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### Authors

Pagnotta, Mattia F

Riddle, Justin

D'Esposito, Mark

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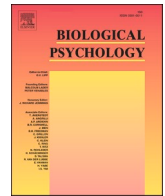
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## Multimodal neuroimaging of hierarchical cognitive control

Mattia F. Pagnotta<sup>a,\*</sup>, Justin Riddle<sup>b,c</sup>, Mark D'Esposito<sup>a,d</sup>

<sup>a</sup> Helen Wills Neuroscience Institute, University of California, Berkeley, CA, USA

<sup>b</sup> Department of Psychology, Florida State University, FL, USA

<sup>c</sup> Program in Neuroscience, Florida State University, FL, USA

<sup>d</sup> Department of Psychology, University of California, Berkeley, CA, USA

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### ABSTRACT

Cognitive control enables us to translate our knowledge into actions, allowing us to flexibly adjust our behavior, according to environmental contexts, our internal goals, and future plans. Multimodal neuroimaging and neurostimulation techniques have proven essential for advancing our understanding of how cognitive control emerges from the coordination of distributed neuronal activities in the brain. In this review, we examine the literature on multimodal studies of cognitive control. We explore how these studies provide converging evidence for a novel, multiplexed model of cognitive control, in which neural oscillations support different levels of control processing along a functionally hierarchical organization of distinct frontoparietal networks.

Flexible goal-directed behavior, called ‘cognitive control’, is the collection of processes that allow us to dynamically interact with the complex world we live in (Badre, 2020; Cohen, 2017). These processes enable us to turn our thoughts into actions in accordance with our current internal goals and future plans. Understanding how cognitive control emerges from the broadly distributed activities of billions of neurons in the brain poses a significant challenge. It involves unraveling the complex mechanisms that allow the coordination of these neuronal activities and deciphering how they collectively translate abstract thoughts and goals into tangible actions.

Neuroimaging methods are indispensable tools for addressing this research challenge. However, each method presents technical and physiological limitations. Previous work has shown that ‘multimodal neuroimaging’—that is, the combination of two or more data sets acquired with different imaging techniques—can provide novel insight into the complex spatio-temporal dynamics of brain processes by leveraging the complementary nature of the information provided by different modalities (Biessmann et al., 2011; Uludağ & Roebroeck, 2014). Reviews on multimodal imaging studies have been previously presented in the context of psychiatric disorders (Liu et al., 2015; Porter et al., 2023; Tulay et al., 2019), stroke (Auriat et al., 2015), and Alzheimer’s Disease (Chételat, 2018), or in the context of specialized approaches, like simultaneous EEG-fMRI (Laufs, 2012; Ritter & Villringer, 2006; Rosenkranz & Lemieux, 2010), PET-MRI (Judenhofer et al.,

2008), and TMS-fMRI (Mizutani-Tiebel et al., 2022; Riddle et al., 2022). Here, instead, we will provide a comprehensive review on how multimodal neuroimaging has contributed to our understanding of the electrophysiological signatures of distinct frontoparietal networks for cognitive control, with a particular focus on ‘hierarchical cognitive control’ (see Box 1).

In this review, we examine the literature on cognitive control, highlighting a functional hierarchical organization of distinct frontoparietal networks (Section 1). We examine leading theories on how neuronal assemblies leverage oscillatory mechanisms to establish inter-areal communication in these frontoparietal networks (Section 2). Further, we review previous studies that employed multimodal imaging techniques and applications to investigate cognitive control (Section 3), as well as the existing research on neurostimulation techniques for causal hypothesis testing of cognitive control processes and functions (Section 4). We examine how the findings and insights derived from these studies contributed to our understanding of the functional organization of distinct frontoparietal networks and their roles in cognitive control processing. Our review supports an updated model of hierarchical cognitive control, leveraging a multiplexing mechanism in which distinct neural oscillations subserve different levels of control processing along a functional hierarchy of brain units.

\* Corresponding author.

E-mail address: [pagnotta@berkeley.edu](mailto:pagnotta@berkeley.edu) (M.F. Pagnotta).

