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THE DEFAULT MODE NETWORK AND THE PROBLEM OF DETERMINING INTRINSIC MENTAL CONTENTS

Abstract. We provide a brief overview of the shift toward the intrinsic view of brain activity, describing in particular the structural and functional connectivity patterns of the “Default mode network” (part I). We then consider the Default mode network in a specifically cognitive setting and ask what changes the focus on the Default mode network and other sorts of intrinsic activity require from models put forward by cognitive neuroscientists (part II).

Keywords: default mode network, intrinsic mental contents, resting state networks, cognitive neuroscience, reactive paradigm in neuroscience.

Introduction

At the end of the 20th century, our knowledge of brain structure and function underwent several crucial revisions on a number of fronts. First, there was the well-known discovery of so-called mirror neurons by Giacomo Rizzolatti’s team, demonstrating that specialized neurons are active in the same way when a person (or a primate) performs a certain action and when she observes another person performing a similar action (see, e.g., Rizzolatti & Craighero, 2004). Another turning point was an existence proof of new neurons in the adult human brain. This discovery, made by Peter Eriksson (Eriksson, Perfilieva, Björk-Eriksson, Alborn, Nordborg, Peterson & Gage, 1998), was a final straw to break the back of a long-standing dogma of no new neurons in the adult mammalian brain. Perhaps most important was the discovery of ongoing intrinsic activity of certain brain areas, first presented by Marcus Raichle’s team under the label of “the default mode network” (DMN; Raichle et al. 2001). This discovery dislodged some well-established beliefs about the nature of brain activity, especially the belief that the brain is just variously responding to the demands of external or bodily environment and that all important states of neural activity are

evoked by such prompting. Raichle and colleagues' research showed that the neuroscientific community had studied the brain only from one side – the side of active stimulation.

As recently documented in an excellent paper by William Bechtel (2013), the shift towards viewing endogenous brain activity as something real and important was surprisingly long in the making.¹ It was already hinted at in the work of the physiologist Thomas Graham Brown, who rebelled against Sherrington's view of brain activity as a set of externally induced reflexes (Burke, 2007; Brown, 1911, 1914; Llinás, 2002, pp. 6f.). It was present in the electroencephalography (EEG) explorations of ongoing electrical activity of the brain (Raichle, 2010). But only with the advent of the DMN idea has the shift really happened. What was previously disregarded or filtered out as mere "noise", disrupting the signals detected in cognitive activations, is now considered to be an important part of the overall picture. Neuroscientists are now busy scrutinizing the ongoing neuronal activity in the brain along with the activity evoked by various cognitive tasks.²

Given this paradigm-like nature of the DMN, it is somewhat surprising that virtually no attention to the phenomenon has been paid by the philosophers of neuroscience. In fact, the only philosophical study explicitly dealing with the DMN and its implications for cognitive architecture that we have been able to find was Bechtel's aforementioned 2013 paper. We will, hence, try to motivate a more intense study of the phenomenon of intrinsic activity from our fellow philosophers. More specifically, we will, first, outline the development of the DMN idea and specify some of the technical details of the functioning of the DMN, especially its structural and functional connectivity patterns (part I). We will then consider the DMN in a specifically cognitive setting and ask what changes the focus on the DMN and other sorts of intrinsic activity requires from models put forward by cognitive neuroscientists (part II).

I. DMN and its *modus operandi*

The reflexive (or reactive, as we will put it) view of brain function played a central role in neuroscience for almost a hundred years. It was well suited for the purposes of the inquiry into the functional specialization of various cerebral regions (for which see, e.g., Finger, 1994). The reactive paradigm enabled experimenters to discover which brain regions are activated when the subject is stimulated in a specific way. This paradigm undoubtedly stands behind many important discoveries and yet, in recent years, it has increas-

ingly come to be viewed as an incomplete tool for discovering brain structure and function. This fascinating history is an object lesson in how the leading paradigm, in the Kuhnian sense, blocks out a potentially valid source of data as utterly irrelevant.

