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Publication Date

2021-05-01

DOI

10.1016/j.neubiorev.2021.02.011

Peer reviewed

A new era for executive function research: On the transition from centralized to distributed executive functioning

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ARTICLE INFO

ABSTRACT

"Executive functions" (EFs) is an umbrella term for higher cognitive control functions such as working memory, inhibition, and cognitive flexibility. One of the most challenging problems in this field of research has been to explain how the wide range of cognitive processes subsumed as EFs are controlled without an all-powerful but ill-defined central executive in the brain. Efforts to localize control mechanisms in circumscribed brain regions have not led to a breakthrough in understanding how the brain controls and regulates itself. We propose to re-conceptualize EFs as emergent consequences of highly distributed brain processes that communicate with a pool of highly connected hub regions, thus precluding the need for a central executive. We further discuss how graph-theory driven analysis of brain networks offers a unique lens on this problem by providing a reference frame to study brain connectivity in EFs in a holistic way and helps to refine our understanding of the mechanisms underlying EFs by providing new, testable hypotheses and resolves empirical and theoretical inconsistencies in the EF literature.

1. Introduction

The ability to exert control over actions is essential for personal autonomy and one of the most impressive yet poorly understood capacities our brains endow us with. The processes that control actions cover a range of cognitive skills referred to as executive functions (EFs) (Diamond, 2013; Powell and Voeller, 2004). While the precise definition of EFs remains a topic of debate (Duncan and Owen, 2000), there is a common consent in terms of the importance of EFs for adaptive behavior in an ever-changing environment (Jurado and Rosselli, 2007; Norman and Shallice, 1986; Rabbitt, 1997). Numerous theoretical frameworks exist to classify different EFs and to describe how they work together (Burgess et al., 2000; Diamond, 2013; Duncan and Owen, 2000; Luria et al., 1966; Miyake et al., 2000; Norman and Shallice, 1986). According to Miyake et al. (2000) and Diamond (2013), at least three core functions of EF can be identified, which are likely to represent distinct cognitive subsystems that nevertheless share a functional overlap to some degree: updating and monitoring of working memory representations, inhibition and interference control, as well as cognitive flexibility and shifting. Working memory (WM) is a cognitive system that enables to manipulate and maintain restricted chunks of information

which are stored in short-term memory (Baddeley et al., 1986; Baddeley and Hitch, 1974; Cowan, 1999; Diamond, 2013; Miller, 1956; Smith and Jonides, 1999). Inhibition has been defined as "being able to control one's attention, behavior, thoughts, and/or emotions to override a strong internal predisposition or external lure, and instead do what's more appropriate or needed" (Diamond, 2013). Cognitive flexibility reflects the ability to consider multiple conflicting representations of a single object or event simultaneously (Jacques and Zelazo, 2005) and selectively switch between actions, perspectives, and strategies for appropriate action in a changing environment (Dajani and Uddin, 2015; Diamond, 2013). In addition to flexibly switching between several laboratory tasks, every-day life as well as modern work environments often require performance on two or more tasks at the same time, e.g. driving while having a telephone conversation or simultaneously controlling several displays in air traffic control. In this multitasking context, efficient EFs are essential to select relevant information from the environment and to adjust performance to environmental demands by flexibly shifting between more serial or more parallel processing strategies (Fischer and Plessow, 2015).

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2. Centralized control in cognition and cognitive neuroscience

Substantial theoretical and experimental progress has been made in the past 50 years to describe how humans control their actions by selecting, processing, and prioritizing task-relevant stimuli (often at the expense of simultaneously present yet less relevant signals), and flexibly adapt to changing demands from the environment (Broadbent, 2013; Deutsch and Deutsch, 1963; Kahneman, 1973; Norman and Shallice, 1986; Schneider and Shiffrin, 1977; Shiffrin and Schneider, 1977; Treisman and Gelade, 1980; Wickens, 1991). Early cognitive models have introduced a hypothetical central executive to their cognitive architectures (Baddeley and Hitch, 1974; Norman and Shallice, 1986). One unifying premise underlying these theories is that some sort of central executive system is required that governs exerted control by "dampening" irrelevant and prioritizing relevant salient information or schemes. But while the necessity of higher-order control functions that control lower-order functions is self-evident, it does not explain how this central executive operates, reducing instead to the question of who is in charge of controlling the central executive. This problem of self-recurrency has been widely acknowledged and has led to the criticism that the central executive resembles an all-powerful but ill-defined "homunculus" that directs all processes that are not "automatic" (Monsell and Driver, 2000a). Any theoretical framework of EFs must therefore not only specify how control operates, how it is implemented at the neurophysiological level, and how it integrates other cognitive processes and their interrelatedness, but also formally address the question of what is controlling the controller in order to avoid an infinite hierarchy of central executives or homunculi (Logie, 2016).

