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LARGE-SCALE DISTRIBUTED NETWORKS AND CEREBRAL HEMISPHERES

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ABSTRACT

The two main large-scale distributed networks, Central Executive (CEN) and Default Mode (DMN) have been extensively studied, but their relationship to hemispheric specialization has not been comprehensively addressed. We present evidence that they are neuroanatomically asymmetric: the CEN components are volumetrically larger in the right hemisphere, and DMN components are volumetrically larger in the left hemisphere. Based on this, the possibility that CEN and DMN are also functionally asymmetric is introduced and implications of the putative functional asymmetry of large-scale distributed networks for refining our understanding of hemispheric specialization are examined.

Among the most significant developments in contemporary neuropsychology and cognitive neuroscience has been a shift of emphasis from specific loci to distributed networks (e.g., Goldman-Rakic, 1988; Fuster, 2003; Bressler & Menon, 2020). Alexander Luria, an early visionary in neuropsychology, anticipated this paradigm shift with his concept of “functional systems” (Luria, 1966), yet as recently as the 1980’s the concept of hard-wired “modularity” remained dominant (Fodor, 1983; Goldberg, 1995). It took the ascendancy of functional neuroimaging to finally dispense with this neurobiologically vacuous notion and for the understanding of neocortical processes as highly distributed networks to take hold.

In this context, two large-scale distributed networks have gained particular interest: Central Executive Network (CEN) and Default Mode Network (DMN). Their functions are different and, in a sense, complementary: the CEN is activated in response to an externally generated cognitive challenge (Fox et al., 2005; Seeley et al., 2007), and DMN is active when an individual is engaged in internally generated cognitive activity (Raichle et al., 2001; Shulman et al., 1997). DMN is presumed to reflect the baseline, internally generated brain activity, which is deactivated during specific, externally introduced cognitive tasks (Raichle & Snyder, 2007). The two types of networks are presumed to be anticorrelated: when CEN is activated, DMN is dampened and vice versa. (Greicius, Krasnow, Reiss, & Menon, 2003; Fox et al., 2005; Sridharan, Levitin, & Menon, 2008).

The description of the exact neuroanatomy of these networks varies from study to study, probably reflecting the fact that CEN and DMN are not truly unique networks but rather classes of networks, just as the corresponding cognitive activities are not unique activities but rather two broad classes of cognitive activities. However, both classes of networks have broadly invariant characteristics. CEN entails a co-activation of dorsolateral/ventrolateral prefrontal and inferoparietal cortices, both of which are found mostly on the lateral, convexital aspect of the hemispheres. By contrast, DMN entails a co-activation of ventromedial/orbitofrontal regions and posterior cingulate/posterior parietal/precuneus regions, both of which are mostly on the mesial aspect of the hemispheres.

Both CEN and DMN are inherently functional constructs, and mapping them on morphological substrates may be difficult, particularly since even the functional delineations of the two large scale networks are not entirely consistent across reports (Bzdok et al., 2015; Buckner & DiNicola, 2019). Additionally, more comprehensive tractography based connectivity studies of the DMN point to the importance of subcortical structures such as the thalamus and basal forebrain (Alves et al., 2019).

Nonetheless, this has not deterred researchers for identifying the morphological substrates of CEN and DMN, albeit in very broad terms. According to Raichle (2015), “the default mode network is divided into roughly three major subdivisions: the ventral medial prefrontal cortex; the dorsal medial prefrontal cortex; and the posterior cingulate cortex and adjacent precuneus plus the lateral parietal cortex”. By contrast the Central Executive Network involves the dorsolateral/ventrolateral prefrontal cortex and posterior parietal cortex (Menon, 2011) (see Fig. 1)

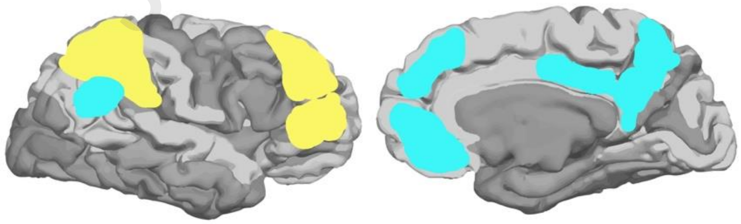

Fig. 1 – Schematic representation of the DMN description by Raichle (2015) and CEN description by Menon (2011). The DMN components are highlighted in aquamarine, CEN components are highlighted in yellow.