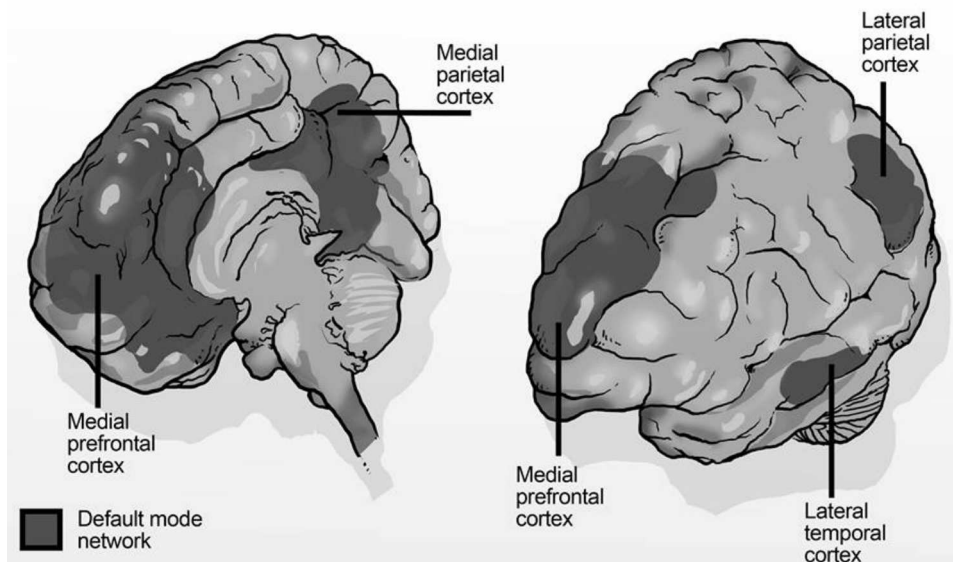
Interestingly enough, Sherrington, a towering figure of the reactive paradigm, was emphasizing that no part of the brain is ever “absolutely at rest” and that the idea of a simple neuronal reflex, neatly isolated from activity in other cerebral regions, is “a convenient ... fiction” (Sherrington, 1906, p. 8). And yet the reactive approach is clearly driving his conception: the ever present and systematically correlated neuronal activity is just a complex set of ongoing reverberations of externally induced responses throughout the brain. The idea that the brain is intrinsically active had to wait until the accidental discovery of fluctuations in activity in certain brain regions – a discovery that, according to some, caused nothing short of a paradigm shift (Raichle, 2009).³

When analyzing data from various fMRI scans, Raichle’s team noticed something strange. A pattern of unexpected, quantitatively identical *decreases* of activity was present in a couple of brain regions when the scanned subject switched from resting state to some cognitive task which required active attention. Such observation sat oddly with the reactive paradigm. If all that goes on in the brain is just a spreading reaction to the stimulus, no systematic activity decrease during performance of a cognitive task is to be expected. Raichle thus came to suspect that the supposed “noise” in the data is actually not noise at all but real neuronal processing with an unknown function – later he, tongue in cheek, dubbed this processing the “brain’s dark energy” (Raichle, 2010). This suspicion formed a background for the formulation of the first explicit hypotheses concerning intrinsic, spontaneous, non-evoked brain activity in a cerebral network which is functionally opposed (“anti-correlated” is the technical term) to other networks implicated in active cognition. Meanwhile, the aforementioned belief that the fluctuating activity patterns are just meaningless noise, attributable primarily to the imperfections of brain imaging technology, was pretty much dislodged. It turned out that there is a systematic coupling of the data obtained from the measurements made with fMRI and with EEG equipment. These independent measurements of the same intrinsic activity were then further buttressed by a similar coupling of data obtained from experiments with monkeys in resting states (i.e., states free from any attention-demanding task). The electrical activity in their visual cortexes was measured with implanted probes while the metabolic changes in their brains were simultaneously tracked in the fMRI scanners.⁴

DMN activity is at its peak when the subjects are instructed simply to rest – to lie down in the scanner and to think of nothing in particular with eyes closed (a similar result can be obtained with visual fixation of a simple target). This intrinsic activity of the DMN is significantly reduced when the subject turns to various cognitive tasks that require attention, and it rises again after the task is completed. Raichle thus concluded that the neural activity of the DMN during rest could be taken to constitute a physiological baseline of brain activity (Raichle et al., 2001; Gusnard & Raichle, 2001). The deactivations in the DMN are then interpreted as deactivations from this baseline. Raichle and colleagues wondered whether the deactivations in the DMN could not actually be interpreted as returns to a baseline level from some unsuspected neuronal activity. However, by carefully comparing the results of numerous scans, they excluded this possibility (Raichle et al., 2001, p. 681).⁵ Surprisingly, activation of the brain areas and networks involved in active responses to stimuli takes up only a tiny fraction (less than 5 percent; Raichle & Mintun, 2006) of overall brain energy consumption, which is huge (about 20 percent of the whole body energy budget). This finding further strengthened the attractiveness of cerebral intrinsic activity as a research programme.

Raichle stresses that while the DMN became an emblem of the intrinsic activity paradigm in contemporary neuroscience, “all parts of the brain exhibit a default mode of functioning that largely reflects their ongoing intrinsic activity” (Raichle & Snyder, 2007, p. 1088). Indeed, research in the first decade of the 2000s identified about a dozen other “resting state networks” (RSN) such as auditory, visual, salience, motor planning, or episodic memory networks (see Sporns, 2011, p. 161; van den Heuvel et al., 2009). Their number will quite probably grow in the future, with “connectomics” quickly becoming one of the prominent foci of contemporary neuroscientific research. For practical reasons, though, we will focus almost exclusively on the DMN in this paper.