One of the most influential theoretical frameworks on the neurophysiological mechanisms of EFs that has pushed beyond the central executive view has been proposed by Miller and Cohen (Miller and Cohen, 2001). This framework emphasizes the importance of the prefrontal cortex (PFC) as a key region to implement a wide range of EFs through active maintenance of goals and the means to achieve them. Rooted in the biased-competition model of selective attention (Desimone and Duncan, 1995), it cast the problem of control as a case of prioritization of competing perceptual or response representations. The role of the PFC is to bias activity in regions responsible for those representation, in accordance with a behavioral goal, that it maintains in memory. Thus, the PFC indirectly acts as a central executive and intervenes in a top-down fashion by selectively prioritizing the relevant process. According to this perspective, exerted control in EF is domain-general and operates on specific subordinated cognitive functions in service of a higher-order task goal. EFs such as inhibition, working memory and cognitive flexibility emerge from the dynamics of the PFC biasing goal-relevant activity patterns in the brain. In the last 20 years, this theoretical model has provided a versatile framework that has generated much empirical evidence supporting the pivotal role of the PFC in many EFs. However, despite progress in understanding the neurophysiological mechanisms of how the PFC represents and implements behavioral goals, the mechanism by which it accounts for EFs remains elusive. Although the PFC may participate to a greater extent than other areas in EFs, increasing evidence suggests that it does not act alone. Damage to the PFC, for instance, may or may not be accompanied by deficits in EFs, and neither site nor size of a prefrontal lesion allow for a clear prediction about the nature of resulting problem in executive functioning (Alvarez and Emory, 2006).

In parallel, the advance of non-invasive neuroimaging techniques such as fMRI, in combination with experimental designs rooted in subtractive logic (Friston et al., 1996; Newman et al., 2001), contributed to the conceptualization of a modular brain architecture (Fodor, 1983; Houk and Wise, 1995; Kanwisher et al., 1997; Minsky, 1988). The results could be construed as a fractionalization of the central executive (Baddeley, 2012; Botvinick et al., 2004, 2001; Braver, 2012; Diamond, 2013; Engle and Kane, 2003; Friston, 1994; Goldman-Rakic et al., 1996; Goschke and Bolte, 2014; Hazy et al., 2007, 2006; Hommel and Wiers,

2017; Koechlin and Summerfield, 2007; Miller and Cohen, 2001; Monsell and Driver, 2000b; Pezzulo et al., 2018; Shenhav et al., 2016, 2013), now a "macroconstruct" in which the central executive consists of discrete subsystems with anatomically segregated and functionally specialized modules. In a typical neuroimaging study, the cognitive process of interest is isolated via correlation to an external manipulation thought to elicit that process, and associated with a brain region of interest. If this association is statistically significant, it is assumed that this process is located within this brain area. This strategy has ascribed different aspects of EFs with specific anatomically circumscribed brain areas. For instance, goal-directed behavior with the ventromedial prefrontal cortex (vmPFC; Hare et al., 2014, 2009; Kahnt et al., 2011; Lim et al., 2011; Sokol-Hessner et al., 2012; Steinbeis et al., 2016; Vassena et al., 2014) and dorsolateral prefrontal cortex (dlPFC; Hare et al., 2014; Kahnt et al., 2011; Milham et al., 2001; Sokol-Hessner et al., 2012; Steinbeis et al., 2016), inhibition with right ventrolateral prefrontal cortex (vlPFC; Aron, 2007; Aron et al., 2014, 2004; Hampshire et al., 2010), conflict monitoring, selective attention, and computation of the expected value of control with anterior cingulate cortex (ACC; Alexander and Brown, 2011; Botvinick et al., 2004; Bush et al., 2002, 1999; Carter and Veen, 2007; Egner and Hirsch, 2005; Kerns, 2004; Kondo et al., 2004; MacDonald et al., 2000; Milham et al., 2001; Ridderinkhof et al., 2004; Shenhav et al., 2016, 2013; van Veen et al., 2001; Vassena et al., 2014; Weissman, 2004; Weissman et al., 2003), and cognitive flexibility and voluntary motor action selection with basal ganglia (BG; Aron et al., 2003; Cameron et al., 2010; Chakravarthy et al., 2010; Pauli et al., 2016; Redgrave et al., 1999; Stocco et al., 2010). The problems with such an approach have been extensively discussed and include subsequent tendencies towards reverse inference and inherent bias in interpretation (Poldrack, 2006; Poldrack and Wagner, 2004). Furthermore, a modular perspective fails to appreciate the activity of this region in the context of the other activities within the brain. The systematic association of a region with an EF such as inhibition could therefore reflect an emergent property of a broader neural network (e.g., involved in detection of salient cues, such as for inhibition; Hampshire et al., 2010), and thus risks to falsely localize higher-level cognitive processes at a lower level of processing (Eisenreich et al., 2017), especially in highly connected regions such as the ACC and basal ganglia.

