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Minds at rest? Social cognition as the default mode of cognizing and its putative relationship to the “default system” of the brain

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ABSTRACT

The “default system” of the brain has been described as a set of regions which are ‘activated’ during rest and ‘deactivated’ during cognitively effortful tasks. To investigate the reliability of task-related deactivations, we performed a meta-analysis across 12 fMRI studies. Our results replicate previous findings by implicating medial frontal and parietal brain regions as part of the “default system”.

However, the cognitive correlates of these deactivations remain unclear. In light of the importance of social cognitive abilities for human beings and their propensity to engage in such activities, we relate our results to findings from neuroimaging studies of social cognition. This demonstrates a remarkable overlap between the brain regions typically involved in social cognitive processes and the “default system”.

We, henceforth, suggest that the physiological ‘baseline’ of the brain is intimately linked to a psychological ‘baseline’: human beings have a predisposition for social cognition as the default mode of cognizing which is implemented in the robust pattern of intrinsic brain activity known as the “default system”.

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1. The “default mode of brain function and its cognitive correlates

Functional neuroimaging studies have typically made use of ‘stimulation paradigms’ to assess task- or stimulus-dependent *increases* in brain activity. Here activations are defined by subtracting activity levels during a reference or control state from those related to a target or experimental condition. The resulting pattern of activations, i.e., increases of neural activity, is generally assumed to reflect the neural correlates of the cognitive processes of interest. Reversely, the subtraction of a task from a control state reveals brain areas in which neural activity *decreases* during the performance of an experimental task, i.e., so-called ‘deactivations’ (Raichle, 1998). Interestingly, such activity *decreases* were observed even in situations when the control state was visual fixation or eye closure, i.e., during so-called ‘resting states’ or states of unconstrained cognition (Shulman et al., 1997). Further investigations confirmed this finding of a network of brain areas (including medial frontal, parietal and temporal areas) whose activity *decreases* during goal-directed tasks (Binder et al., 1999; Fransson, 2006; Gould, Brown, Owen, Bullmore, & Howard, 2006; Greicius, Krasnow, Reiss, & Menon, 2003; Gusnard, Akbudak, Shulman, & Raichle, 2001; Gusnard & Raichle, 2001; Mason et al., 2007; Mazoyer et al., 2001; McKiernan, Kaufman, Kucera-Thompson, & Binder, 2003). To rule out that the observed signal decreases might be activations in a strict sense, present in the absence of a task, PET studies were undertaken and demonstrated that from a physiological perspective these areas could not be distinguished

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from other areas. Raichle and colleagues (2001), therefore, concluded that the task-specific regional decreases represented sustained as opposed to transiently activated “default functions” attenuated only in those instants when neural resources have to be temporarily re-allocated to meet the demands of an experimental task. The constellation of brain areas showing higher intrinsic activity during ‘resting states’ and decreases of activity when task performance requires increases of activity in other regions has come to be known as the “default system” (DS) of the brain (Raichle & Snyder, 2007; Raichle et al., 2001).

Apart from describing a more or less circumscribed network of brain areas showing these characteristics, it has also been emphasized that *all* brain areas have a high level of organized default functional activity (Hunter et al., 2006; Raichle & Snyder, 2007). The idea of “default functions” thereby supports the view that the brain’s function is not only reflexive, i.e., occurring in response to external stimulation, but also intrinsic, i.e., relying upon spontaneous, endogenous operations that might subserve the maintenance of, response to, and prediction of information (Bar, 2007). Concordingly, it has been pointed out that the differential neural activity that corresponds to external stimulation is relatively small in comparison to the activity which the brain continuously expends at rest (Raichle, 2006; Raichle & Mintun, 2006). As a consequence, there is now an increasing interest in the investigation of *decreases* in brain activity during task-performance, the neural correlates of ‘resting states’ or states of unconstrained cognition and possible interactions.