The DMN is the largest resting state network, spanning prefrontal to parietal and temporal areas along the brain midline.⁶ Other RSNs are smaller and local, and are associated with specific activities such as processing of auditory information in the auditory RSN. The DMN displays remarkable stability both across a single individual at different times and across groups of subjects and during a variety of cognitive tasks. It is composed primarily of the medial prefrontal cortex (mPFC), ventral medial prefrontal cortex (vmPFC), medial temporal lobes, posterior cingulate cortex (pCC), posterior inferior parietal lobule (pIPL), and hippocampal formation (HF) (see, e.g., Buckner, 2008).⁷ As revealed in studies using



Diffusion Tensor Imaging (DTI) technology (tracking the direction of diffusion of water molecules in brain tissue), these parts of the DMN are anatomically connected via white matter axon tracts. This structural connectivity enables their *functional* connectivity, i.e., synchronized coactivity (Greicius et al., 2003; van den Heuvel, 2009).⁸ The term “network” is thus not a mere metaphor: there is a physical connection between the various parts of the DMN.⁹

II. DMN in cognitive contexts

II.1. Mutual influence of the DMN and task-oriented networks

As Raichle and Snyder put it in their review article, “task-related responses in any part of the nervous system should ultimately be understood in relation to local intrinsic activity” (2007, Appendix A, p. 1088). A burgeoning research programme fitting this description already exists.

A fruitful approach within this programme is to focus on variations of results between different trials with identical stimulus. This method enables us to precisely trace the patterns of interaction between intrinsic and evoked brain activity. This approach reveals a substantive and non-random contribution of intrinsic activity to cognitive operations, i.e., its modulation. Depending on the nature of pre-task activity in the DMN and its fluctua-

tions, neural signals in some task-positive areas, and even some behavioral effects – success or failure in a task, e.g. – can be predicted. Anticevic et al. (2012, p. 585) claim that lower pre-task activity in the DMN is typically associated with more successful performance across a number of cognitive tasks, and vice versa. The 2007 study by a Belgian team of researchers led by Mélanie Boly supports this theory. The team studied in particular the impact of the DMN activity on detection of somatosensory stimuli and the level of felt painfulness. The subjects were stimulated with a non-invasive laser on the dorsum of their left hand. The stimuli were graded according to intensity, on a scale of discrete levels ranging from 0 (unperceived) to 5 (distinctly perceived and quite painful). The published findings confirm a dynamic anti-correlation pattern between lateral, externally oriented brain networks and medial, DMN regions. The neuroscientists measured the level of activity three seconds before the onset of laser stimulation. They concluded that the higher the activity in the DMN before the stimulation, the lower the success in the assigned task (that is, in plain terms, the stimulus is likely to go unnoticed). And vice versa, decreased activity in the DMN before stimulation facilitates perception of somatosensory stimulus.¹⁰

This was an example of how a prior activity in the DMN influences subsequent cognitive processing. Other researchers focus on a reversed scenario, that is, on how intrinsic brain activity is influenced by a performed task. Northoff et al. (2010, p. 280) describe an experiment in which the subject was presented with a “working memory task” (the subject was asked to determine whether a stimulus matched another one previously perceived). An impact of the task on the activity within the DMN was found, indicating the presence of “stimulus-rest” interaction. In this case, the increased post-task activity in the DMN is presumably due to consolidation of the learned information in memory. Yet another approach is to try to disentangle intrinsic and evoked activity *during the very task*. Raichle and Snyder (2007, Appendix A, 1089) envisage a future in which experimental strategies develop to such an extent that “distinctions between intrinsic and evoked [activity] during task performance may ... become increasingly feasible in the context of functional neuroimaging”.¹¹

What do these intriguing results tell us about the standard working methods of cognitive neuroscience? Do they put pressure on scientists to change their approach in dramatic ways? This does not seem to be the case. The results obtained within the older, reactive paradigm of cognitive neuroscience remain valid and will, doubtlessly, bear more fruit in the future. The new intrinsic paradigm is, hence, not completely revolutionary. The

challenge is rather to expand the field of focus and to take intrinsic activity into account, both in experimental designs and in theories of cognitive architecture. Also, a reversal of research priorities is increasingly becoming a real possibility. Raichle has taken a lead in stressing that intrinsic activity, in the DMN and elsewhere in the brain, is not just a curious pendant of task-evoked activity, but is actually an essential and dominant aspect of brain function. And Raichle is not alone: for example, members of the Boly team boldly state that “baseline brain-activity fluctuations may profoundly modify our conscious perception of the external world” (2007, p. 12187). Thus, there seems to be no future in the supposition that intrinsic brain activity is of marginal interest only.