Although it is intuitive to assume that conceptually distinct EFs must also have distinct anatomical representations (Botvinick and Cohen, 2014), attempts to identify neuroanatomical correlates of the central executive (Baddeley, 2012; Botvinick et al., 2004, 2001; Braver, 2012; Diamond, 2013; Engle and Kane, 2003; Friston, 1994; Goldman-Rakic et al., 1996; Goschke and Bolte, 2014; Hazy et al., 2007, 2006; Hommel and Wiers, 2017; Koechlin and Summerfield, 2007; Miller and Cohen, 2001; Monsell and Driver, 2000b; Pezzulo et al., 2018; Shenhav et al., 2016, 2013) have not yet led to breakthroughs to describe their neurophysiological mechanisms. The idea of subsystems that provide specialized, subsidiary central executive functions is challenged by empirical evidence suggesting that the same putative brain correlates for EFs such as the PFC and ACC have been associated with functionally different EFs (Alexander and Brown, 2011; Botvinick et al., 2004; Braver, 2012; Bush et al., 1999; Carter and Veen, 2007; Hare et al., 2009; Kahnt et al., 2011; Kerns, 2004; Kondo et al., 2004; Lim et al., 2011; MacDonald et al., 2000; Milham et al., 2001; Ridderinkhof et al., 2004; Shenhav et al., 2016, 2013; Steinbeis et al., 2016; van Veen et al., 2001; Vassena et al., 2014; Weissman, 2004; Weissman et al., 2003). This raises the question how a plethora of diverse EFs can arise from a rather static neuroanatomical architecture (Park and Friston, 2013). In complement, different EFs such as inhibition, flexibility, and working memory have been shown to activate large proportions of the cerebrum and converge within PFC, ACC, and posterior parietal cortex (Niendam et al., 2012). Moreover, the putative brain areas underlying EFs also show large functional overlap, such as in goal directed behavior (ACC; Carter and Veen, 2007; dlPFC; Hare et al., 2014; Kahnt et al., 2011; Sokol-Hessner et al., 2012; Steinbeis et al., 2016); vmPFC; Hare et al.,

2014, 2009; Kahnt et al., 2011; Sokol-Hessner et al., 2012; Steinbeis et al., 2016), prediction and evaluation of an action (ACC; Alexander and Brown, 2011; Bush et al., 2002; Ridderinkhof et al., 2004; Shenhav et al., 2016, 2013; Vassena et al., 2014); vmPFC; Vassena et al., 2014), and selective attention (ACC; Bush et al., 1999; Milham et al., 2001; Weissman, 2004; Weissman et al., 2003); vmPFC; Lim et al., 2011; dlPFC; Milham et al., 2001), which challenges the functional specificity of these regions. Arguably, the focus on activity of specific regions of interests or single event-related components has therefore substantially limited the possibility to identifying the neural correlates of EFs from a whole brain perspective.

