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Consciousness in a multilevel architecture: Evidence from the right side of the brain

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ABSTRACT

By taking into account Bruce Bridgeman's interest in an evolutionary framing of human cognition, we examine effective (cause-and-effect) connectivity among cortical structures related to different parts of the triune phylogenetic stratification: archicortex, paleocortex and neocortex. Using resting-state functional magnetic resonance imaging data from 25 healthy subjects and spectral Dynamic Causal Modeling, we report interactions among 10 symmetrical left and right brain areas. Our results testify to general rightward and top-down biases in excitatory interactions of these structures during resting state, when self-related contemplation prevails over more objectified conceptual thinking. The right hippocampus is the only structure that shows bottom-up excitatory influences extending to the frontopolar cortex. The right ventrolateral cortex also plays a prominent role as it interacts with the majority of nodes within and between evolutionary distinct brain subdivisions. These results suggest the existence of several levels of cognitive-affective organization in the human brain and their profound lateralization.

1. Introduction

Two dominant vectors in the lifework of Bruce Bridgman were studies of visual perception and the search for an evolutionary explanation of language, consciousness and cognition. BMV has benefited personally and scientifically from a long collaboration with Bruce Bridgman. This collaboration was focused on the problems of visual psychophysics (e.g. Bridgeman, Van der Heijden, & Velichkovsky, 1994; Pannasch, Selden, Velichkovsky, & Bridgeman, 2011) but there was always our common interest in the evolution of consciousness and cognition in the background. When working on research papers, Bruce advocated for replacing undefined "it may be" by more the assertive "it can be" or even "it is". We followed this recommendation in the present article, though it is devoted to still unresolved and highly speculative matters. From the early days of psychology and neurology, one particular approach to

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conceptualize mind evolution is in terms of several evolutionary steps, or levels continuing to shape brain connectivity and cognitive-affective organization in the modern humans (Bridgeman, Cellerier, Paillard, & Velichkovsky, 2000).

Presuming that there is such a “vertical dimension” of brain-and-mind functioning, what could the granularity and distinct characteristics of levels be? Over four decades ago, Gregory Razran (1971) reviewed more than 1500 studies on learning and memory, concluding that there must be a hierarchy of learning processes with several levels, which can be related to the evolutionary stage when they first appear. In another attempt to understand multiple stages of brain evolution, one of the founders of biomechanics, Nikolai Bernstein (1947), described four levels involved in construction of human movements: A. Paleokinetic regulation, B. Synergies, C. Spatial field, and D. Object actions. He linked the levels C and D to functions of parietal and temporal cortices. Bernstein also supposed that “one or two” levels of “higher symbolic coordinations” might be localized “above” level D, the Object actions. In their here-and-now functioning, levels are functionally organized in a temporary figure-ground structure. Depending on the task at hand, one of the levels, possessing operational resources with the best fit to ones demanded by the task solution, takes over the lead. This means that we are aware of the meaningful content of goals (the goals’ “what” but not “how”) that the currently leading level is pursuing. Other levels work in background mode whereby their operations remain unconscious. When the situation changes, any level may receive the leading status and therefore its goals become conscious. Considering this feature, Bernstein’s hierarchy is a heterarchy from the system theoretical point of view (Velichkovsky, 2002).

These early intuitions stemmed from biomechanical research and neuropsychological observations. Some of them have subsequently gained experimental support. For example, grasping movements show a dependence of finer object-adjusted hand movements (Bernstein's level of objects action D) on the global translatory motion of the arm to a location in space (level of spatial field, or level C) (Jeannerod, 1997). As a whole, both of these hypothetical mechanisms in Bernstein’s theory strikingly resemble the dorsal and ventral pathways discussed in contemporary neuroscience (Parr & Friston, 2017; Ungerleider, & Haxby, 1994) and their respective ambient and focal modes of perceptual awareness (Velichkovsky, Joos, Helmert, & Pannasch, 2005). The functional imaging revolution in research methods has promoted the view of the brain as organized into a multilevel networks architecture, e.g. by description of two action counterparts to dorsal and ventral streams in perception (Fox, Corbetta, Snyder, Vincent, & Raichle, 2006). At the same time, the unified dorsal vs. ventral dichotomy is too narrow for a functional description of even the posterior parts of the human brain, especially with respect to functionality of the tertiary multimodal areas around the temporoparietal junction such as the right inferior parietal lobe (Singh-Curry, & Husain, 2009).

