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Opinion

The Dorsal Frontoparietal Network: A Core System for Emulated Action

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The dorsal frontoparietal network (dFPN) of the human brain assumes a puzzling variety of functions, including motor planning and imagery, mental rotation, spatial attention, and working memory. How can a single network engage in such a diversity of roles? We propose that cognitive computations relying on the dFPN can be pinned down to a core function underlying offline motor planning: action emulation. Emulation creates a dynamic representation of abstract movement kinematics, sustains the internal manipulation of this representation, and ensures its maintenance over short time periods. Based on these fundamental characteristics, the dFPN has evolved from a pure motor control network into a domain-general system supporting various cognitive and motor functions.

The Domain-General Role of Dorsal Frontoparietal Cortex

Human cognition is sustained by structurally and functionally organized networks of the brain, often labeled using broad anatomical or functional descriptors [1–3]. One of the most prominent, the **dFPN** (see Glossary), connects the superior parietal cortex with dorsal **premotor cortex** (PMd) [4]. These regions exhibit a strongly correlated pattern of activation at rest and during various motor or cognitive tasks, such as reaching and grasping, **saccades** and spatial attention, mental rotation, or working memory. The reasons for this diversity of activations remain obscure, because most studies of the dFPN have focused on a specific cognitive domain, such as attention [5,6], executive function [2], or cognitive control [7,8]. Here, we propose that, to understand the role of the dFPN, we should proceed backwards and examine the joint characteristics of distinct cognitive operations that may lead to overlapping activations in this cortical area. Common activations more likely reflect a shared computational process than distinct and independent processes [9,10]. This assumption rests on the principle of cognitive economy, which says that brain systems save processing load and capacity by sharing resources between different tasks. Complex cognition is rooted within elementary 'core' functions and is structured hierarchically, where more general-purpose and elaborate functions emerge from combinations of more basic processes.

We further propose that the dFPN evolved as an extension of a simple action-control network connecting the **posterior parietal cortex** (PPC) with the PMd, and that the cognitive functions of this network are rooted within its fundamental capacity to support planning and imagining actions. We use the term '**emulation**' to denote this core function of the dFPN [11,12]. Action emulation comprises the potential to establish a dynamic internal representation of movement, and to manipulate and maintain this representation over time. These fundamental characteristics of action emulation have driven the transformation of the dFPN from a motor network into a domain-general system.

Trends

Abundant functional imaging research supports a comprehensive role of the dFPN in multiple motor and cognitive functions.

These functions can be pinned down to a common 'core' computation whose essential role it is to establish abstract representations of movement kinematics: action emulation.

Through synergy and recombination of basic cognitive components, more complex functions emerge from action emulation during child development.

The dFPN eventually assumes a domain-general role in spatial attention and working memory, laying the foundation for general reasoning, decision making, and intelligence.

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An Outline of the Emulation Account of dFPN Function