## 1. Cognitive control and the hierarchical organization of the frontal and parietal lobes

In primates, the lateral prefrontal cortex (LPFC) plays a pivotal role in the coordination of cognitive control (Badre, 2020; Duncan, 2010; Miller & Cohen, 2001). The LPFC maintains and integrates information related to the contexts of our environment by providing ‘abstract rules’ that can be cued by the interaction between contextual understanding and sensory inputs (Bunge, 2004; Fuster, 2000; Wallis et al., 2001). It is important to note that the LPFC neither works in isolation nor functions as a unitary controller. Instead, the LPFC displays complex connectivity patterns with many other brain areas, including structures in the parietal and temporal lobes (Menon & D’Esposito, 2022). Further, previous evidence suggests that the LPFC control system is best conceptualized as a collection of specialized units characterized by a meaningful functional organization, rather than acting as a unitary controller (Badre & Nee, 2018). Neuroimaging data obtained using functional magnetic resonance imaging (fMRI), and behavioral studies of patients with frontal lesions, demonstrated that the frontal lobes are organized hierarchically along a rostrocaudal axis, characterized by a functional gradient from caudal to rostral areas, corresponding to the abstractness of action representations and control (Fig. 1A)—that is, the level of abstraction of control increases moving from caudal frontal areas that are in closer proximity to sensorimotor cortex to rostral areas that are more distant from the sensorimotor cortex (Badre, 2008; Badre et al., 2009; Badre & D’Esposito, 2007; Koechlin et al., 2003). While different models have been proposed to explain the principles by which the control signals are integrated in the frontal lobes (see Box 2), most of them agree that there is a functional macroscale gradient along their rostrocaudal axis (but see the ‘multiple demand’ system, in Box 2).

In the context of this rostrocaudal axis of abstraction, a recent review of fMRI studies (Badre & Nee, 2018) proposes that the frontal lobes comprise three major functional zones in the frontal cortex to support hierarchical control (Fig. 1B): i) a caudal zone, ii) an intermediary zone, and iii) a rostral zone. The caudal zone includes motor and premotor areas proposed to support ‘sensorimotor control’, which is the control of stimulus-response associations or rules, i.e., the pairings between stimulus information and appropriate (planned) response or action. The intermediary zone includes the mid-dorsolateral PFC (mid-DLPFC) proposed to support ‘contextual control’, which is the control of current actions depending on internally maintained contexts. Finally, the rostral zone includes the rostrolateral-PFC (RLPFC) proposed to support

‘schematic and temporal control’, which involves future-oriented control over actions, based on superordinate or model-based knowledge (‘schemas’). The original models of the frontal hierarchy hypothesized that this most anterior portion of the frontal cortex, RLPFC, is at the top of the hierarchy (Badre, 2008; Badre et al., 2009; Badre & D’Esposito, 2007; Koechlin et al., 2003) (see also Box 2). More recent empirical evidence, however, challenges the assumptions of a simple unidimensional rostrocaudal gradient of control, in which RLPFC is at the top of the hierarchy. A series of studies used fMRI to analyze connectivity patterns among frontal regions and transcranial magnetic stimulation (TMS) to disrupt activity in these regions (Nee & D’Esposito, 2016, 2017), providing evidence that the top of the frontal hierarchy is not in RLPFC. Instead, the mid-DLPFC appears to constitute the apex of the frontal hierarchy of control processing (Fig. 1B), serving as a convergence zone from more posterior and more anterior regions, which represent more concrete contextual information and more abstract information, respectively (Badre & Nee, 2018; Nee & D’Esposito, 2016, 2017). Different levels of representations may thus be integrated in the mid-DLPFC.

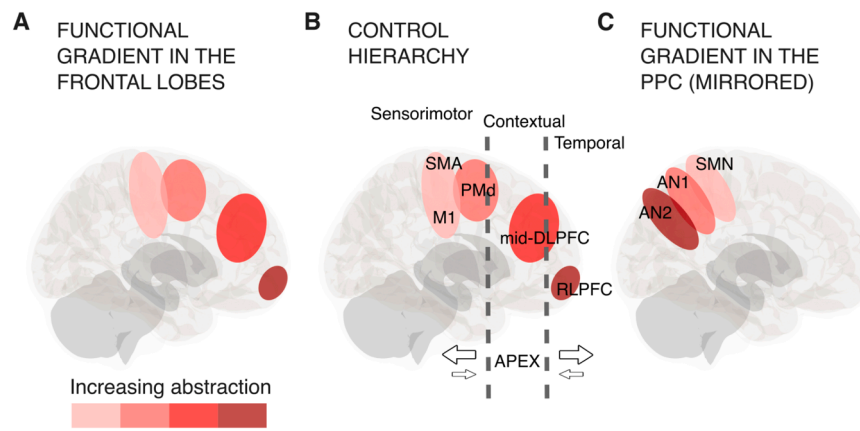
Previous fMRI studies also showed that the hierarchical organization of these functional units observed in the frontal lobes is mirrored in the posterior parietal cortices, progressing from rostral to caudal-lateral areas as a function of the abstractness of control (Fig. 1C) (Choi et al., 2018; Nee, 2021). These findings suggest that these lateral frontal control zones are embedded within frontoparietal association networks, whose interactions with the parietal cortex can support different levels of control processing, providing a parallel and distributed processing organization (Badre & Desrochers, 2019). This organization of functional units extends also to subcortical structures, primarily the basal ganglia and the thalamus, each with a hierarchical organization mirroring the cortex (Alexander et al., 1986; Choi et al., 2012; Haber, 2003). This brain architecture is characterized by multiple hierarchically organized loops, each loop comprising projections from frontal and parietal areas through the striatum to the thalamus and back to the cortex. Within each loop, there is a convergence of anatomical projections from frontal and parietal areas into the nuclei of the striatum (Choi et al., 2017).