The predominant affiliation of CEN components with the lateral aspect of the hemispheres, and of DMN components with the mesial aspect of the hemispheres has been noted by numerous authors (Raichle et al., 2001; Vincent et al., 2008; Lu et al., 2012) The reciprocal affiliation of CEN and DMN with, respectively, the lateral vs mesial aspects of cerebral hemispheres, appears to be one of their distinguishing characteristics.

Obviously, the components of CEN and DMN networks are present in both cerebral hemispheres, and a question then arises how symmetric they are. To the best of our knowledge, this rather natural question has not been comprehensively addressed in the research literature up to date. However, morphometric data exist, which may shed light on the issue. Additional inspection of the data published in an earlier morphometric study (Goldberg et al., 2013) suggests that the neuroanatomical components of both CEN and DMN are characterized by significant asymmetries: ventrolateral frontal, dorsolateral frontal, and inferoparietal regions (all components of CEN) are volumetrically larger in the right hemisphere; whereas orbitofrontal/ventromedial frontal regions and posterior cingulate/precuneus (all components of DMN) are volumetrically larger in the left hemispheres (Fig. 2).

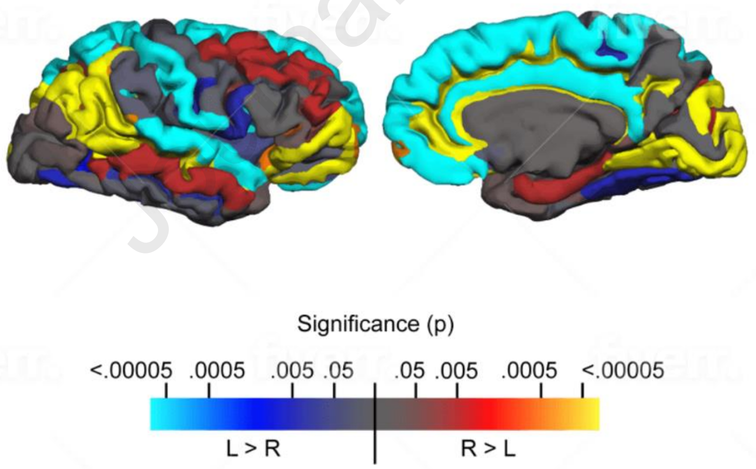

Fig. 2 - Regional cortical volume asymmetries in the two hemispheres. Direction of differences and significance levels are coded according to the color bar below. Adapted from "Hemispheric asymmetries of cortical volume in the human brain," by Goldberg et al., 2013, *Cortex*, 49(1), pp. 200-210.

After a rigorous Bonferroni correction for multiple comparisons, the following asymmetries were confirmed at $p < .05$ level: the superior frontal gyrus, superior frontal sulcus, frontomarginal sulcus, suborbital sulcus, gyrus rectus, postcentral gyrus, postcentral sulcus, cingulate gyrus, paracentral gyrus, subcentral gyrus, transverse temporal gyri, superior temporal gyrus (lateral aspect), planum temporale, superior parietal gyrus, anterior occipital sulcus, ascending ramus of the lateral fissure, and circular insular sulcus (superior and inferior aspects) were larger in the left than right (L > R) hemisphere across the whole sample (all p values < .00067). Conversely, the inferior parietal gyrus, superior occipital gyrus, lingual gyrus, calcarine sulcus, lateral fissure (posterior segment), collateral transverse sulcus, middle frontal sulcus, subparietal sulcus, anterior subcentral sulcus, superior temporal sulcus, cingulate sulcus, the lateral aspect of orbital gyri, pericallosal sulcus, and Jensen sulcus were larger in the right than left (R > L) hemispheres (all p values < .00067). Of those, the lateral aspect of the orbital gyrus and the inferior parietal gyrus are components of CEN and are volumetrically larger in the right hemisphere. By contrast, gyrus rectus, posterior portion of the cingulate gyrus, and the paracentral gyrus (the mesial aspect of parietal lobe) are components of DMN and are larger in the left hemisphere. The regions found to be volumetrically larger in the right hemisphere are located mostly on the lateral aspect of the hemisphere. By contrast, the regions found to be volumetrically larger in the left hemisphere are located mostly on the mesial aspect of the hemisphere. (Goldberg et al., 2013)