Action emulation is the abstract, offline representation of movements expressed in terms of their pragmatics (action goals) and kinematics (movement patterns). The term 'emulation' is borrowed from computer science, where it describes the ability of a program to imitate the behavior of other programs. The existence of emulation processes in motor planning is inferred from the observation that motor control relies on predictions of the consequences of motor plans (Figure 1A). Performing a skilled action requires online adaptation and control, and relies on continuous sensory feedback available during the movement [13]. Since feedback processes have limited value as predictors of the future impact of an action [14], models of action control propose that motor planning entails the anticipation of the predicted state of an effector compared with its desired state [15]. This comparison is accomplished through a **forward model** of the motor-to-sensory transformation required for successful action [16,17]. An emulator receives input from processes involved in motor planning and computes a forward model of proprioceptive and kinematic output just as though the movement had been
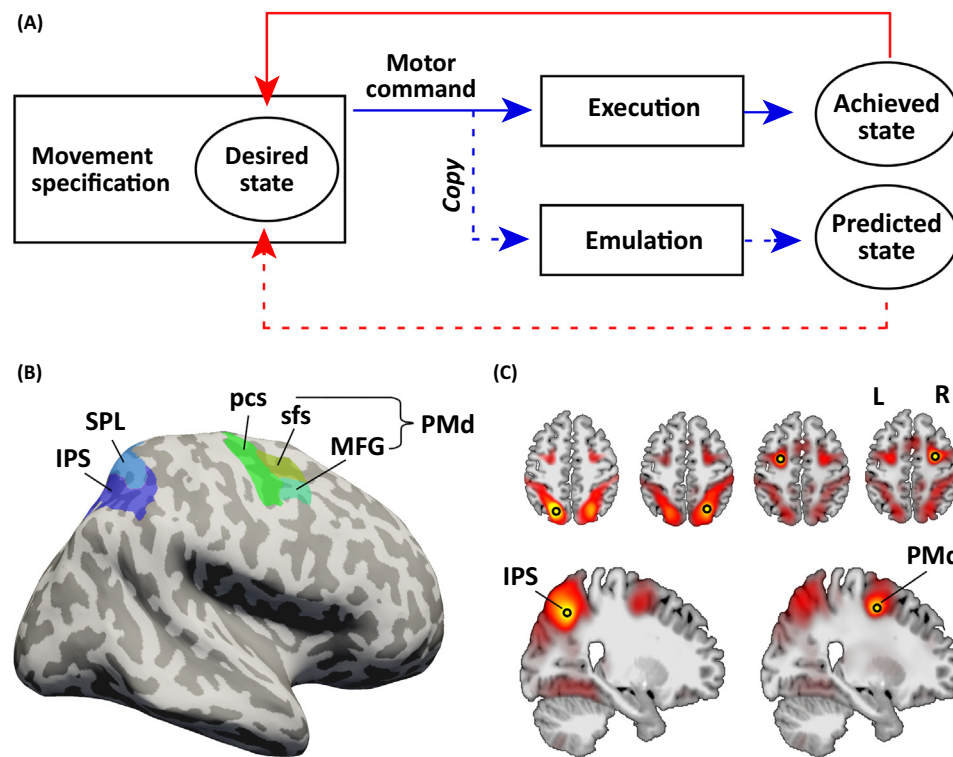
Figure 1. Action Emulation and the Dorsal Frontoparietal Network (dFPN). (A) Simplified model of motor planning, movement execution, and emulation. Movements specified in terms of spatiotemporal and kinematic properties define a desired state and determine the associated motor command, which sends feedforward (blue) input to execution systems and an **efference copy** of this input to the emulation system. Both systems produce output in the form of new states of the effector, which are compared with the desired state via feedback loops (red). (B) The anatomical definition of the dFPN as derived from resting-state fMRI connectivity, shown on a flattened brain. The superior parietal lobule (SPL) and intraparietal sulcus (IPS) constitute the parietal node of the dFPN (blue), while dorsal premotor cortex (PMd) lying in the caudal middle frontal gyrus (MFG) and adjacent sulci comprises its anterior node (green). The frontal eye field (FEF) is located at the junction between the superior frontal sulcus (sfs) and the precentral sulcus (pcs). (C) Resting-state connectivity of the dFPN based on data from 1000 subjects. The figure shows voxels of significant coactivation with a specific 'seed' voxel (small circle), which was placed manually at selected regions within the IPS or the PMd of the left/right cerebral hemisphere. Irrespective of the location of the seed, the results identify the same intrinsic organization of functional connectivity between dorsal frontoparietal regions and across both cerebral hemispheres (data were generated in Neurosynth [140] and are based on a large-scale connectivity study by Yeo *et al.* [1]).