The wealth of studies providing evidence for the existence of a DS of the brain stands in contrast to the dearth of concepts regarding its cognitive and behavioural correlates. It has been suggested that decreases in brain activity during a task might be related to the re-allocation of resources to those brain areas which are differentially activated by task performance while internal and/or semantic processing that occurs during ‘resting states’ is suspended (Binder et al., 1999; McKiernan, D’Angelo, Kaufman, & Binder, 2006; McKiernan et al., 2003). Others have described the DS as contributing to the “continuous simulation of behavior” (Ingvar, 1985), “an inner rehearsal as well as an optimization of cognitive and behavioral serial programs for the individual’s future” (Gusnard et al., 2001), “inner speech” (Greicius, Srivastava, Reiss, & Menon, 2004; Mazoyer et al., 2001), “facilitation of responses to stimuli”, “maintenance of information for interpreting, responding to, and even predicting environmental demands” (Gusnard, 2005) or “chronic self-evaluation” (Beer, 2007). Similarly, it has been suggested that the DS might be involved in modulating attention, reviewing past knowledge and planning of future behavior (Cavanna & Trimble, 2006; Weissman, Roberts, Visscher, & Woldorff, 2006). While activity decreases in the DS during cognitively effortful, stimulus-dependent processing, “stimulus-independent thoughts” (SIT) that may be experienced as ‘mind-wandering’ or ‘day-dreaming’ have actually been shown to lead to a differential increase of activity in the DS (Mason et al., 2007). This led to the suggestion that people may have a proclivity to let their minds wander to which they ‘automatically’ return when not forced to attend to external stimulation according to instructions of an experimenter.

Taken together the nature of the cognitive correlates of the DS of the brain remains elusive. Answers to this important question need to account for the fact that the human brain not only serves to process external sensory information acutely, but also to address ‘problems’—possibly over a longer time scale—that are, at least in part, independent of external sensory stimulation (Raichle & Snyder, 2007). Indeed, “internally oriented” processes have been suggested to be of particular importance for human cognition and evolution (Binder et al., 1999). Psychological research not only suggests that internalized activity comprises a large part of the information-processing capacities of humans during daily life, but that deprivation of external sensory input or the increasing predictability of such events may result in an increase of internally generated activity (Antrobus, 1968; Filler & Giambra, 1973; Singer, 1993; Teasdale et al., 1995). We here pursue the idea that the physiological ‘baseline’ of the DS of the brain may correspond to a psychological ‘baseline’ of internally oriented cognition. What do we mean, however, when we say that cognition is internally oriented as opposed to externally driven? What might the contents of such an internal orientation be?

2. Self-consciousness and its social dimension

We suppose that a continuum exists between full ‘immersion’ in the stimulus-dependent performance of a given task on the one hand and stimulus-independent or unconstrained cognition on the other. During the former our cognitive resources could be thought of as bound by perceiving, adequately representing and responding to external stimulation to such a degree that we are completely immersed in this activity. During the latter, a relative lack of external stimulation may drive us to refer to endogenous sources of information or internally generated representations. This dichotomy has been described in terms of “perceptual”, i.e., *externally* driven, versus “conceptual”, i.e., *internally* driven processing (Binder et al., 1999). Yet another suggestion—which might be particularly valuable in conceptually connecting internal processing and the use of external sensory information—makes reference to the idea of “Bayesian inferences” which allow us to generate internal representations or models of the world whose predictions are then compared to the available empirical evidence (Kilner, Friston, & Frith, 2007).

With regard to a more integrative description of internally oriented cognition, the notion of ‘being a self’ or having self-consciousness can be useful (Gusnard, 2005). Self-consciousness has been defined as the implicit and explicit awareness of one’s own mental or bodily states, whereas the ability to explicitly meta-represent one’s mental or bodily states as one’s own refers to a special case of self-consciousness (Newen & Vogeley, 2003; Vogeley & Fink, 2003; Vogeley & Newen, *in press*). Providing integrated internal representations of the outside world and of our organism can be regarded as the central function of human self-consciousness offering important advantages for survival such as planning, decision-making and behavioral control in response to external demands (Vogeley, Kurthen, Falkai, & Maier, 1999). But also in the absence of external

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