Thus, an anatomical double-dissociation is present: CEN components are volumetrically larger in the right hemisphere, and DMN components are larger in the left hemisphere. Both the components of CEN and the regions found to be larger in the right hemisphere are located predominantly on the lateral aspect of the hemispheres. These include the ventrolateral and dorsolateral prefrontal cortices, as well as posterior inferoparietal regions. By contrast, the components of DMN and the regions found to be larger in the left hemisphere are located predominantly on the mesial aspect of the hemispheres. These include ventral medial and dorsal medial prefrontal cortices, as well as posterior cingulate and precuneus regions. The above-mentioned regions exhibiting reciprocal volumetric asymmetry in the earlier study by Goldberg et al. (2013) closely align with the commonly identified morphological substrates of the two main large-scale distributed networks.

While the data supporting this conclusion were presented in the original paper by Goldberg et al. (2013), the conclusion itself, about the opposing lateralization of neuroanatomical substrates of CEN and DMN, has not been explicitly articulated in that paper. We believe that the point is sufficiently important in its potential implications to warrant this comment.

The question then arises whether the *neuroanatomical* double-dissociation is accompanied by a *functional* double-dissociation between CEN and DMN in the two cerebral hemispheres. While inferring function from anatomy is inevitably a potentially hazardous exercise, numerous studies exist demonstrating that individual differences in the size of a neuroanatomical structure are often positively correlated with the level of performance on the cognitive tasks reflecting its function. Accordingly, Schremm et al. (2018) found that, in native speakers, cortical thickness of the left planum temporale is positively related to individual word tone processing performance. However, when processing pseudowords, it is the cortical thickness of a different brain region - the left pars opercularis of the left inferior gyrus - that predicts individual performance. Likewise, Maguire et al. (2000) found significantly increased gray matter volume in the brains of taxi drivers compared with those of controls in the right and the left hippocampi, likely due to their professional dependence on navigational skills, this also implying an association between task proficiency and regional volume size.

Aligned with the above, Schneider et al. (2002) detected enlarged gray matter volume of the anteromedial portion of Heschl's gyrus in professional musicians and Draganski et al. (2004) reported increased gray matter volume in the mid-temporal area (hMT/V5) and in the left posterior intraparietal sulcus resulting from juggling training. Blackmon et al. (2010) demonstrated that better performance on a phonetically irregular oral word reading task is associated with increased cortical thickness in the angular gyrus/posterior superior temporal gyrus (AG/p-STG) and anterior superior temporal gyrus (aSTG). Studies on introspection have shown that our ability to introspect about self-performance is correlated with gray matter volume in the anterior prefrontal cortex (Fleming et al., 2010).

Therefore, it is reasonable to ascertain, at least as a hypothesis, the possibility that a functional double-dissociation between CEN and DMN exists, which parallels the structural double-dissociation between them. According to this possibility, while both networks are bilaterally represented, the right hemisphere is dominant in supporting CEN, and the left hemisphere is dominant in supporting DMN. Given the current interest in these large-scale networks, this hypothesis may warrant a re-analysis of existing, previously acquired functional neuroimaging data, as well as the design of future studies directly examining the CEN-DMN dynamics in relationship to cerebral hemispheres. Interestingly, we were able to find at least one direct claim, albeit not in a peer-reviewed publication, that in the connectome CEN is more extensively represented in the right hemisphere (Omniscient Neurotechnology, 2022a), and DMN in the left hemisphere (Omniscient Neurotechnology, 2022b). This is broadly consistent with tractographic findings by de Schotten et al. (2011) of the rightward asymmetry of the fronto-parietal component of the arcuate fasciculum, located on the lateral aspect of the hemisphere, as is CEN. By contrast, tractographic studies of cingulum, which like DMN is located on the mesial aspect of the hemispere, revealed complete or partial leftward asymmetry (Gong et al., 2005; de Schotten et al., 2011).