Glossary

Dorsal frontoparietal network (dFPN): functional network connecting the superior parietal cortex with the dorsal premotor cortex.
Efference copy: internal copy of a motor plan that becomes available to sensory and cognitive systems generating a prediction of movement outcome.
Emulation: abstract representation and offline maintenance of the kinematic properties of a movement plan.
Forward model: mental representation of a movement plan that allows predicting action outcomes by comparing a predicted state with the desired final state of a motor effector.
Intraparietal sulcus (IPS): fissure dividing the posterior parietal lobe into a superior and inferior part.
N-back task: experimental paradigm requiring subjects to decide whether the current stimulus (e.g., a number) matches an item presented *N* steps earlier in a continuous sequence.
Optic ataxia: a disorder of visually guided movement observed in patients with PPC damage, mainly affecting reaching and pointing toward objects in the peripheral visual field.
Posterior parietal cortex (PPC): portion of the parietal lobe that mainly comprises polymodal association cortex and is located posterior to the primary somatosensory cortex.
Premotor cortex: portion of frontal cortex that lies anterior to the primary motor cortex and covers Brodmann area 6 and parts of area 8 at the lateral surface of the brain.
Premotor theory of attention: hypothesis postulating a causal link between motor programs for eye movements and spatial attention.
Saccade: a fast, ballistic eye movement that directs the fovea toward a stimulus of interest. Saccades may be triggered reflexively by an abruptly appearing stimulus or voluntarily by conscious plans.
Simulation theory: proposal that movement-related brain activity can be reproduced mentally without the necessity to execute the movement.
Superior parietal lobule: portion of the parietal lobe delimited by the postcentral sulcus, the intraparietal sulcus, and the parietooccipital sulcus.

performed [12]. We conceive emulation as a central process that deals specifically with dynamic motor representations, irrespective of the action trigger and the output effector. Evidence for such abstract motor representations comes from studies showing invariant brain activity in frontoparietal cortex for imagined versus performed [18], self-initiated versus externally triggered [19], and right- versus left-hand movements [20].

The emulation account of higher cognition is based on the further assumptions that cognitive development depends on the reenactment of sensorimotor experiences [21,22], and that increasingly complex behavior emerges through the recombination of existing core functions. During child development, new capacities do not emerge in the form of entirely novel computational processes, but through recombination of elementary motor control and object representation functions and their expression in a new context [23]. This notion of synergy through cognitive recombination differs from competitive accounts of culturally driven abilities, such as reading and numerical cognition, which may rival with and eventually supersede phylogenetically older functions [24,25]. We argue instead for a relation of complementarity and gradual diversification of dFPN function. The ability to imagine motor acts provides an excellent illustration of cognitive synergy, because it results from conjoint activation of movement kinematics, proprioceptive signals, and a visual representation of the own limb [26,27]. Motor imagery is the mental rehearsal of manual actions, such as aiming, moving, or rotating objects, akin to the **simulation** of real movements [21,28–30]. Likewise, the **premotor theory** conceives spatial attention as simulated eye movements, where the attentional focus of an 'inner eye' reproduces spatiotemporal dynamics of saccades [31]. While simulation has been proposed to underlie a variety of perceptual, motor, and introspective states [21], we understand emulation as a purely motor process that is independent of action triggers and effectors.

The emulation account posits that the manipulation of objects not only shapes the ability of the child to replay object manipulations mentally, but also to establish a modal representation (as opposed to a symbolic representation [32,33]) of action and object properties that can be used for higher-order computations. Instead of culminating in a real movement, emulated motor plans activated during mental imagery act upon visual images generated by the extrastriate cortex and the PPC [34], thus making possible the manipulation, transformation, or maintenance of images in mind. For example, an emulated motor plan generated for a rotation movement may be applied to an imagined action (locking the door) or to an imagined object (rotating a street map to its canonical orientation). Under this account, mental rotation and spatial working memory are akin to an emulation process applied on mental images. Thus, the functional diversity of the dFPN emerges from the synergistic activation of motor and perceptual representations, their mental manipulation, and maintenance. Through the recombination of elementary cognitive capacities, a domain-specific system present in the child is gradually transformed into a cognitively flexible and diversified system in the adult.