Increasing evidence suggests that these putative brain areas underlying EFs seem to interact. The ACC, for instance, has been found to support PFC in maintaining and updating task-relevant representation in working memory (Banich et al., 2000; D'Esposito and Postle, 2015; Egner and Hirsch, 2005) and signal the need for control (Botvinick et al., 2004; Hazy et al., 2007). Furthermore, studies indicate that cognitive flexibility is orchestrated within BG (Aron et al., 2003), but also supported by PFC (Chakravarthy et al., 2010; Stocco et al., 2010) and ACC (Nicolle and Baxter, 2003). Similarly, close interrelation between PFC and BG were found to support WM processes (Ashby et al., 2005; Baier et al., 2010; Chang et al., 2007; Frank et al., 2001; McNab and Klingberg, 2007; Schroll et al., 2012; Schroll and Hamker, 2013; Voytek and Knight, 2010). Thus, once again, the data suggest that pivotal brain areas that contribute significantly to EFs, such as PFC, ACC, and basal ganglia, act within spatially distributed networks and include other structures that may also be relevant to explain EFs. This point is echoed in studies of neuropsychiatric disorders that exhibit impairments in EFs, and that reveal aberrant development and functional connectivity in spatially distributed brain networks (Assaf et al., 2010; Baker et al., 2014; Bassett et al., 2012; Cerliani et al., 2015; Chai et al., 2011; Cherkassky et al., 2006; dos Santos Siqueira et al., 2014; Du et al., 2016; Fan et al., 2012; Fassbender et al., 2009; Franzen et al., 2013; Garrity et al., 2007; Hull et al., 2017; Itahashi et al., 2014; Jafri et al., 2008; Jang et al., 2011; Liddle et al., 2011; Lin et al., 2015; Manoliu et al., 2014; Meda et al., 2014; Murias et al., 2007; Öngür et al., 2010; Orliac et al., 2013; Paakki et al., 2010; Pomarol-Clotet et al., 2008; Roiser et al., 2013; Rotarska-Jagiela et al., 2010; Salgado-Pineda et al., 2011; Sripada et al., 2014; Sun et al., 2014; Swanson et al., 2011; Tian et al., 2008; Tu et al., 2013; Uddin et al., 2008; van Buuren et al., 2012; Wang et al., 2005; Weng et al., 2010; Whitfield-Gabrieli et al., 2009; Wilson et al., 2011; Woodward et al., 2011).

Thus, mounting evidence suggest that there is no single brain region that sits at the control apex, and, furthermore, efforts to define EF-dedicated neuroanatomical substrates have not been conclusive. The question of how EFs are generated by the brain persists. In the following sections we consider an alternate view to centralized or localized EFs. We argue based on suggestions from the cognitive and computational literature(Barnard and Bowman, 2004; Eisenreich et al., 2017; Vandierendonck, 2016), and in line with the recognized significance of functional connectivity patterns to neural organization and function (Collin et al., 2014; Margulies et al., 2016; van den Heuvel et al., 2012; van den Heuvel and Sporns, 2013), that EFs are neither a strictly top-down generated process nor one that can be localized in specific brain correlates, but rather that EFs are the *emerging consequence* of communication within a broad network of spatially and functionally dispersed brain areas that integrate different aspects of EFs.

3. Distributed control and executive functions

A core assumption underlying many theoretical frameworks on EFs is of hierarchical architecture, namely, that brain areas or circuits underlying EFs regulate, but do not participate in the more basic cognitive processes that they control (Botvinick et al., 2001; Miller and Cohen, 2001; Fig. 1A). This top-down view, by design, relies on a centrally operating executive. However, Barnard and Bowman (2004);
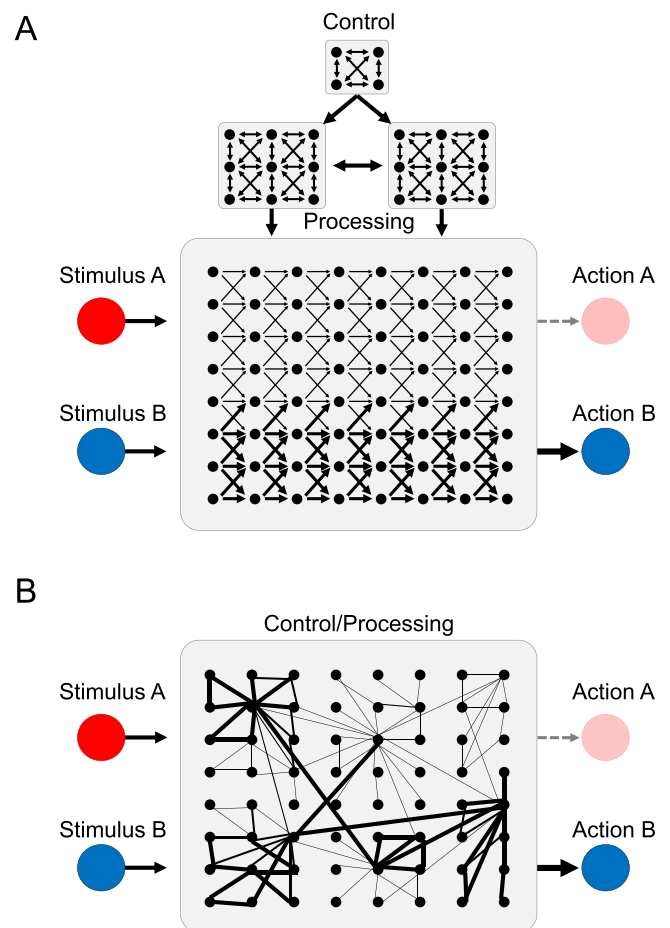

Fig. 1. Organization of a modular executive control network vs. a distributed control network, in which two stimuli (stimulus A and stimulus B) lead to an action outcome (action A vs. action B). A. Top-down controlled, hierarchically organized control-modules govern automatized processing. In this system, control and processing elements are distinct and localized to specific areas. B. Distributed control networks, in which control and processing elements are combined in individual agents. These agents form individual clusters. Adapted and modified from Eisenreich et al. (2017).