Assuming that the opposing functional lateralization of CEN and DMN is confirmed, how will it impact our broader understanding of hemispheric specialization? For one, it will suggest that the right cerebral hemisphere is more closely involved in responding to cognitive demands as they arise from the outside world (Shulman et al., 2010). This is consistent with the suggestions about the privileged role of the right hemisphere in attention to the outside world, as well as about its privileged role dealing with cognitive novelty (Goldberg & Costa, 1981; Goldberg et al., 1994). By contrast, it will emphasize the role of the left hemisphere in internally generated cognitive processes driven by representations already present in the individual's cognitive repertoire and reflecting the subject's needs and priorities (Goldberg & Costa, 1981).

The existence of major distributed networks has been demonstrated in several primate species (Barks, Parr, & Rilling, 2013; Mantini et al., 2011; Vincent et al., 2007). Demonstration of the lateralization of the main large distributed networks helps place the topic of hemispheric specialization into a broader evolutionary context. One of the major limitations of the classic notions linking the left hemisphere to language and the right hemisphere to non-verbal process is the fact that it is devoid of evolutionary universality (Goldberg & Costa, 1981; Goldberg et al, 1994). Indeed, the verbal-nonverbal dichotomy is meaningful for humans but is meaningless outside of our species since other species do not possess language. By contrast, unlike language in its narrow definition, the ability to form internal representations is universal, shared by all species capable of learning. While human language is a powerful tool for forming and manipulating internal representations, it is not a necessary prerequisite thereof. Unlike the verbal-nonverbal distinction, the distinction between internally motivated cognition and cognition driven by external demands is meaningful across multiple species.

Bilateral brain architecture is a universal feature conserved throughout evolution across multiple species, and so is the asymmetric nature of this architecture. Evidence exists of hemispheric asymmetries, both structural and functional, in multiple vertebrate species including baboons (Fagot & Vauclair, 1994), orangutans (LeMay & Geschwind, 1975), chimpanzees (Gannon, Holloway, Broadfield, & Braun, 1998), macaques (Croxson, Forkel, Cerliani, & Thiebaut de Schotten, 2018), rats (Klur et al., 2009), dolphins (Sakai, Hishii, Takeda, & Kohshima, 2006), songbirds (Bell, Phan, & Vicario, 2015), and zebrafish (Dadda et al., 2010), Some of these asymmetries are invariant across species.

Therefore, any comprehensive understanding of hemispheric specialization should account for evolutionary continuity of the underlying principles, something the traditional language-nonlanguage dichotomy fails to do (e.g., de Waal, 2016). Placed in a broad evolutionary context, the dominant role of the left hemisphere in language in humans may be a special case of a more fundamental role of the left hemisphere in supporting and managing previously formed mental representations already stored in the organism’s central nervous system, verbal and non-verbal alike (Goldberg, Vaughan, & Gerstman, 1978), and in initiating behaviors driven by such representations. More precise characterization of the relative hemispheric contribution to CEN and DMN may help advance our understanding of their place in cognition, as well as of the fundamental functional relations between the two cerebral hemispheres.

Furthermore, recognition of reciprocally asymmetric nature of the main large-scale networks will place hemispheric specialization into the context of current central themes in cognitive neuroscience, and by so doing will help revive an interest in hemispheric specialization, a topic which, after many years in the focus of neuropsychological research, has been all but abandoned in today’s cognitive neuroscience – not because all the salient issues were successfully resolved, but because they were not.

Ultimately, any conclusive demonstration of the reciprocally asymmetric nature of the large-scale distributed networks will require functional neuroimaging approaches. Several neurological conditions are characterized by distinct variants with asymmetric neuroanatomical and neurocognitive expressions. These include left vs right hemi-parkinsonian syndromes (Hovik, Øie, & Goldberg, 2017; Varanese et al., 2010) and tics- vs exploratory behaviors-dominated variants of Tourette syndrome (Hovik, Øie, & Goldberg, 2017; Sacks, 1992). Examining the asymmetric characteristics of the large-scale distributed networks in such clinical disorders may shed further light on the cortical organization of these networks and their role in health and disease. Encouraging such studies and providing the rationale for them is among the motivations for this paper.

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