC; see below) was selectively engaged in the self-related condition. Similarly, a PET study that used a comparable paradigm [14] observed activation in the OMPFC and anterior cingulate, but also in the right ventrolateral prefrontal cortex. Using auditorily delivered statements, another investigation compared judgments about one's own abilities, traits and attitudes (such as '*I can be trusted*') with a semantic judgment task [31]. The self-referential condition was associated with activation in the OMPFC (as well as DMPFC and PC; see below) relative to the control condition. Similarly, Kjaer *et al.* [32] observed OMPFC activation when comparing reflection on one's own personality traits with reflection on those of a well-known individual (for example, the Queen of Denmark).

The OMPFC is also implicated in the processing of emotional stimuli. There are reasons to regard emotional stimuli as (implicitly) self-referential. First, they are crucial to the individual in that they guide decision-making and efficient behavioral responses [5,8,33,34]. Second, emotional stimuli are mentally significant for a person, as 'one cannot formulate and use adequate theories of one's own mind if something like the somatic markers fails' (Damasio [5], p. 219). We consider it plausible to assume that stimuli are processed on a self–non-self continuum. Emotional stimuli might be on the 'self' side of the central point, whereas, for example, stimuli presented in a semantic judgment task [31] might lie on the 'non-self' side.

The engagement of the OMPFC in emotional processing is independent of the sensory modality (for example, visual, gustatory, etc.), the method of induction (verbal vs. non-verbal; current events vs. recall of past events) and the accompanying task (emotional judgment, non-emotional judgment, or passive perception) [33,35,36]. It might thus be inferred that the OMPFC is associated with the general representation of emotional stimuli. The OMFPC might be viewed as a convergence zone that receives interoceptive (for example, temperature, proprioception) and exteroceptive (for example, auditory, visual) data [8,16]. This would allow for the representation of multimodal stimuli and for their labelling as self-referential. This function is also suggested by the involvement of the OMPFC in reward processing [33] where stimuli are represented with respect to one's own behavioral goals [37].

Supragenual anterior cingulate cortex and monitoring

The SAC has been associated with monitoring and control functions, such as response selection and inhibition, conflict monitoring, error detection and performance monitoring [38–41]. A variety of cognitive and emotional tasks revealed increased activity in the SAC to self-referential stimuli compared with non-self-referential stimuli [42]. Although different modalities were involved and different tasks used, all these studies had in common that subjects were required to attentively observe (i.e. monitor) self-referential as opposed to non-self-referential stimuli. Stimuli included auditory verbal feedback [43], short stories [44], sensory stimuli [45,46], actions (agency) [18], facial self-recognition [25] and emotional pictures [47]. A more complex self-monitoring task elicited SAC activation during error detection and during increased response competition [40]. We can conclude that the monitoring function of the SAC is associated with a preference for self-referential stimuli irrespective of the sensory modality or the task involved.

It has been suggested that the internal monitoring of one's own actions is disrupted in patients with schizophrenia [48]. This mechanism might potentially underlie positive symptoms in which putatively self-generated actions are attributed to an external agent. In accordance with this model, a recent fMRI study on schizophrenic

patients revealed impaired activation in the SAC during a performance monitoring task [48].

Dorsomedial prefrontal cortex and evaluation

The DMPFC is involved in the evaluation of self-referential stimuli. For example, subjects required to monitor and judge whether auditory verbal feedback was their own or another person's voice, showed activation in the DMPFC (and SAC; see above) [43]. In the above mentioned self-evaluation tasks, Kelley *et al.* [15] and Johnson *et al.* [31] found that the DMPFC (and OMPFC; see above) was selectively engaged in the self-related condition. Similarly, DMPFC activation was observed during evaluation of self-referential statements (for example, '*I like Leipzig*: yes/no') compared with memory retrieval trials [49]. In a recent study, subjects had to judge whether positive and negative personality trait adjectives described themselves properly [50]. As a control, subjects were asked if the adjectives described generally desirable traits. The DMPFC (and PC; see below) was specifically activated during the self-referential evaluation irrespective of the valence of the presented words.

The DMPFC is also involved in the judgment of emotional stimuli. Emotional judgment is associated with DMPFC activation compared with non-emotional judgment [35,47,51]. Particularly strong emotional engagement is apparently required for moral judgment, which might involve self-referential evaluation. Consistent with this notion, DMPFC activation was observed during moral judgment [52].

Similarly, theory-of-mind judgments produce activation in the DMPFC [18,42,53]. It might be speculated that this reflects self-referential evaluation, as the mental state of others seems to resonate with one's own mental state during mind reading. However, when investigating theory of mind and self-perspective in a two-way factorial design, Vogeley *et al.* [44] observed the interaction effect in the right prefrontal cortex. Besides these regions, mind-reading was found to involve the SAC, PC, superior temporal sulci, and temporal poles bilaterally [18,42,44,53,54].

Posterior cingulate cortex and integration

Neuroimaging studies suggest a role for the posterior cingulate cortex (PC) and the adjacent precuneus in integrating self-referential stimuli in the context of one's own person. This was investigated in a variety of tasks:

Self-reflection tasks [31] require the integration of self-referential stimuli in the context of personal attitudes, goals and traits. For example, activation in the PC and adjacent precuneus was observed when subjects had to indicate whether a word or statement was self-descriptive or not [26,31,50]. Similarly, reflection on one's own personality traits was associated with activation in the precuneus (and OMPFC) when compared with reflection on traits of the Danish Queen [32].