Vandierendonck (2016) and Eisenreich et al. (2017), have argued that EFs can also be a result of a conceptually and anatomically distributed control system (DCS). One such DCS view is inspired from early connectionist models (Hopfield, 1982; James and Rumelhart, 1986), in which control and controlled processes are co-localized within large numbers of dispersed elements (Fig. 1B). In contrast to a hierarchical architecture where core brain regions are assumed to solely exert control on more basic processes, in a DCS, each element can be a controller and an element that is being controlled. In computational models of distributed control, the state of the overall system is often independent from any constituting element (Barnard and Bowman, 2004). In other words, in such systems, behavioral control is analogous to the state of the overall system, and is therefore an emergent function arising from the interaction of all elements (McClelland et al., 2010; Mitchell, 2009). Recent evidence of distributed control in nonbrain biological systems such as in schools of fish, flocks of birds, swarms of insects (Couzin, 2009; Eisenreich et al., 2017; Passino et al., 2008), and herds of baboons (Couzin and Krause, 2003; Strandburg-Peshkin et al., 2015) and in distributed deep learning algorithms (LeCun et al., 2015) highlight the strength and plausibility of a DCS view. Apparent control in these biological distributed systems is often realized via a couple of simple rules that guide the indirect coordination between agents or actions. In schools of fish or flocks of birds, the control over the shape of the swarm

and the moving direction is a consequence of the distance kept between adjacent agents and the rule about when to change direction (i.e. follow the group average; Couzin and Krause, 2003). These rules enable fast communication of information (e.g. about the direction of movement) across all agents, without reliance on a top-down controller.

Can a DCS framework explain EFs? EFs can be conceptualized as a consequence of the interaction between distributed elements, thus avoiding the problem of any central executive or central executive subsystem. Increasingly evidence suggests that, indeed, properties of EF generation in the brain are consistent with properties of a DCS. One such principle is that all elements can be controlled or be a controller, or, in other words, the emergent property can be observed in any subset of the system. Several studies have highlighted that prefrontal regions, a putative apex of the central executive, as well as posterior regions seem to exhibit both basic and control processing (Awh and Jonides, 2001; Cisek and Kalaska, 2010; Postle, 2006; Sleezer and Hayden, 2016). In line with the DCS view, it has been suggested that working memory (WM), a core EF, is a general property of the cortex, not limited to specific regions (Lee and Baker, 2016; Postle, 2006). This proposal shifts perspective of WM from localized to a highly distributed process wherein information can be maintained in any system engaged in the initial perceptual processing, including any region contributing to the initial percept (Lee and Baker, 2016). The second key principle of a DCS is the existence of local rules capable of generating the emergent phenomenon, such as the distance kept between adjacent agents in a swarm. In the brain, from single neuron firing to neuron populations and between brain area communications, each level is a complex function of its lower level constituents and embedded in a larger-scale organization (Buzsáki, 2006). In this context, EFs such as the initiation vs. the inhibition of an action or switching to another action might be the emergent behavioral outcome from simpler local neurophysiological mechanisms of the participating brain areas, for instance via neuronal interactions resulting in local gain modulation (Abbott, 1997; Chance et al., 2002; Donner and Nieuwenhuis, 2013; Saalmann and Kastner, 2009; Salinas and Thier, 2000) and the collective state of each contributing neuron (Buzsáki, 2006). In particular, evidence supporting biased competition among neuronal populations in generating initiation or inhibition in selective attention (Desimone, 1998; Desimone and Duncan, 1995), suggests that such competition is a general property of neurons across the brain, not limited to any central controller. From this perspective, the emergence of executive control patterns (e.g. initiating or inhibiting an action or switching to another action) observed in putative control structures like the PFC, ACC, and basal ganglia may reflect the overall state of the system, in the same way a single fish in a swarm or a single bird in a flock reflects the state of the overall system (i.e. the trajectory of the movement), without the requirement to be on top of the hierarchy in the control system.