Cortico-striatal feedback loops may coordinate interactions within the parallel networks of the rostral-caudal frontal and caudal-rostral parietal cortex (Choi et al., 2018; Hwang & Shine, Cole, et al., 2022; Shine et al., 2023), enabling us to integrate contextual, memory, and sensory representations from various distributed areas, thereby adapting

### Box 1

Key concepts and definitions.

- **Control, contextual:** control of current actions depending on internally maintained contexts. It is supported by an associative frontoparietal network, which encompasses the mid-DLPFC.
- **Control, schematic/temporal:** control based on superordinate or model-based knowledge encoded in schemas. It is supported by a second associative frontoparietal network, which is more distant from the sensorimotor cortex compared to the network supporting contextual control and encompasses the RLPFC.
- **Control, sensorimotor:** control over the pairings between stimulus information and planned action—that is, basic stimulus-response relationships. It is supported by a network of areas that encompass the motor and premotor cortex.
- **Dimension task:** task in which the participants are asked to respond to a series of colored squares containing two objects. Here, the participants have to compare the two objects and indicate whether they match or not along one of multiple perceptual dimensions (features such as texture, shape, orientation, and size), based on previously learned color-to-dimension mappings (Badre & D’Esposito, 2007).
- **Hierarchical cognitive control:** control organization in which multiple internal goals or contextual contingencies must be related to one another.
- **Policy:** relationship between a context and an appropriate course of action, in the context of a goal.
- **Policy abstraction:** degree to which a policy relates contexts to classes of more specific, simpler policies. This can be manipulated in the lab in terms of levels of contingencies, whereby rules of higher-order contextual contingencies require selecting over sets of other policies—that is, the depth of the decision tree relating contexts to actions.
- **Response task:** task in which the participants are asked to respond to a series of colored squares (visual stimuli) with a response on a keypad (action), based on previously learned color-to-response mappings (Badre & D’Esposito, 2007).



**Fig. 1.** The organization of control abstraction. **A** Functional gradient of abstraction of the action representations from caudal to rostral areas in the frontal lobes (Badre & D’Esposito, 2007). **B** Control hierarchy in the frontal cortex, highlighting the three major functional zones according to (Badre & Nee, 2018), as well as the mid-DLPFC comprising an apex of the frontal hierarchy of control processing (Nee & D’Esposito, 2016, 2017). SMA: supplementary motor areas, M1: primary motor cortex, PMd: premotor cortex, and RL-PFC: rostralateral-PFC. **C** Functional gradient of abstraction progressing from rostral to caudal-lateral areas in the posterior parietal cortices (PPC). Highlighted are the cortical regions from the somatomotor-related network (SMN) and Association Networks 1 and 2 (AN1/AN2) (Choi et al., 2018).

our behavior according to multiple contingencies (Badre, 2020; Badre & Desrochers, 2019; Badre & Nee, 2018). The striatum may also implement mechanisms of gating, controlling which information is input and output from working memory, to regulate the interactions among these separate parallel networks (Chatham & Badre, 2015), by supporting rule learning as well as the generalization of control policies (Badre, 2020; Badre et al., 2010; Badre & Frank, 2012; Collins & Frank, 2013; Frank & Badre, 2012). With this nesting of parallel networks, it becomes essential for the brain to separate the control signals associated with different control levels. This is crucial in areas that integrate signals from different levels of control processing, such as the mid-DLPFC (Badre & Nee, 2018; Nee & D’Esposito, 2016, 2017), as well as mirrored intermediary areas in the posterior parietal cortex (Nee, 2021). In telecommunications and computer networking, the method of combining two or more signals into a single transmission channel while maintaining their independence is referred to as ‘multiplexing’. The brain is thought to implement some forms of multiplexing as efficient neural coding strategies, to obviate its intrinsic biological limits and constraints in terms of number of neurons and their maximum firing-rate (Lankarany et al., 2019; Panzeri et al., 2010). Multiplexing can facilitate selective neural communication by leveraging different network oscillations (Akam & Kullmann, 2014).