II.2. The proper functions of the DMN and the methodological challenges of its study

The discovery of intrinsic brain activity in the DMN has inevitably raised a question: what is the function (or functions) of this large neural network? One answer to this question suggests itself naturally. Subjects scanned in the “resting state” are largely free from exogenous influences and the need to respond to them. But, of course, their stream of consciousness is typically far from empty. It is thus tempting to use introspection as a clue as to what the brain is so busy at processing. Unfortunately, this way of uncovering the functions of the DMN was dampered by the discovery that intrinsic activity in the DMN is traceable even in unconscious states of human or animal subjects, such as in the initial phases of sleep or anesthesia (see Raichle, 2010, p. 183, for references).¹² It would thus be a mistake to conclude that the DMN is devoted solely to a conscious processing of thoughts, memories, and images, accessible via introspection. Raichle hints at a “more fundamental ... property of brain functional organisation” than the conscious one. But what is it? Could it all be just “maintenance” work, oiling of the cerebral wheelwork (such as facilitation of responses to stimuli by sculpting neuronal communication pathways, perhaps by continuously balancing between excitatory and inhibitory action)? This is very probably part of the truth. But still, many researchers believe that intrinsic activity in the DMN has a cognitive dimension, too. Numerous recent studies claim to have identified one or more cognitive functions of the DMN, such as self-referential thinking (Gusnard & Raichle, 2001; Molnar-Szakacs & Arzy, 2009), “mind-wandering” (Mason et al., 2007), recollecting one’s past, imagining and predicting future events (Greicius & Menon, 2004; Addis et al., 2007; Raichle, 2010), “theory of mind” (Spreng et al., 2009; Mars et al., 2012), and other cognitive ac-

tivities. None of these hypotheses, though, is a safe bet yet, for identifying the actual content of spontaneous intrinsic activity is far from trivial. With exogenous stimulation, the situation is different. There we have a clearly identified stimulus and correlated neuronal activity, traceable with standard methods of cognitive neuroscience. In the case of the DMN, there is no public stimulus, only the neuronal activity; the objective correlation between the two components is missing. That is why the critics of intrinsic activity research programmes fear that pending the standard task manipulation designs, “the resting activity would [be] treated as a single, broadly defined state and would, consequently, [be] inexplicable” (Morcom & Fletcher, 2007b, p. 1097).

Now, we believe that the discovery of the DMN and ongoing intrinsic activity is an important neuroscientific breakthrough. On the other hand, it has brought in its wake some serious methodological problems. These problems concern mental contents – let us call them intrinsic mental contents (IMC) – that are allegedly produced within the DMN.

The contemporary philosophy of neuroscience is dominated by the mechanistic approach (see Craver & Kaplan, 2011). This approach aims to identify which mechanisms are responsible for producing a particular phenomenon observable in the behaviour of a complex system. The crucial step is to identify the “locus of control”, that is, a system (or part of a system) that we take to be responsible for producing the phenomenon (Bechtel & Richardson, 2010, p. 39). The DMN is being taken to be the locus of control for, e.g., self-referential thoughts. Mechanistic explanation emphasizes the strategies of *decomposition* and *localization*. Decomposition is hierarchical; it divides the system into its parts, and these are subsequently also decomposed for the purpose of understanding the mechanisms involved. The decomposition is complemented by localization of the specific functions of the decomposed parts of the system. When localization is the goal, the scientists use two experimental methods that both involve manipulating the system. The first one is *inhibition*. This method looks on the observable behavior of a system when some specific part of it is missing or inhibited. The difference between the behavior of a normal and deficient/inhibited system gives us some idea about the function of missing or inhibited areas and paves the way for first localization hypotheses. The second, complementary method is based on *excitation* and activation experiments. By stimulating the brain, we can, with the help of various neuroimaging tools, observe which parts of the brain are activated. Bechtel and Richardson stress that decomposition and localization are not without problems, but still they remain the basic strategies of research into complex systems.

Unfortunately, in the case of the DMN, we cannot use these experimental methods. We can decompose the DMN into its anatomical nodes (such as mPFC, vmPFC, pCC, etc.). But what then? When we activate the neural structures of a resting subject we are no longer testing intrinsic activity but evoked activity. Inhibition of DMN activity, on the other hand, leads to sleep or a disrupted level of consciousness (Vanhaudenhuyse et al., 2010), and thus to the disappearance of the mental phenomena of interest. Couldn't we determine the functions of the DMN by looking at the typical tasks the various parts of the network are usually devoted to according to cognitive neuroscience? Well, no, we couldn't. Functions of the nodes of the DMN cannot be identified with functions present when its regions are coactivated by stimulation and cognitive tasks. Many studies by cognitive neuroscientists (for example Addis et al., 2007; Saxe & Kanwisher, 2003; Greene et al., 2001, etc.), cited by authors working on the DMN, are based on stimulation and evoked activity, but this is a methodological flaw. Intrinsic activity is anti-correlated to evoked activity; hence, assuming that a neural region has the same function in evoked and intrinsic activity is misguided.¹³ Any direct gauging of IMC by traditional methods of cognitive neuroscience is thus precluded.¹⁴

II.3. New method for scientific testing of intrinsic activity needed

Due to this lack of reliable testing methods, the theories concerning the functions of the DMN and other intrinsically active networks and brain parts are to a large extent sheer guesswork. New methods capable of identifying IMC without direct excitation or inhibition need to be developed. In the remainder of this paper, we discuss one attempt along these lines which was presented in a recent paper by Demis Hassabis and his collaborators.