This notion of motor-to-cognitive diversification makes several predictions. First, since imagined and real actions rely on the same motor plan, they should be strongly interdependent. Second, cognitive functions, such as spatial attention, mental rotation, and working memory, should emerge from motor competency during child development. Finally, dFPN damage should lead to correlated deficits of motor planning and cognitive functions supposed to rely on this network. Before addressing these predictions, we present neuroimaging findings showing the large variety of motor and cognitive functions that are sustained by the dFPN.

The dFPN Is a Common Substrate for Motor and Cognitive Processes

One of the central tenets that the action emulation account has in common with other accounts is that a more complex cognitive process may emerge from simpler processes if it shares neural sources and uses overlapping computational mechanisms. Resting-state fMRI connectivity

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**Box 1. The Equivocal Anatomy of Brain Networks**

Anatomical definitions of cortical networks vary in the function of the applied method. Resting-state functional connectivity data, task-induced fMRI activations, and diffusion-tensor imaging (DTI) provide complementary, yet only partly overlapping approaches. For example, analyses of fMRI connectivity identify cortical areas communicating with each other, while DTI examines large subcortical fiber tracts, but has less statistical precision regarding their cortical origins. Task-induced activations vary as a function of the experimental paradigm and do not necessarily respect the boundaries of areas defined by structural or functional connectivity [121,122]. Comparative anatomical studies of the monkey brain add another problem, which has to do with evolutionary changes of frontoparietal anatomy. For example, the frontal eye field (FEF) of the rhesus monkey is located anteroventrally to the PMd, while its location in humans is more superior and posterior [123]. The human parietal lobe also shows evidence for evolutionary expansion from the inferior to the superior parietal cortex, in particular regarding the planning of reaching and grasping movements [41]. Finally, evolutionary adaptations have led to less functional specialization of dFPN regions in humans: in the monkey, specialized regions for reaching and grasping can be distinguished, whereas, in humans, the presence of reach and grasp-related activity is more diffuse and distributed across parietal cortex [41,124].

Given these ambiguities, we here apply a heuristic approach and define the superior parietal lobule and the intraparietal cortex (Brodmann area 7 and the border region of areas 40, 39, and 19) as the parietal part of the dFPN and the dorsal frontal cortex (area 6 and the posterior portion of area 8) as its premotor part (see Figure 1 in main text). This heuristically defined network partially overlaps with a dorsodorsal frontoparietal network postulated based on single-neuron studies [125] and a task-evoked dorsal attention network identified using fMRI [5].

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defines the anatomy of the dFPN (Box 1) and provides tentative support for this assumption. Although resting-state oscillations do not inform about the cognitive processes occurring in a network, they suggest that spontaneous activity between interconnected regions is highly coordinated and, hence, that they might be engaged in common functions [7,35–37] (Figure 1B,C).

However, more direct evidence comes from active-state studies. Task-related activations associated with the execution of simple arm movements (pointing or reaching), hand movements (grasping), or coordinated hand–finger movements (writing or drawing) are found in the superior parietal cortex, **intraparietal sulcus** (IPS), and precuneus [38–40]. Similarly, the PMd is activated by these three types of motor activity [41] (Figure 2A). Another important finding is that reach- and grasp-related activity engages the dFPN to a similar degree, whether movements are performed in the dark or while the arm is visible [40], and when movements are delayed (requiring active maintenance in working memory) [42], or merely observed [43]. In addition, activity of the PMd, **superior parietal lobule** (SPL), and IPS is a strong predictor of different kinds of motor learning [44]. Together, these findings support the involvement of a process that relies on the abstract representation of movement kinematics, irrespective of the effector, visual feedback, or actual movement execution.