Another key property of a DCS is its robustness to perturbations. In contrast to centralized systems, in which a nonbrain biological systems such as swarm would be vulnerable to the loss of its leading agent, a swarm organized as a DCS has been shown to be robust to degradation (Sumpter, 2006). Similarly, decentralized (i.e. distributed) networks have been shown to be resilient systems which are capable of absorbing large external perturbations without undergoing functional breakdown (Achard, 2006; Bassett and Bullmore, 2006; Bullmore and Sporns, 2009; Buzsáki, 2006). A DCS network organization in the brain may therefore explain how EFs can be preserved to some extent in the face of pathological attack by lesion and substance-related disorders (Ahmadlou et al., 2013; Wang et al., 2015; Yuan et al., 2010), neuropsychological disorders like ADHD (Ahmadlou et al., 2012; Liu et al., 2015; Wang et al., 2009; Xia et al., 2014), schizophrenia (Liu et al., 2008; Michel-oyannis et al., 2006; Rubinov et al., 2009; Shim et al., 2014), and restless legs syndrome (Choi et al., 2017), aberrant development such as in autism (Barttfeld et al., 2011; Itahashi et al., 2014), and cognitive decline such as Alzheimer's (Frantzidis et al., 2014; Stam et al., 2006; Vecchio et al., 2016; Wei et al., 2015; Zeng et al., 2015) and Parkinson's

disease (Berman et al., 2016; Lebedev et al., 2014). As noted previously, damage to the PFC, as well, may or may not be accompanied by deficits in EFs, and neither site nor size of a prefrontal lesion allow for a clear prediction about the nature of resulting problem in executive functioning (Alvarez and Emory, 2006). Thus, EFs do exemplify some robustness in the human brain. One way to investigate the robustness of EFs as a DCS is using 'lesioned' networks in computational models, which investigate how an observed profile of anatomical or functional dysconnectivity in a mature network might have been generated by earlier developmental abnormalities (Achard, 2006; Honey and Sporns, 2008; Kaiser et al., 2007; Ravasz and Barabási, 2003; Sporns, 2006). In order to explore the effect of acute damage on overall performance in EFs, nodes or connections are deleted. The vulnerability of a network to damage is then assessed by comparing its efficiency after the lesioning to its intact behavior. In an anatomically informed computational model, in line with the DCS view, deletion of nodes did not impair EFs.

4. A new era for executive functions

Despite the appeal of the DCS view as an elegant theoretical solution for the aforementioned problems with centralized EF frameworks, and despite indirect evidence for the viability of DCS as a putative alternative, direct empirical studies of the neurophysiological mechanisms of a DCS governing EFs are scarce. This may be attributed in part to limited awareness of this framework in the field and in part to inherent difficulties in translating DCS concepts, such as the existence of organizing rules, to testable hypotheses. A key challenge is to derive descriptive measures that could provide testable hypothesis of the organizational rules that drive the network towards emergence of EFs. However, one promising approach to investigate EFs from a DCS perspective is the application of methods from network science, primarily graph theory, to neuroimaging data. A DCS conceptualizes executive functioning as an eminent property of multiple interacting elements of the brain. This is analogous to the network science framework, which aims to summarize, via a family of derived metrics, the organizing principles of a set of connected nodes. Hence, the graph theory framework is naturally aligned with a distributed perspective on EFs, with derived metrics potentially capturing the organizing principles or local rules that guide the behavior of the system. The task then becomes to model the brain as a network in which brain areas or constellations act as nodes (i.e. agents) and functional communication among these nodes are represented as edges, and, critically, to relate the static and dynamic features of the resulting network to EFs. In contrast to putting emphasis on the identification of specialized subsystems of EFs that are assumed to exert control over basic processes, a network analytical approach puts focus on how these brain regions or sub-systems (i.e. network nodes) communicate (i.e. are connected) with each other.

From a network perspective, this means that functionally different EFs such as inhibition, and cognitive flexibility can recruit a set of similar or overlapping brain structures (i.e. PFC, ACC, and other regions), but the connectivity patterns within these networks between perceptual input and motor output are functionally different. The connectivity patterns between the involved agents can, in principle, either result in refraining from an action (i.e. inhibition) or shifting to another action (i.e. cognitive flexibility). In other words, we hypothesize that the emergence of a given EF may lie in a given network state, as determined by organizing rules.