Hassabis et al. (2013) were working with subjects trained in a specific way. During pre-scan training the participants learned the personalities of four imaginary people. Every such personality was associated with twelve statements characterizing him or her. Six of these statements were related to agreeableness,¹⁵ another six to extraversion.¹⁶ In the next phase, participants were asked to vividly imagine twelve common everyday locations – for example a bank, a bar, a school, etc. (They were instructed to mentally construct novel locations, not to draw on their memories of real places.) During fMRI scanning sessions, participants were presented with short text cues containing information about one of the four personalities involved in some course of action in one of the preimagined locations;¹⁷ they were asked to mentally play out the event, focusing on the actions, feelings, and thoughts of the imaginary protagonist for a period of ten seconds. In a variant of the

experiment, participants were asked to imagine either themselves instead of any of the four protagonists, or an empty location.

The mental simulations were all associated with increased Blood Oxygen Level Dependent signal in regions that make up the DMN. Differences in measurement between the three scenarios – (i) one of the four protagonists, (ii) the subject herself, (iii) the empty scene – led to two further questions: (A) Where in the brain is the personality information represented? and (B) Where is the information concerning the identity of a person represented?¹⁸ The answer to the first question is that simulations of personalities with high and low agreeableness can be clearly distinguished through observation of the dorsal mPFC and left Lateral Temporal Cortex and personalities with high and low extraversion can be distinguished by observing the pCC. The answer to the second question is that the identity of the four persons can be uniquely determined by looking at the activity in the anterior and dorsal mPFC. “In other words, based on brain activation patterns alone, we were able to infer which of the 4 protagonists the participants were imagining.”¹⁹

The study by Hassabis and colleagues not only demonstrated where the brain represents and stores models of personalities and what sub-regions of the DMN are engaged in these matters, but also opened the possibility of scrutinizing intrinsic brain activity and determining its cognitive function without using the traditional manipulation methods of cognitive neuroscience such as excitation or inhibition. Hassabis and his collaborators achieved this by “smuggling” various representations into parts of the DMN during the pre-scan training period. The neural correlates of these representations could then be objectively observed in the fMRI images.

It could be objected, and rightly so, that the smuggling approach is not *entirely* new in its methods. During the pre-scan training phase, participants are explicitly instructed to mentally simulate certain events. This part of the experiment could, perhaps, be interpreted as a procedure within the framework of the evoked, goal-oriented experimental paradigm. Moreover, it violates the condition of spontaneousness of cognitive activity, the condition associated with IMC. On the other hand, during the scanning phase the participants are in behavioral rest (lying quietly in scanners and imagining the scenes), so in this respect the experiment resembles the usual method of studying the DMN and intrinsic activity. There is no excitation, no external stimuli to attend to. The experiment is thus a mixture of traditional and new approach. We suggest that the experiment (and other, similar ones) can be seen as a first step towards a methodologically sound scientific study of IMC. We are sceptical that it would be possible to

go much further, methodologically, and sidestep the smuggling phase altogether. Still, the future might bring unsuspected developments in this field of study.

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N O T E S

¹ For another summary of this development see Callard et al. (2012).

² In the paper, we will use the term “intrinsic activity” for brain activity not elicited by external events or bodily demands. The term “endogenous activity”, used by Bechtel, is also apposite, but the neuroscientific community prefers the former term.

³ In the following brief account of the development of the DMN theory we will confine ourselves mainly to the contributions of Marcus Raichle and his team. However, a pioneering work of Bharat Biswal and his colleagues at the Biophysics Research Institute of the Medical College of Wisconsin from the mid-nineties should certainly form a part of the fuller account. See Biswal et al. (1995).

⁴ See Smith (2012) for a lively account of this development and for references to some technical literature.