The emulation account also posits that the crucial step in the elaboration of cognitive representations of actions is simulation and, hence, that brain regions involved in action execution should also be recruited by motor imagery. Indeed, imagined and executed actions activate the PMd and the parietal cortex comparably [26,45] and this holds even when advanced multivariate techniques are applied [18,46,47]. An early study also observed nearly identical activations of the SPL and PMd when subjects imagined rotating their hand (requiring motor imagery) or mentally rotated depicted tools (requiring purely perceptual transformations) [48]. A more recent meta-analysis confirmed that mental rotation activates primarily the superior parietal and intraparietal cortex, as well as the premotor cortex [49]. Thus, the dFPN appears to offer the neural substrate for functions that support motor actions, their mental replay, and non-motor mental manipulation. This conclusion is further supported by neuroimaging studies of spatial working memory. To mentally rotate an object subjects must maintain its internal representation in mind while manipulating this representation. The focus of many working-memory studies has been on prefrontal cortex; however, meta-analyses on large numbers of neuroimaging studies show that the maintenance and mental manipulation of the contents of working memory not
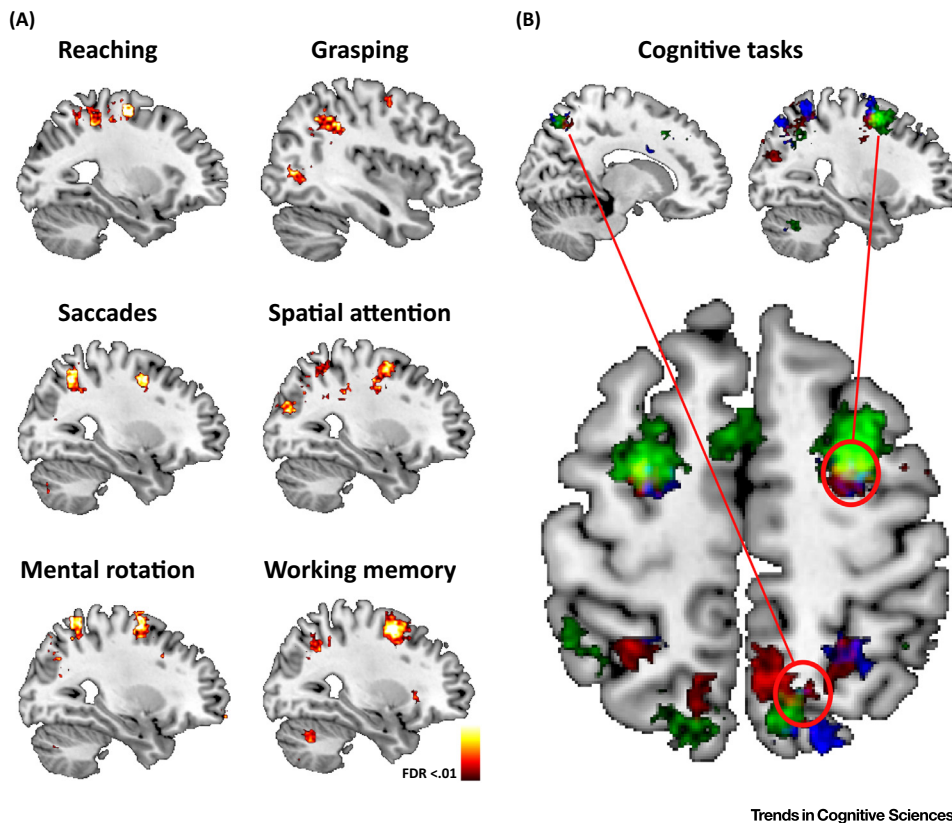
Figure 2. Task-Evoked Activations of the Dorsal Frontoparietal Network (dFPN). (A) Meta-analytic results of studies targeting different motor (reaching, grasping, and saccades) and cognitive tasks (spatial attention, mental rotation, and working memory). Meta-analyses were generated in Neurosynth [140], whereby studies of clinical populations, children, or older participants, as well as studies that did not contain whole-brain analyses were excluded. The respective numbers of studies contributing to these meta-analyses were: ten (reaching); 22 (grasping); 18 (saccades); 25 (spatial attention); 12 (mental rotation), and 72 (working memory). (B) Comparison of activations induced by three cognitive functions supported by the dFPN: spatial attention (red), mental rotation (blue), and working memory (green).