Of central relevance for our analysis is the discovery of a widely distributed network of brain structures, which is active during rest and inwardly-directed tasks such as contemplation, introspection and planning for the future (Gusnard, Akbudak, Shulman, & Raichle, 2001; Raichle, et al., 2001). This network is best known for its activation during conditions of relative rest and external inactivity and has thus been termed the Default Mode Network (DMN) (Raichle et al., 2001). The DMN comprises multiple interacting structures (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010). Most of them are located around the brain’s midline, like the medial prefrontal cortex, the posterior cingulate cortex, and the ventral precuneus, but the DMN also includes portions of the temporo-parietal junction, namely the left and right inferior parietal cortex (IPCl and IPCr, correspondingly). With respect to the hippocampal formation, rank correlations of activity have also revealed the basic pattern of activation/deactivation characteristic of the DMN (Greicius, Supekar, Menon, & Dougherty, 2009; Vincent, Bloomer, Hinson, & Bergmann, 2006). A number of hypotheses on the functionality of the DMN have been formulated mostly relating it to higher-order aspects of consciousness and self-related mental activities (Raichle, 2015; Schilbach, Eickhoff, Rotarska-Jagiela, Fink, & Vogeley, 2008).

Semiotic aspects of resting-state activity have not yet been studied systematically. In a pioneering brain mapping study of natural speech semantics, Alexander Huth and colleagues (Huth, de Heer, Griffiths, Theunissen, & Gallant, 2016) have recently demonstrated that the distribution of global semantic dimensions over the surface of the human cerebral cortex coincided with outlines of the DMN. Thus, the DMN could well suit the role of the upper-level mechanisms of “symbolic coordinations” anticipated by Bernstein (1947). Surprisingly, no leftward bias for natural speech categories was observed by Huth et al. (2016) but instead a broad distribution of semantic representations was found across both hemispheres. Moreover, an asymmetry for categories with attributes ‘mental”, “emotional”, and “social” seemed to be present in the data with a focus around the right temporoparietal junction. The study used a flat projection of categories on the cortex and it is therefore impossible to determine whether underlying limbic structures such as hippocampus were involved.

The role of these structures can, however, be substantial as it has been shown in our study of effective (cause-and-effect) connectivity of the left and right hippocampal formation (HIPl and HIPr, respectively) within the DMN (Ushakov et al., 2016). In that study, we applied spectral Dynamic Causal Modeling (DCM) to resting-state functional magnetic resonance imaging (fMRI) data. The main idea of DCM is to evaluate parameters of a biologically validated model of the neuronal system so that it can predict the observed fMRI data in the best way (Friston, Kahan, Biswal, & Razi, 2014; Sharaev, Zavyalova, Ushakov, Kartashov, & Velichkovsky, 2016). Our study was conducted in a group of 30 healthy right-handed subjects and comprised the DCM analysis of two 5-nodes and one 6-nodes interactions. The winning models demonstrated a significant asymmetry in the effective connectivity between hippocampi and the main multimodal regions of the posterior neocortex, IPCl and IPCr. While HIPl demonstrated bidirectional interaction with IPCl, there was no inflow to HIPl from IPCr. This means that in terms of spatial representation HIPl has access to information only from the right hemispace of the surrounding. On the contrary, HIPr was affected by inputs from both IPCl and IPCr that could lead to a holistic multimodal representation including both hemispaces (for a detailed analysis, see Ushakov et al., 2016).

The pattern of causal relationships characteristic of the hippocampal formation can be important for a causal explanation of various neglect phenomena and for a possible division of the brain mechanisms depending on their evolutionary origin in two or more large-scale functional groups, *aka* levels. In the present study, we extended our analysis of lateralization in effective connectivity under resting state beyond the borders of the core DMN, by including in a series of spectral DCM analyses interactions