One important characteristic of networks, and putative organizing rule, is the structural and functional efficiency of its architecture. From an evolutionary perspective, brain networks have been evolved to maximize the diversity of possible functional circuits (i.e. enabling functionally different EFs), while minimizing the diversity of structural circuits (i.e. enabling efficient assembly and encoding) (Sporns and Kötter, 2004). Thus, the brain seeks towards minimal complexity of neural architecture with maximal richness of function. This may explain why putative brain correlates of specific EFs (i.e. PFC and ACC) have

also been associated with other functionally different EFs (Alexander and Brown, 2011; Botvinick et al., 2004; Braver, 2012; Bush et al., 1999; Carter and Veen, 2007; Hare et al., 2009; Kahnt et al., 2011; Kerns, 2004; Kondo et al., 2004; Lim et al., 2011; MacDonald et al., 2000; Milham et al., 2001; Ridderinkhof et al., 2004; Shenhav et al., 2016, 2013; Steinbeis et al., 2016; van Veen et al., 2001; Vassena et al., 2014; Weissman, 2004; Weissman et al., 2003). From a graph theoretical perspective, the efficiency of large-scale communication between different brain areas is defined by the number of connections necessary to connect all neurons, a measure that is referred to as average synaptic path length (Fig. 2A). Additionally, metabolic efficiency in brain networks is realized by predominantly local connectivity (Yoshimura et al., 2005) or local clustering (Fig. 2B), which avoids metabolically expensive long-range axonal connections (Kalisman et al., 2005). However, a purely local clustering in the network would dramatically increase the average number of connections necessary to connect all neurons (i.e. the average path length). Thus, two network organization principles—local clustering and average path length —compete with each other to providing network communication that is metabolically efficient (i.e. high local clustering), but also enables effective large-scale communication (i.e. low average path length). Networks, which enable efficient large-scale traffic while maintaining mainly local connectivity are called 'small-world' networks (Watts and Strogatz, 1998; Fig. 2E). Despite considerable heterogeneity in the methodological approaches, there is an encouraging degree of convergence between small-world properties on the structural (Chen et al., 2008; Hagmann et al., 2007; He et al., 2007b; Iturria-Medina et al., 2008, 2007; Sporns and Kötter, 2004) as well as on the functional brain network level (Ferrarini et al., 2009; Liu et al., 2008; Meunier et al., 2009; Salvador, 2004; Schwarz et al., 2008; Wang et al., 2009; Xia et al., 2014). Thus, the small-world properties of neural networks may be a key organizing principle that provides a functional link between brain structure and EFs (Beste et al., 2019). Namely, we suggest that EFs are the result of the brain's need to be structurally and functionally efficient. Recent findings highlight that the efficiency of how brain networks communicate (i.e. the small-world network characteristic) is strongly related to the demand on EFs. Differences in small-world properties have been shown for different demands on EFs (Beste et al., 2019; Wolff et al., 2017; Zink et al., 2018). Higher demand on inhibition (Hong et al., 2016), cognitive flexibility and WM capacity, for instance, have been found to lead to decreased

small-world properties in the involved functional networks (Wolff et al., 2017), suggesting that EFs emerge when the brain is tipped away from a small-world state. This would predict that training EF capacities should lead to more efficient (i.e. more 'small-worldish') functional network communication. Consistent with this prediction, training in EFs such as WM capacity has shown to improve the efficiency of functional networks in the brain (Langer et al., 2013).