only engage the dorsal and ventral prefrontal cortex, but also consistently activate the dFPN [50–54]. Importantly, paradigms such as the **N-back task** activate the dFPN in the left and right hemisphere to a similar degree, whether subjects rehearse spatial (e.g., shapes or faces), verbal (letters, words, or numbers), or auditory material, supporting a common domain-general mechanism [52,55]. A further argument favoring such a mechanism is that delayed activity is observed in the same dFPN regions whether participants are employed in working memory, oculomotor, or spatial attention tasks [56,57]. Finally, the same dFPN regions exhibit persistent activity when subjects rehearse motor plans or spatial locations, suggesting that motor and spatial working memory rely on the same neural substrate [58–60] and that action-related codes are used to retain spatial information [61].

Thus, an overwhelming number of neuroimaging studies indicate that motor planning and imagery, mental rotation, and spatial working memory similarly engage the dFPN, providing a strong argument for the view that these cognitive processes may build on a common underlying core function. A similar line of evidence comes from studies of the saccade system and its link with spatial attention. Meta-analyses of functional imaging data [62] and studies comparing saccades with shifts of attention in similar paradigms [63,64] show a nearly complete overlap of activations in the FEF, IPS, and superior parietal cortex.

Our discussion has focused on the dFPN and, therefore, we have left out additional activations observed in the supplementary motor area (associated with reaching, saccades, and working memory), primary motor and somatosensory cortex (reaching and grasping), and the dorso-lateral prefrontal cortex (working memory). Nevertheless, comparing the three cognitive tasks under the focus of the present analysis (mental rotation, working memory, and spatial attention) reveals a striking overlap of activations in the anterior and posterior portion of the dFPN (Figure 2B), supporting a shared cognitive component.

Interdependencies between Motor and Cognitive Functions Sustained by the dFPN

The first prediction of the emulation account is that behavioral studies should support a common functional origin of real and simulated action. Given that simulated movement cannot be directly observed, much of the evidence favoring this point is deduced from reaction times for real and imagined actions [65]. For example, the duration of real movements and estimated durations of imagined movements are indistinguishable for horizontal, uphill or downhill walking [66], hand rotation [67], mental rehearsal of a finger opposition sequence [68], or pointing movements with different weights applied to the arm [69]. These studies suggest a great deal of isomorphism between imagined and executed action.

A second line of evidence for the similarity between real and imagined action is the observation of motor compatibility effects. Imagined rotational movements interfere with the execution of spatially incompatible real movements [67,70,71], and the development of such interference effects in children confirms the second prediction of the emulation account (Box 2). Interestingly, interference is already present during the planning phase of the movement, indicating that real and imagined movements share common action goals and, therefore, that motor imagery relies on emulation [70]. This is further supported by the observation that internally rehearsed action has similar effects on bodily functions as real action, such as effort-related increases of heart rate and respiratory frequency [72,73]. Finally, motor imagery is impaired by amputation

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Box 2. The dFPN and Cognitive Development

A shared idea among developmental scientists is that abstract, conceptual structures emerge from basic sensorimotor skills [22,126,127]. This notion presupposes that cognitive systems evolve under pressure for information-processing efficiency, to which they react by expanding the scope of already existing functions. Therefore, the prediction is that the emergence of cognitive functions follows from the development of motor functions. Unfortunately, this progression is difficult to study because of the early age at which rudimentary cognitive capacities emerge. For example, appreciable working-memory span has been measured at 6 months [128]. Spatial orienting of attention can be observed at 5 months [129] and, at 7 months, infants adjust their grasp when reaching for objects in the dark, suggesting that they use a mental representation of object size to adapt their action [130]. At 22 months, infants rotate objects to fit them through holes, whereas the earliest evidence of active mental rotation emerges between 4 and 5 years [131,132]. By contrast, grasping and kicking movements having a measurable aim can be observed as early as 2–3 months [22], reflexive saccades before 4 months, and voluntary saccades at 7 months [133]. However, the order of appearance is not a strong argument for a causal relationship between functions.