## 2. Brain rhythms in hierarchical cognitive control

Voltage-gated ion channels depolarize and hyperpolarize the membrane of neurons, giving rise to oscillatory transmembrane currents and extracellular fields that can be measured using electric recording techniques (Buzsáki et al., 2012; Destexhe & Sejnowski, 2003; Glickfeld et al., 2009; Trevelyan, 2009). Rhythmic electrical activities are ubiquitous across spatial scales in the brain and their behavioral correlates are mostly preserved across mammalian brains (Buzsáki, 2006). The emergence of oscillatory activity in neuronal populations is fundamental for orchestrating information processing by temporally locking to environmental information (Fiebelkorn et al., 2018; Helfrich et al., 2017) and potentially binding neuronal representations (Clouter et al., 2017). Neural oscillations also play a role in coordinating large-scale brain networks, effectively binding distributed cell assemblies across widespread regions—that is, oscillations enable the formation of transient “neuronal partnerships” (Buzsáki, 2010; Buzsáki & Draguhn, 2004; Buzsáki & Wang, 2012). A fundamental mechanism underlying cognitive function is how neurons come together in assembly behavior.

Multiple mechanisms for neuronal communication have been formulated and experimentally substantiated based on the concept that

inter-areal communication in the brain is subserved by neuronal rhythmic synchronization. Among them, the ‘communication through coherence’ hypothesis proposes that the dynamic emergence of coherence between gamma-band oscillations, typically from 30–100 Hz, gives rise to communication between neuronal groups (Fries, 2005)—that is, gamma phase coherence between two groups of neurons produces temporal windows for input and output between the two groups, effectively establishing selective routing of information through the brain (Fries, 2009; Womelsdorf et al., 2007). An additional oscillatory mechanism for selectively routing information is that alpha-band oscillations (~8–12 Hz) hinder the communication of local activity to interconnected groups of neurons by creating a form of ‘pulsed inhibition’ that selectively conserves resource allocation (Jensen & Mazaheri, 2010). This ‘gating by inhibition’ hypothesis is based on the relationship between gamma oscillations and local neuronal computations and circuit operations (Buzsáki & Wang, 2012). It also relies on the observation that increases in gamma-band activity typically co-occur with a decrease in the power of alpha oscillations and vice versa. This general pattern of anti-correlated dynamics which has been observed in numerous cognitive processes, including visual attention (Pagnotta et al., 2020; Pascucci et al., 2018) and working memory (Brincat et al., 2021; Lundqvist et al., 2016, 2018). The gating by inhibition hypothesis is also supported by evidence that there are attention-related, top-down influences from higher-order to lower-order areas that control the alpha-driven gating of sensory processing in the latter (Halgren et al., 2019; Pagnotta et al., 2022).

In consideration of the gating by inhibition hypothesis, a new formulation of the communication through coherence recognizes a differential but central role of alpha and beta oscillations (~8–20 Hz) in mediating predominantly top-down-directed influences, which exert control over gamma influences that are predominantly bottom-up-directed (Fries, 2015). This distinction between alpha/beta and gamma influences was supported by previous electrophysiology studies in nonhuman primates, showing that functional influences among visual areas are subserved by distinct brain rhythms (Bastos et al., 2015; van Kerkoerle et al., 2014). In particular, these studies showed that high-frequency gamma oscillations and low-frequency theta oscillations predominantly subserve information processing in the feedforward direction (from low-level to higher areas of the visual cortex), conveying sensory signals. In contrast, alpha and beta oscillations more strongly subserve feedback influences (from high-level to low-level areas), modulating the feedforward signaling according to the current behavioral context. Recent evidence further suggests that theta rhythms

**Box 2**

Alternative models of control integration.

**Models based on a macroscale gradient**

- 1) The ‘**cascade model**’ proposes that temporally distinct control signals progress from anterior to posterior regions, integrating information along the way (Koechlin et al., 2003; Koechlin & Summerfield, 2007). This model posits that the RL PFC forms the apex of the control hierarchy and influences the mid-DLPFC, which in turn influences premotor areas, and so forth moving towards the motor cortex.
- 2) The ‘**abstract representational hierarchy**’ proposes that prefrontal regions are distinguished by the level of abstraction at which representations compete during action selection (Badre, 2008; Badre & D’Esposito, 2007, 2009). In this model, the most rostral area (RLPFC) constitutes the apex of the hierarchy of control processing, exerting widespread influences that can coordinate brain-wide activity and influence ongoing processing in more caudal areas (lower-order).
- 3) A third model proposes that there is a ‘**nested structure to macroscale gradients**’ in the brain (Nee, 2021; Nee & D’Esposito, 2016, 2017), in which frontoparietal areas situated in intermediary zones (including the mid-DLPFC) are essential for the integration of control signals from different levels of action representations.