⁵ But how to identify a baseline of neuronal activity when the standard method of cognitive subtraction – in which one subtracts the scan readings for a suitably defined control state, usually some type of a resting state, from the readings for the task at hand – cannot be applied in this case? There is no control state for a control state, viz. for the “resting” state. The baseline has to be identified in some other way. Raichle and his team decided to focus on metabolic signatures of resting state activity, especially on the extraction of oxygen from the blood delivered to the brain. Evoked activation is associated with increased blood flow in specific cerebral regions. This increased blood flow is also accompanied by higher glucose utilization and increased oxygen availability. The ratio of oxygen extracted and used by the region to the overall amount of oxygen delivered by blood to the region is called Oxygen Extraction Fraction (OEF). OEF in a region decreases when the region is activated, for the blood supply of oxygen increases more than can be utilised by the given region. One can thus use OEF as a direct measure of activity increase – or, as the matter stands, decrease in the studied area. For more technical details see the lucid account in Raichle et al. (2001). For criticism of the baseline idea see Morcom and Fletcher (2007a).

⁶ “Resting state network” is pretty much a misnomer, as Spreng (2009) emphasises. The activity of the DMN and other brain areas and networks during the so-called rest is far from restful. The important distinction is not between rest and activity, but between intrinsic and evoked activity. However, the term “resting network” became entrenched and is widely used by contemporary neuroscientists. One should keep in mind that “rest” is here a *behavioral* description, meaning simply an absence of stimulus-driven or goal-oriented activity on the part of the subject of an experiment.

⁷ We should like to stress that what we are presenting here is a somewhat simplified, neat picture of the DMN anatomy and function. The actual details are less clear-cut. For example, some areas of the DMN might be involved in positive tasks recruitment, thus defying the “task-negative” label. Also, brain areas are only gradually, non-discretely differentiated according to the nature and level of intrinsic activity, with the DMN displaying a fairly stable, but not an entirely static pattern. For details see the review studies of Northoff et al. (2010) and Sadaghiani et al. (2010).

⁸ Structural connectivity constraints, though not entirely, predict the functional connectivity; see Deco et al. (2013).

⁹ Recent work has confirmed that this connectivity is not inborn, but develops through ontogeny; see Fair et al. (2008) and Kelly et al. (2009).

¹⁰ Common sense suggests that the more one concentrates on one’s own inner thought processes (an activity thought to be characteristic of DMN), the higher the chance that she will miss or misidentify the stimulus. This view is explicitly endorsed by Boly et al. (2007): “Our results are likely to reflect a competition between conscious access to external stimuli and self-referential processes” (p. 12189). However, this simple picture is contradicted by Sadaghiani et al. (2009), who report that, in their experiment, higher activity in the precuneus/pCC part of the DMN actually preceded *more successful* answers (“hits”) in a sound perception task. This indicates that the nature of the cognitive task studied needs to be taken into account. However, this finding is consistent with the prevalent notion that *in most cases*, DMN deactivation eases the execution of a cognitive task. It is just one of the ever-present reminders that things are not as clear-cut as we would, perhaps, have wished, and that the context and difficulty of a cognitive task matters.

¹¹ An attempt along these lines was made in an influential study by Fox, Snyder, Zacks and Raichle (2006). They claim that “spontaneous and task-related activity are linearly superimposed in the human brain” (p. 23). We won’t dwell on the details of this study, because the team focused on motor brain regions instead of the DMN.

¹² Interestingly, as the study of Silvina Horovitz and her colleagues demonstrated, during deep, dreamless sleep, DMN does not stop being active, either. What happens is that the frontal areas of the DMN so to speak decouple from the rest of the network, whereas the parts more to the rear of the brain (viz., bilateral inferior parietal cortices/angular gyri and posterior cingulate cortex) even *strengthen* their correlations (Horovitz et al., 2009, p. 11376).

¹³ Moreover, thanks to experiments on neural coactivations, we know that specific neural regions can be involved in a number of behaviors and therefore are not responsible for only one cognitive function. It all depends on the coactivity pattern. A coactivation of cerebral region A with regions B and C might produce certain cognitive phenomenon, whereas its coactivation with D and E might give rise to completely different phenomenon. Differences in cognitive contexts thus correlate with differences in how the parts of the DMN are connected with each other and with other brain areas.

¹⁴ What about the introspective reports of the subjects, couldn’t they be of help? We acknowledge that such a source of data might well turn out to be valid, perhaps even indispensable in the study of conscious intrinsic activity. However, to base the whole theory of IMC on nothing but introspection would not be scientifically responsible, what with the well-known unreliability and severe limits of introspective reports.

¹⁵ E.g., “Likes to cooperate with others” or “Can be cold and aloof.”

¹⁶ E.g., “Is outgoing, sociable” or “Is sometimes shy, inhibited.”

¹⁷ Example: “in the street – sees a homeless vet asking for changes – Sarah”.

¹⁸ Personality information is a cluster of personality traits (sociable, aggressive, etc.), whereas identity information fixes whether the person in question is Sarah, Mary, or John.

¹⁹ Although the identity of the protagonist imagined in any of the scanning sessions was contained in the text cue (see note 17), the researchers were trying to determine the identity by looking at the brain scans alone. Hassabis confirms this in an e-mail correspondence.