Only recently did studies with young children find more direct support that cognition emerges from motor function. Motor competency in 5–6-year olds predicts their mental rotation ability [134]. At 18 months, measures of kinematic control during reaching predict working-memory and response inhibition accuracy, suggesting a direct link between prospective motor control and the emergence of executive functions [126]. Another study found that compatibility effects between mental object rotation and concurrent manual rotation were largest at 5 years, somewhat smaller at 8 years, and disappeared during early adolescence, suggesting a gradual independence of mental manipulation from motor experience with increasing age [131]. A similar interpretation is supported by functional imaging studies. Although it has already segregated from other intrinsic networks within the first year of life [135–137], the dFPN and other higher-order cognitive networks mature later than somatosensory, auditory, and visual networks [138]. In addition, compared with adults, children show greater connectivity within the dFPN, while adults have greater connectivity with regions outside this network [139]. These findings support the view that, during childhood, the dFPN evolves from a functionally isolated network to a permeable system supporting flexible interactions with other cognitive systems.

[74] or chronic pain [75] of the limb whose movement is simulated, suggesting that motor imagery (just as real action) relies on an intact body schema.

Although not as well examined as the relation between real and imagined action, all other functions subserved by the dFPN show a strong degree of interdependency. For example, grasping-related properties of objects facilitate appropriate actions and visual recognition, suggesting that object affordances automatically activate action systems [76–78]. Imagery of rotated body parts and mental object rotation depend similarly on angular disparity [48]. Spatial attention enhances perceptual identification similarly as saccades [79,80], and eye movements and shifts of attention cannot be made in opposite directions [81,82]. Dual-task interference between spatial attention and working memory is evident in visual processing [83,84] or when subjects shift attention or execute saccades while attempting to maintain spatial targets in working memory [85]. Furthermore, shifting the focus of attention during a short maintenance interval impairs recognition of a spatial target held in working memory [53,86]. Finally, mental rotation disrupts target maintenance in visual working memory [87] and the deployment of attention toward an abruptly appearing target [88]. In sum, temporal correspondence, spatial compatibility and dual-task interference effects all indicate that cognitive and motor functions of the dFPN have a common cognitive source.

Structural and Virtual Damage of the dFPN

The emulation account further predicts that action planning, mental rotation, spatial attention, and working memory should all suffer following damage to the dorsal premotor and parietal cortex. PPC lesions lead to severe deficits of goal-oriented movements, known as **optic ataxia**, which are particularly evident in peripheral vision and when online correction of movement is required [89,90]. Electrical stimulation of the PPC evokes an intention to move, or even the belief that the contralateral limb has moved, but not actual movement [91]. By contrast, damage to the PMd leads to impairments of selection among alternative motor schemas [92] and electrical stimulation of this region triggers limb, mouth, or eye movements [91]. Consequently, PPC activity has been related to motor preparation and online correction, while the PMd has been proposed to have a preliminary role in movement selection and triggering [17,93]. Damage affecting fibers connecting the PPC with the PMd impairs motor imagery ability [94], while isolated PMd damage affects corporeal awareness and motor imagery but leaves mental object rotation intact [95]. By contrast, damage to the PPC or transient disruption of this region with transcranial magnetic stimulation led to more general deficits in manipulating mental images, whether these do or do not comprise the own body [96,97].