Some of the discrepancies between models may be attributed to the different forms of tasks used to test abstraction and their emphasis (Badre & D’Esposito, 2009). For example, in a recent study (Pitts & Nee, 2022), the participants had to maintain context-task set mappings specific to the block (‘episodic control’) and use this temporal information to select task sets (contextual). While this form of control operates over timeframes that are equivalent to those of temporal control in previous studies (Badre & Nee, 2018), the study showed that the activations elicited by episodic control are largely overlapping with those elicited by contextual control (Pitts & Nee, 2022), in contrast to previous studies (Nee & D’Esposito, 2016, 2017). Nonetheless, effective connectivity modeling revealed a functional architecture similar to previous findings, confirming that the mid-DLPFC exerts the most widespread influences throughout frontal areas. This review focuses on the macroscale aspects of the hierarchical organization of the brain supporting cognitive control. One open question is related to the actual spatial resolution of the observed macroscale cortical gradients (see also (Nee, 2021)). For example, different types of neurons along the functional gradient in the frontal lobes (see Fig. 1A) might respond uniquely to different levels of abstractness of action representations, similar to how the hippocampus has neurons with varying place-field sizes (Strange et al., 2014). This would suggest that there might be a smooth gradient that spans regions along the rostrocaudal axis of the frontal lobes. However, a recent study analyzed the physiological properties of individual neurons in the PFC of nonhuman primates and found that these properties are best described by an areal gradient rather than a smooth gradient (Tan et al., 2023). While future studies employing single-unit recordings may further elucidate the exact spatial resolution of the functional gradient, these findings support the idea that the resolution of macroscale gradients is at the areal level and that the functional abstraction gradient is an emergent property arising from functionally distinct regions.

**Multiple demand (MD) system** An influential alternative to the gradient hypothesis is the ‘**multiple demand**’ (MD) system. The MD system encompasses a set of cortical regions that are active in cognitive tasks with different demands (Duncan, 2010). These regions have been localized around the inferior frontal sulcus (IFS, which is part of the DLPFC), the anterior insula and frontal operculum (AI/FO), the dorsal anterior cingulate cortex and the pre-supplementary motor area (dACC/pre-SMA), and the intraparietal sulcus (IPS), by fMRI studies (Crittenden & Duncan, 2014; Duncan, 2010). The MD pattern hypothesis differs conceptually from the rostrocaudal gradient models in that the observed frontoparietal system plays a core integrative role and can be recruited as a whole even by very simple task demands. The core regions of the MD system are characterized by strong functional connectivity among themselves (Assem et al., 2020). Additionally, more anterior frontal regions in the RL PFC are activated as task difficulty increases (Crittenden & Duncan, 2014), which, despite the different conceptual approach of the model, aligns with a top-to-bottom hierarchical organization. A recent study found a consistent rostro-caudal functional differentiation in this network, due to factors such as complexity, time pressure, and reward (Shashidhara et al., 2019), not directly attributable to a policy abstraction hierarchy. As previously discussed, discrepancies between the models may be attributed to specific aspects of the experimental protocols. If that is the case, it indicates that policy abstraction might not be the only relevant factor for the organization of the frontal lobes (see also (Badre, 2024; Badre & Nee, 2018)). Future research may explicitly test the role of these different factors in the functional organization of frontal and parietal lobes, by leveraging the multimodal and neurostimulation approaches outlined in the rest of this paper.

(~3–7 Hz) play a role in attentional sampling by providing a regular reset of the gamma phase when new information should be attended to, dynamically modulating the strength of gamma-band synchronization. This has been supported by ample evidence of an involvement of theta oscillations in the modulation of perceptual sensitivity under conditions that promote ‘sustained’ attention at a cued location (Fiebelkorn et al., 2018; Fiebelkorn & Kastner, 2019; Helfrich et al., 2018). These studies used intracranial data collected from humans and nonhuman primates and showed that theta oscillations periodically shape perceptual sensitivity even during states of sustained spatial attention. This promotes either attention-related sampling at the cued, behaviorally relevant location or attentional shifts to another location. Together, the findings of these studies highlight the central functional role of low-frequency oscillations in organizing communication between neural populations within large-scale networks.