Autobiographical memory tasks involve the cued retrieval of self-referential data embedded in a rich context of personal information. They require the integration of self-referential cues (for example, familiar names) in the autobiographical context of a person. Accordingly, the retrieval of such memories leads to PC activation [53].

Finally, *emotional and moral judgment tasks* presuppose the integration of current self-referential stimuli (for example, an emotional picture or a moral dilemma) in the broader emotional or moral context of the person. Consequently, several emotional and moral evaluation studies [52,54] revealed activation in the PC (and DMPFC; see above).

Conceptual implications

Process specificity in the CMS

In the case of the lateral prefrontal regions, the concepts of domain specificity and process specificity have been discussed in the literature [55]. Process specificity suggests a functional organization regarding specific psychological processes (such as storage and manipulation of information in working memory) in different regions, independently of the processed contents. By contrast, domain specificity reflects functional organization with regard to the content (such as verbal and spatial domains in working memory) in different regions, independently of the required processes. What concept of functional organization applies to the CMS? The presented data favors a model of process specificity for the CMS because the subprocesses can be characterized as supramodal and thus domain-independent. Accordingly, different CMS are associated with specific self-referential subprocesses (representation, monitoring, evaluation and integration).

OMPFC as the cortical entrance door to consciousness

A close linkage between OMPFC and self has previously been proposed by Schore [16], who characterizes the OMPFC as the 'entrance door' to consciousness. He assumes that the convergence of intero- and exteroceptive stimuli in the OMPFC might not yet be conscious but rather preconscious. According to this view, subsequent processing in other regions is required for self-referential processing to become conscious. Because of its crucial involvement in working memory, a role here for the lateral prefrontal cortex has been suggested [8,12,56], and the right hemisphere seems to be predominantly implicated [13,16]. In additon to the lateral prefrontal regions, other subunits of the CMS (SAC, DMPFC and PC) might also contribute to the conscious awareness of self-referential stimuli and ultimately to self-consciousness.

The proposal of the OMPFC as the 'entrance door' to self-referential processing is in accordance with results from intracranial recording and EEG/MEG studies [57]. OMPFC activity was observed as early as 200 ms after the onset of emotional stimuli. By contrast, lateral prefrontal regions and more posteriorly located CMS showed delayed responses (300–800 ms). This could imply that self-referential stimuli have to be represented and labelled as self-referential (in the OMPFC) before they can be further processed in adjacent cortical regions [2]. One may subsequently predict that deficits in the OMPFC will interrupt early processing of self-referential stimuli.

CMS: physiological and psychological baseline

All of the CMS discussed here exhibit a high level of neural activity during so-called resting conditions such as a fixation task [27,28,51]. Together with the medial and

Box 2. Questions for future research

- How do the CMS interact with each other? What is the exact spatiotemporal pattern of neural activity within the CMS? Is there a direction of activity spread?
- Is there a hemispheric specialization within the CMS with regard to the processing of self-referential stimuli?
- What is the exact relation between preconsciousness, consciousness and neural processing in CMS?
- How are activation and deactivation modulated between lateral and medial prefrontal cortical regions? Is there a reciprocal pattern of activation?
- How are CMS functionally related to the right parietal cortex and temporo-parietal region?
- Is neural activity in CMS modulated by the amygdala? What is the functional relationship between CMS and subcortical regions (hypothalamus, periaquaeductal grey, locus coeruleus)?
- Is the neural processing in CMS disturbed in neuropsychiatric disorders involving self-referential processing (for example, major depressive disorder, post-traumatic stress disorder, phobia, anxiety disorder, catatonia)?

lateral parietal areas, they show the highest level of neural activity during the resting state. This high level of neural activity has been characterized as the 'physiological baseline' or 'default mode' of the brain [27,28].

Given this high baseline activity, it should come as no surprise that CMS are mainly modulated by deactivation. In the OMPFC, various non-self-referential cognitive tasks (reading and generation of nouns; coherence judgments) elicit large signal decreases [27,35,51,58]. By contrast, smaller signal decreases are seen during the processing of self-referential stimuli [15,35], which is occasionally interpreted as 'activation' in the self-referential condition relative to control tasks. Similarly to the OMPFC, non-self-referential stimuli induce prominent deactivation in other CMS (SAC, DMPFC, PC) [27,28]. Unlike the OMPFC, however, these regions demonstrate increases in activity during the processing of self-referential stimuli [47,51,59].

What is the psychological correlate of the 'physiological baseline'? Is there a 'psychological baseline'? One of the challenges for the future (see Box 2) will be to link empirically the 'physiological baseline' to our subjective experience. Psychologically, the continuous high level of neural activity has to be systematically related to ongoing processing of self-referential stimuli. Will this continuous baseline activity in CMS finally account for the 'core self' [3,5] and (in the phrase used by William James) the 'continuous stream of subjective experience'? Temporary suppression of self-referential processing might then correspond to deactivation in CMS. This might reflect the temporary eclipse of subjective experience during non-self-referential tasks, that is, tasks with strong cognitive and behavioral demands.

Conclusions

Continously ongoing processing of self-referential stimuli might be considered a fundamental component in the constitution of a permanent self. We suggest that the processing of self-referential stimuli can be characterized by four subprocesses – representation, monitoring, evaluation and integration. These processes can be related to distinct regions within the CMS. This leads to the understanding of the CMS as a functional unit. The OMPFC may be considered as the 'entrance door' to the CMS which, as a unit, is characterized by process specificity and high baseline activity. The latter has been described as 'physiological baseline' that could account for the continuous processing of self-referential stimuli reflecting a 'psychological baseline'.

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