REFERENCES

- Addis, D. R., Wong, A. T., & Schacter, D. L. (2007). Remembering the past and imagining the future: Common and distinct neural substrates during event construction and elaboration. *Neuropsychologia*, 45(7), 1363–1377.
- Anticevic, A., Cole, M. W., Murray, J. D., Corlett, P. R., Wang, X.-J., & Krystal, J. H. (2012). The role of default network deactivation in cognition and disease. *Trends in Cognitive Sciences*, 16(12), 584–592.
- Bechtel, W. (2013). The endogenously active brain: The need for an alternative cognitive architecture. *Philosophia Scientiae*, 17–2 (2), 3–30.
- Bechtel, W., & Richardson, R. C. (2010). *Discovering complexity: Decomposition and localization as strategies in scientific research*. Cambridge, MA: MIT Press.
- Biswal, B., Yetkin, F. Z., Haughton, V. M., & Hyde, J. S. (1995). Functional connectivity in the motor cortex of resting human brain using echo-planar MRI. *Magnetic Resonance in Medicine*, 34(4), 537–41.
- Boly, M., Balteau, E., Schnakers, C., Degueldre, C., Moonen, G., Luxen, A., Phillips, C., Peigneux, P., Maquet, P., & Laureys, S. (2007). Baseline brain activity fluctuations predict somatosensory perception in humans. *Proceedings of the National Academy of Sciences of the United States of America*, 104(29), 12187–12192.
- Brown, T. G. (1911). The intrinsic factors in the act of progression in the mammal. *Proceedings of the Royal Society of London. Series B*, 84(572), 308–319.
- Brown, T. G. (1914). On the nature of the fundamental activity of nervous centers. *The Journal of Physiology*, 48(1), 18–46.
- Buckner, R. L., Andrews-Hanna, J. R., & Schacter, D. L. (2008). The brain's default network: Anatomy, function, and relevance to disease. *Annals of the New York Academy of Sciences*, 1124, 1–38.
- Burke, R. E., (2007). Sir Charles Sherrington's *Integrative action of the nervous system*: A centenary appreciation. *Brain*, 130(4), 887–894.
- Callard, F., Smallwood J., & Margulies, D. S. (2012). Default positions: How neuroscience's historical legacy has hampered investigation of the resting mind. *Frontiers in Psychology*, 3, Article 321, 1–6.
- Craver, C. F., & Kaplan, D. M. (2011). Towards a mechanistic philosophy of neuroscience. In S. French & J. Saatsi (Eds.), *The Continuum companion to the philosophy of science* (pp. 268–291). London and New York: Continuum International Publishing Group.

- Deco, G., Jirsa, V. K., & McIntosh, A. R. (2013). Resting brains never rest: Computational insights into potential cognitive architectures. *Trends in Neurosciences*, 36(5), 268–274.
- Eriksson, P. S., Perfilieva, E., Björk-Eriksson, T., Alborn, A. M., Nordborg, C., Peterson, D. A., & Gage, F. H. (1998). Neurogenesis in the adult human hippocampus. *Nature Medicine*, 4(11), 1313–1317.
- Fair, D. A., Cohen, A. L., Dosenbach, N. U. F., Church, J. A., Miezin, F. M., Barch, D. M., Raichle, M. E., Petersen, S. E., & Schlaggar, B. L. (2008). The maturing architecture of the brain's default network. *Proceedings of the National Academy of Sciences of the United States of America*, 105(10), 4028–4032.
- Finger, S. (1994). *Origins of neuroscience: A history of explorations into brain function*. Oxford: Oxford University Press.
- Fox, M. D., Snyder, A. Z., Zacks, J. M., & Raichle, M. (2006). Coherent spontaneous activity accounts for trial-to-trial variability in human evoked brain responses. *Nature Neuroscience*, 9(1), 23–25.
- Greene, J. D., Sommerville, R. B., Nystrom, L. E., Darley, J. M., & Cohen, J. D. (2001). An fMRI investigation of emotional engagement in moral judgment. *Science*, 293, 14 September, 2105–2108.
- Greicius, M. D., Krasnow, B., Reiss, A. L., & Menon, V. (2003). Functional connectivity in the resting brain: A network analysis of the default mode hypothesis. *Proceedings of the National Academy of Sciences of the United States of America*, 100(1), 253–258.
- Greicius, M. D., & Menon, V. (2004). Default-mode activity during a passive sensory task: Uncoupled from deactivation but impacting activation. *Journal of Cognitive Neuroscience*, 16(9), 1484–1492.
- Gusnard, D. A., & Raichle, M. E. (2001). Searching for a baseline: Functional imaging and the resting human brain. *Nature Reviews Neuroscience*, 2(10), 685–694.
- Hassabis, D., Spreng, R. N., Rusu, A. A., Robbins, C. A., Mar, R. A., & Schacter, D. L. (2013). Imagine all the people: How the brain creates and uses personality models to predict behavior. *Cerebral Cortex*, in press. doi:10.1093/cercor/bht042.
- van den Heuvel, M. P., Mandl, R. C. W., Kahn, R. S., & Hulshoff Pol, H. E. (2009). Functionally linked resting-state networks reflect the underlying structural connectivity architecture of the human brain. *Human Brain Mapping*, 30(10), 3127–3141.
- Horovitz, S. G., Braun, A. R., Carr, W. S., Picchioni, D., Balkin, T. J., Fukunaga, M., & Duyn, J. H. (2009). Decoupling of the brain's default mode network during deep sleep. *Proceedings of the National Academy of Sciences of the United States of America*, 106(27), 11376–11381.