The hypotheses of communication through coherence and gating by inhibition led to a novel framework, suggesting that neuronal

communication occurs within multiple parallel frequency bands and is also ‘nested’ within specific frequency-band pairs. In this framework, the phase synchronization of low-frequency oscillations (e.g., delta/theta ~0.5–7 Hz, alpha, and beta) serves as a temporal reference for the neuronal information carried by the activity at higher frequencies (Bonfond et al., 2017). This hypothesis is supported by evidence of ‘phase coding’ mechanisms based on the cross-frequency coupling between low-frequency and high-frequency oscillations (Canolty & Knight, 2010; Jensen et al., 2012, 2014; Szczepanski et al., 2014; Voytek et al., 2010). In particular, phase-amplitude coupling represents a specific form of cross-frequency coupling in which the phase of a low-frequency oscillation modulates the amplitude of an oscillation at higher frequency. This coupling mechanism may be the way in which distinct large-scale networks bias the extracellular membrane potentials in local cortical circuits, by modulating the firing probability across neuronal assemblies (Akam & Kullmann, 2014; Buzsáki, 2010).

The nested-oscillations hypothesis provides an account of how

neuronal assemblies leverage oscillatory timing to establish inter-areal communication, mediated by slower oscillations. In particular, low-frequency delta-to-theta oscillations are proposed to subservise synchronization mechanisms among distributed large-scale functional networks (Cavanagh & Frank, 2014; Helfrich & Knight, 2016) and may thus provide parallel frequency channels for information transmission related to different levels of hierarchical control (Akam & Kullmann, 2010, 2014). A human intracranial electroencephalography (iEEG) study aimed to characterize these oscillatory neural dynamics in the context of hierarchical cognitive control (Voytek et al., 2015). Voytek and colleagues employed electrocorticography (ECoG) recordings collected in four human participants performing hierarchical control tasks, while the participants underwent surgical procedures and treatments for medically refractory epilepsy. The participants performed ‘response’ and ‘dimension’ tasks, previously defined by Badre and colleagues (Badre et al., 2009; Badre & D’Esposito, 2007) (see Box 1), which engage two hierarchically-related levels of abstraction: sensorimotor and contextual cognitive control (Badre & Nee, 2018). The findings of this study showed that a more abstract rule resulted in stronger phase coding theta-band (4–8 Hz) influences between LPFC and premotor/primary-motor cortices, with a stronger directionality from the former to the latter, where the phase of low-frequency theta oscillations in LPFC was coupled with high gamma amplitude in motor cortices (Fig. 2) (Voytek et al., 2015). This study, however, did not directly compare the oscillatory dynamics between the two levels of control processing (sensorimotor vs. contextual). Further, it did not investigate the potential involvement of the parietal cortex, due to limited electrode coverage in these areas.

Another study attempted to fill these gaps and explicitly compared the two levels of control and their respective oscillatory dynamics using electroencephalography (EEG) (Riddle, Vogelsang, et al., 2020). This EEG study implemented an experimental design similar to the one used by the previous ECoG study (Voytek et al., 2015) using response and dimension tasks, but the participant’s behavioral performance was matched between the two tasks, which was not accomplished in the ECoG study. This reduced possible confounding effects of task difficulty to more precisely isolate the control processing of abstract rules (contextual). Increased theta-band power (4–6 Hz) in frontal midline electrodes was associated with sensorimotor control, while a higher level of contextual control was distinctively associated with increased delta power (2–3 Hz). Further, the functional specificity of low-frequency delta and theta rhythms was demonstrated by showing phase-amplitude coupling modulations with beta and gamma rhythms, respectively (Riddle et al., 2020). The distinction between delta and theta oscillations in this task was subsequently replicated in an independent sample of participants (Riddle et al., 2021). These findings raise the following question: do these different low-frequency rhythms (delta

and theta) serve as communication channels for distinct frontoparietal networks involved in cognitive control?

### 3. What has multimodal imaging told us about cognitive control?

Cognitive control has often been studied in humans with EEG and fMRI, individually. Due to the inherent limitations of employing each method in isolation, however, our knowledge of the systems-level mechanisms governing cognitive control remains limited if we rely only on a single modality approach. To overcome this limitation, some studies of cognitive control have combined multimodal imaging combining fMRI and EEG measurements, either in parallel studies or simultaneous approaches. The non-simultaneous combination of EEG and fMRI—using the same experiment but different participants—allows researchers to characterize the complex dynamics of cognitive control from two complementary perspectives, as well as to inform the analysis of one modality based on the results from the other (e.g., see (Pagnotta et al., 2024), discussed below). However, this approach presents some limitations related to the confounding effects introduced by the variability in brain responses across participants. While combining separate EEG and fMRI recordings from the same participants can help to reduce these effects, only simultaneous acquisitions can ensure that the signals reflect the exact same brain activity state. This simultaneous approach, however, comes with several technical challenges and requires the careful use of sophisticated artifact reduction algorithms to ensure sufficient data quality (Laufs, 2012; Ritter & Villringer, 2006). Further, to maximally leverage simultaneous acquisition, analyses should ideally include an investigation of single-trial variance (e.g., delta power is greater for trials with greater BOLD activation in the mid-DLPFC) or individual differences analysis (e.g., delta power is greater in participants with greater BOLD activation in the mid-DLPFC), otherwise the benefit is simply controlling for group differences.