PPC and PMd lesions also have distinct effects on the programming and execution of gaze shifts. Unilateral damage to the intraparietal cortex [98] or FEF [99] leads to delayed and hypometric contralesional saccades, but the reasons for these modifications appear to be different. While patients with parietal damage fail to compute target position in retinocentric coordinates, PMd damage affects the maintenance [100,101] and voluntary triggering [98,102] of motor plans necessary to initiate saccades. A more severe oculomotor impairment is observed following bilateral PPC damage. These patients show abnormally prolonged fixations, erratic gaze paths, an inability to localize visual targets, or even a complete absence of gaze shifts toward the periphery [103,104]. Oculomotor deficits are invariably accompanied by impairments of spatial attention and, given the interdependency between spatial attention and saccades, they are often impossible to disentangle. Thus, FEF damage affects visual search [105] and the capture of attention by relevant distracters [106], suggesting that this region contributes to modulation of spatial attention even if saccades are not required. Unilateral PPC damage has more profound consequences, because it increases the interference of a concurrent ipsilateral distracter with processing of contralateral targets and strongly

biases attention toward the lesion side [107–109]. Literally devastating are the consequences of bilateral PPC damage: patients are almost unable to keep more than one stimulus within their attentional focus, to shift attention between stimuli, or to localize correctly the features of individual objects [4,110]. Thus, dFPN damage leads to distinctive impairments of motor and cognitive functions, supporting a domain-general role of this network. In addition, damage to the PMd and the PPC compromises the maintenance and manipulation of spatial information in working memory. While monkey studies emphasized the role of dorsolateral prefrontal cortex in working memory, recent human brain lesion studies have found impaired performance in rehearsal and maintenance tasks only when damage encroached on the PMd [111–113], disconnected fiber tracts between the PMd and the PPC [114], or directly affected the left or right superior parietal cortex [115,116].

A weakness of these studies is that most of them did not examine the effects of dFPN damage on more than one cognitive function. Therefore, it is not clear to what extent impairment in one function predicts impairment in another function. Nevertheless, these neuropsychological findings support the conclusion that dFPN damage has widespread consequences on motor and cognitive functions relying on emulation. These findings also suggest a collaborative role of the PMd and the PPC for action planning and selection, attentional control, and the manipulation and maintenance of mental contents.

Concluding Remarks

Domain-general cognitive systems are a distinctive feature of the human mind, forming the bedrock for the remarkable evolutionary expansion of reasoning capacity and general intelligence in humans. How domain-general properties are acquired has been a source of much theorizing. Functional imaging, behavioral, developmental, and human lesion studies support the hypothesis that the domain-general role of the dFPN evolved through synergy between isolated cognitive components and the core function of this network in action emulation. The framework presented here could be extended to a discussion of cognitive control, number processing, or logical inference, which also partly rely on the dFPN. Could action emulation be at the origin of even more complex functions than those discussed here? How did the dFPN adapt locally to the diversification of its functional roles? What is the relation between domain-general thinking and the dynamic reconfiguration of brain networks during learning [117] and different task requirements [2]? These and many additional questions emerge once one accepts the concept and utility of core functions (see Outstanding Questions).

Doubtlessly our proposal has its limitations. In particular, it relies on concepts such as 'attention' or 'imagery', which are too broad to address the diversity of underlying cognitive computations [118–120]. However, studying common neural and cognitive sources instead of coarsely defined individual functions provides a way to get rid of such fuzzy concepts and to replace them with a taxonomy that is derived from an empirical analysis of behavioral and neural data. The identification of core functions of the brain, such as action emulation, is one step in this direction.

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Outstanding Questions

What are the core functions of the brain besides action emulation?

How do cognitive modules reorganize during development to allow the emergence of new functional computations?

Can the idea of cognitive synergy and emergence of new functions be applied to other brain networks?

How does the dynamic reorganization of functional brain networks according to task demand relate to the use of cognitive resources and functions?

What is the driving force for hemispheric asymmetry and why does it affect some cognitive functions (attention or mental rotation) more than others (working memory)?

Is the spatial working memory system of the dFPN capable of maintaining phonological codes and, thus, to support verbal working memory?

Do symbolic representations of numbers and magnitude have their origins in action emulation?

How does the domain-general function of the dFPN support human reasoning and intelligence?

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