- Kelly, A. M. C., Di Martino, A., Uddin, L. Q., Shehzad, Z., Gee, D. G., Reiss, P. T., Margulies, D. S., Castellanos, F. X., & Milham, M. P. (2009). Development of anterior cingulate functional connectivity from late childhood to early adulthood. *Cerebral Cortex*, 19(3), 640–657.
- Llinás, R. (2002). *I of the vortex*. Cambridge, MA: MIT Press.
- Mars, R. B., Neubert, F.-X., Noonan, M. P., Sallet, J., Toni, I., & Rushworth, M. F. S. (2012). On the relationship between the “default mode network” and the “social brain”. *Frontiers in Human Neuroscience*, 6, Article 189, 1–9.
- Mason, M., Norton, M. I., Van Horn, J. D., Wegner, D. M., Grafton, S. T., & Macrae, C. N. (2007). Wandering minds: The default network and stimulus-independent thought. *Science*, 315, 19 January, 393–395.
- Molnar-Szakacs, I., & Arzy, S. (2009). Searching for an integrated self-representation. *Communicative and Integrative Biology*, 2(4), 365–367.
- Morcom, A., & Fletcher, P. C. (2007a). Does the brain have a baseline? Why we should be resisting a rest. *NeuroImage*, 37(4), 1073–1082.
- Morcom, A., & Fletcher, P. C. (2007b). Cognitive neuroscience: The case for design rather than default. *NeuroImage*, 37(4), 1097–1099.
- Northoff G., Quin, P., & Nakao, T. (2010). Rest-stimulus interaction in the brain: A review. *Trends in Neurosciences*, 33(6), 277–284.
- Raichle, M. E. (2009). A paradigm shift in functional brain imaging. *The Journal of Neuroscience*, 29(41), 12729–12734.
- Raichle, M. E (2010). Two views of brain function. *Trends in Cognitive Sciences*, 14(4), 180–190.
- Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America*, 98(2), 676–682.
- Raichle, M. E., & Mintun, M. A. (2006). Brain work and brain imaging. *Annual Review of Neuroscience*, 29, 449–476.
- Raichle, M., & Snyder, A. Z. (2007). A default mode of brain function: A brief history of an evolving idea. *NeuroImage*, 37(4), 1083–1090.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27, 169–192.
- Sadaghiani, S., Hesselmann, G., & Kleinschmidt, A. (2009). Distributed and antagonistic contributions of ongoing activity fluctuations to auditory stimulus detection. *The Journal of Neuroscience*, 29(42), 13410–13417.
- Sadaghiani, S., Hesselmann, G., Friston, K. J., & Kleinschmidt, A. (2010). The relation of ongoing brain activity, evoked neural responses, and cognition. *Frontiers on Systems Neuroscience*, 4, Article 4, 1–14.

- Saxe, R., & Kanwisher, N. (2003). People thinking about thinking people: The role of the temporo-parietal junction in “theory of mind”. *Neuroimage*, 19(4), 1835–1842.
- Sherrington, C. (1906). *The integrative action of the nervous system*. New Haven: Yale University Press.
- Smith, K. (2012). Idle minds. *Nature*, 489, 19 September, 356–358.
- Sporns, Olaf. (2011). *Networks of the brain*. Cambridge, MA: MIT Press.
- Spreng, R. N. (2012). The fallacy of a “task-negative” network. *Frontiers in Psychology*, 3, Article 145, 1–5.
- Spreng, R. N., Mar, R. A., & Kim, A. S. N. (2009). The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: A quantitative meta-analysis. *Journal of Cognitive Neuroscience*, 21(3), 489–510.
- Vanhaudenhuyse, A., Noirhomme, Q., Tschibanda, L. J., Bruno, M. A., Boveroux, P., Schnakers, C., Soddu, A., Perlberg, V., Ledoux, D., Brichant, J. F., Moonen, G., Maquet, P., Greicius, M. D., Laureys, S., & Boly, M. (2010). Default network connectivity reflects the level of consciousness in non-communicative brain-damaged patients. *Brain*, 133(1), 161–71.