Regardless of how the two modalities are combined, previous EEG-fMRI studies have provided novel insights into the spatio-temporal dynamics of cognitive control. For example, attentional control was studied using simultaneous EEG-fMRI, revealing that fMRI activity in visual cortical regions contralateral to the cued location of the attended visual stimulus covaried positively with occipital EEG gamma activity, while in ipsilateral visual cortical regions it covaried negatively with occipital EEG alpha activity. These findings are consistent with attention-related enhancement and suppression of the relevant and irrelevant visual hemifield, respectively (Green et al., 2017). While each of these methods has intrinsic limitations (the most prominent being low spatial resolution for EEG and low temporal resolution for fMRI), combining them in a multimodal approach allowed the investigation of the cortical oscillatory dynamics underlying spatial attention, and how these are coordinated by subcortical structures. The EEG temporal resolution allowed for the characterization of attention-related modulations of cortical oscillations and the correlation of these modulations with changes in neural activity (as derived from fMRI). Further, fMRI enabled the investigation of modulations in subcortical processes. In addition to discovering an inverse relationship between alpha and gamma activity in attentional control, this study implicated the pulvinar nucleus of the thalamus as a control structure that mediates the observed spatially specific, attention-related oscillatory modulations.

Only a limited number of studies that implemented a multimodal approach have examined cognitive control, and they have not done so explicitly within the context of a hierarchical organization of control processing. For example, some studies characterized the timing of different control signals, as well as the involvement of frontal theta oscillations in mediating cognitive control processes. One study used EEG and fMRI data, collected using a unimodal (rather than simultaneous), counterbalanced design, to examine the role of the anterior cingulate cortex (ACC) during error-monitoring (Edwards et al., 2012). Using joint

#### THETA–GAMMA COUPLING

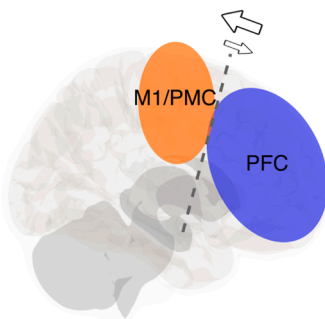
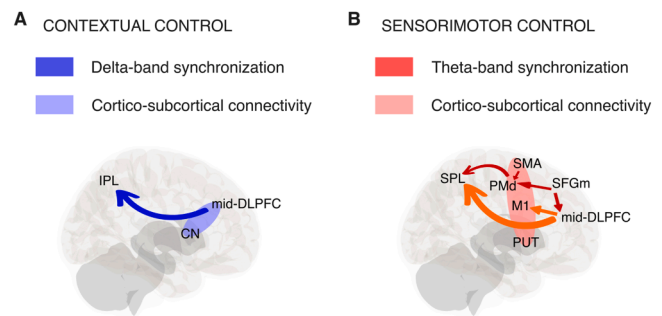


Fig. 2. Phase coding theta influences in the frontal cortex. Schematic representation of the key findings from (Voytek et al., 2015), showing stronger directionality in the theta-gamma phase amplitude coupling from LPFC to premotor/primary-motor cortices (PMC/M1), than vice versa.

Independent Component Analysis to couple EEG event-related potentials with fMRI activation maps, this study showed that cognitive error processing first occurs simultaneously in the LPFC and caudal ACC (considered the ACC ‘cognitive division’, as opposed to the more rostral ‘affective division’), and is then followed by affective processing during error monitoring in rostral ACC. A simultaneous EEG-fMRI study was used to untangle the relationships between frontal midline theta measured by EEG and activity measured with fMRI for conflict- and error-related processing during conflict tasks (Beldzik et al., 2022). Researchers found that the pre-response conflict-related theta power was negatively correlated to fMRI activity in the dorsomedial prefrontal cortex (dmPFC), while post-response error-related theta was characterized by a short duration response that was positively correlated with fMRI activity in the cognitive division of the ACC, which has also been referred to as anterior midcingulate cortex (amCC). These findings suggest a separation of processing among frontal midline areas, with error-related theta power possibly reflecting a quick transient modulation in the theta range. A similar negative correlation between frontal midline theta and fMRI activity was also reported using simultaneous EEG-fMRI, during a working memory task (Scheeringa et al., 2009) and Go/NoGo tasks (Algermissen et al., 2022). The Go/NoGo study found that trial-by-trial fluctuations in the late frontal midline theta, around the time of response, are best predicted by activity in the striatum, suggesting that this component may reflect the involvement of frontostriatal loops in action selection processes.