Of particular interest, small-world architecture results in a system that is neither exclusively top-down in information flow, or exclusively distributed. The system necessitates the existence of so-called hub nodes, that are highly connected and serve a key role in facilitating the balance between high-local clustering and low average path length (van den Heuvel and Sporns, 2013; Fig. 2C). However, such hub-nodes, due to their high-connectivity, can, in a way, exert control over less-strongly connected nodes along the action cascade and thus may play a key role in driving the functional connectivity state of the system and the emergence of behavior (Fig. 2C). Supporting this notion, in a simulated model, deletion of well-connected nodes produced disruptions of functional connectivity (Falcon et al., 2015; Honey and Sporns, 2008; Jirsa et al., 2010) consistent with reported effects of focal human brain lesions on EFs (He et al., 2007a). These facts have also led to the proposal that there exists a connective core network, that is a metabolically costly yet highly integratory collective of brain regions, whose anatomical wiring and topological position within the brain network supports brain-wide communicability and which exerts control over brain dynamics and cortical states (Collin et al., 2014; de Reus and van den Heuvel, 2014; Senden et al., 2017; Shine et al., 2018; van den Heuvel et al., 2012; van den Heuvel and Sporns, 2013). Here we additionally suggest that such a network drives brain states in observance of or striding towards a small-world state, with no single region acting as a core executive or solely responsible solely for the maintenance of behavioral goals (e.g., PFC). It is sensible to suppose that regions previously associated with EFs (i.e. PFC, ACC, basal ganglia) contribute to this network, though the identity of this network, or networks, remains an open question. A large scale meta-analysis of fMRI literature has shown that a superordinate fronto-cingulo-parietal network underlies a range of different EFs such as inhibition, flexibility, and working memory, consistent with expectation, but also integrating the inherent biases in published literature (Niendam et al., 2012). In contrast, in an original research study, Dosenbach et al. (2007), used network analyses on a set of 39 predefined
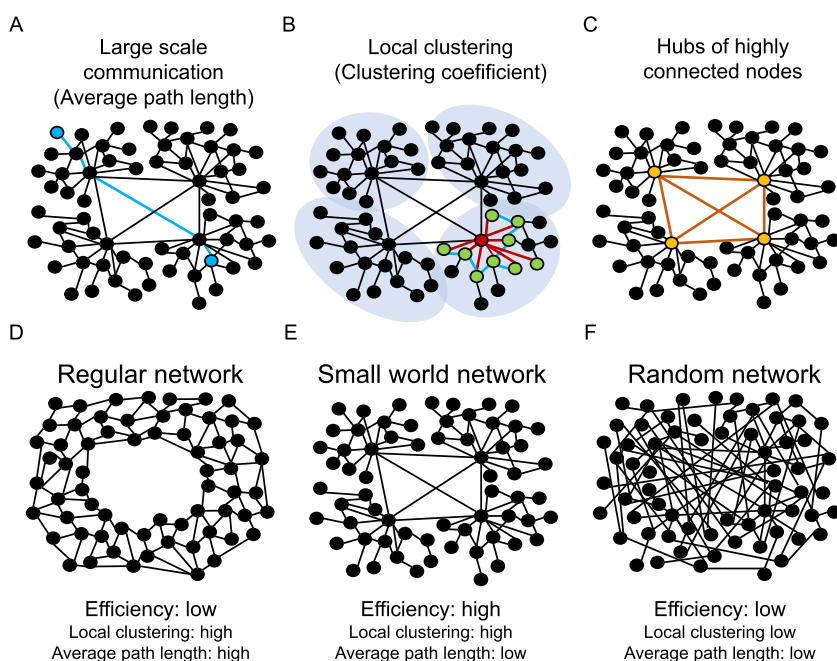

Fig. 2. Graph theoretical characteristics of distributed control networks in the brain. Functional integration capacity in neural networks can be quantified by the average path length (A), which describes the average number of edges (marked in blue) to connect each node to any other node in the network (marked in blue). Functional separation capacity in neural networks can be quantified by the clustering coefficient (B), which describes the interconnectivity of neighboring nodes. The clustering coefficient is exemplified in (B), where connections for one node (marked in red) to its immediate neighbors (marked in green) are colored in red and the connections between these neighbors are marked in blue. All real networks lie on a spectrum between very regularly and very randomly connected. Regular networks (D) exhibit a high clustering coefficient and a high average path length. Random networks (F) show a low clustering coefficient and a low average path length. According to Watts and Strogatz (1998), a network shows small-world network properties (E) when it demonstrates a high clustering coefficient as in regular networks and a low average path length as in very random networks. In case a network shows small-world properties, highly connected nodes form hubs that integrate high local connections with long range connections (C).

regions of interests (ROIs) to reveal two separate networks of ROIs that both showed small-world characteristics: A frontoparietal network that included dlPFC that was more strongly associated with control adaptation and another network including the ACC, that was more strongly associated with WM processes. These data raise the open question of whether there exists a single superordinate EF network, whether multiple networks exist for different EFs or whether, as we suggest here, EFs are purely emergent phenomena with no underlying network, that arise when the brain responds to disturbances of its small-world state.

5. Conclusion

Despite the experimental and theoretical progress in research on EFs, efforts to identify circumscribed brain areas associated with executive functioning have not satisfactorily described the neurophysiological mechanisms that drive EFs. Increasing evidence from neuroimaging suggests instead that the dynamics of a superordinate, spatially distributed brain network, or networks, underlie EFs. A paradigm change from a centralized view, in which single areas exert top down control over the more basic processes they regulate, towards a distributed control system view, in which each brain network agent controls and is being controlled, provide a new perspective on mechanisms of how EFs emerge, with small-world organization a putative driving principle. Emerging studies that leverage network science, and emphasize emergent network dynamics, pave the wave to a new era of EF research.

Acknowledgements

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