To the best of our knowledge, only one study adopted a multimodal approach using EEG and fMRI to directly investigate the spatio-temporal dynamics of hierarchical cognitive control. In a follow-up to our EEG studies on hierarchical control discussed above (Riddle et al., 2020; Riddle et al., 2021), we re-analyzed the EEG data from the original study and a new fMRI dataset, collected from a different group of participants performing the same experiment (Pagnotta et al., 2024). We employed source-reconstruction techniques in EEG data to characterize the oscillatory dynamics of different levels of control processing. This was achieved by using cortical regions of interest, identified in a data-driven way using the fMRI data. Overall, we found spatial alignment between the brain regions with the greatest activity during contextual control, observed in fMRI, and the brain regions with the greatest increase in delta-band power from these same conditions, estimated using EEG source-reconstruction techniques. Similar spatial alignment was also observed during sensorimotor control when comparing the modulation of theta-band power between fMRI and source-reconstructed EEG, here, in areas of the frontal lobes that are close to the sensorimotor cortex. EEG connectivity analyses showed a multiplexing of the control signals for contextual and sensorimotor control. We found a separation of delta and theta oscillations for mediating large-scale synchronization that underlies these two levels of control in distinct frontoparietal association networks (Fig. 3). One of the frontoparietal networks included predominantly areas that are positioned laterally and more distant from the sensorimotor cortex (LPFC and inferior parietal lobule–IPL), while the other network primarily included frontoparietal areas that are in the proximity of the sensorimotor cortex and the frontal midline (dorsal premotor cortex–PMD, supplementary motor area–SMA, superior frontal gyrus–SFG, and superior parietal lobule–SPL). These networks are consistent with the rostral-caudal hierarchical organization discussed in the previous section. Low-frequency oscillations enable network connectivity and distinguish hierarchical levels, leveraging different oscillatory frequencies in the theta-band (lower in the hierarchy and related to sensorimotor control) and in the delta-band (higher in the hierarchy and related to contextual control). Each network and level of cognitive control was also associated with increased cortico-subcortical functional connectivity with specific portions of the dorsal striatum, as revealed by fMRI connectivity analyses (Fig. 3): caudate nucleus for contextual control and putamen for sensorimotor control. These findings, enabled by multimodal imaging, provide supportive evidence for multiplexing of cognitive control signals in frontostriatal loops. Furthermore, these two



**Fig. 3.** Model of multiplexed hierarchical control. Schematic representation of the key findings from (Pagnotta et al., 2024), showing a multiplexing of the control signals for distinct levels of control processing (contextual and sensorimotor). **A** Contextual control (higher in the hierarchy) is associated with increased delta-band synchronization between the mid-DLPFC and the inferior parietal lobule (IPL), as well as with increased cortico-subcortical functional connectivity with the caudate nucleus (CN). **B** Sensorimotor control (lower in the hierarchy) is associated with increased theta-band synchronization among areas that are in the proximity of the sensorimotor cortex and the frontal midline (dorsal premotor cortex–PMD, supplementary motor area–SMA, medial superior frontal gyrus–SFGm, and superior parietal lobule–SPL), as well as with increased cortico-subcortical functional connectivity with the putamen (PUT).

networks are not entirely disjoint. We found a convergence of signals for the two levels of control in the mid-LPFC. In this area, we observed delta and theta-band modulations in both oscillatory power and functional connectivity, depending on the specific level of control: contextual and sensorimotor, respectively.

In summary, leveraging their spatial resolution, previous fMRI studies have demonstrated that distinct frontoparietal association networks are involved in hierarchical cognitive control and subserve different levels of control processing along a functional hierarchy (Badre, 2008; Badre & D’Esposito, 2007; Badre & Nee, 2018; Koehnlin et al., 2003; Nee, 2021; Nee & D’Esposito, 2016). Leveraging the temporal resolution of EEG, previous studies demonstrated that distinct oscillatory signatures map to different levels of control processing (Riddle et al., 2020; Riddle et al., 2021). Our multimodal study, combining fMRI and EEG, provides stronger support that distinct oscillatory signatures subserve functional connectivity across the different networks supporting hierarchical control, consistent with a multiplexing mechanism (Pagnotta et al., 2024). In this study, the temporal dynamics of the two levels of control processing (sensorimotor and contextual) largely overlapped in time, although careful analysis in EEG revealed a tendency for sequential activation of these levels of control. Sensorimotor control engaged later than contextual control, characterized by dynamics locked to the behavioral response, whereas contextual control engaged earlier and was locked to the stimulus. However, the specific sequencing of control processes may be specific to the task. In the hierarchical cognitive control task described here, participants must first establish a context based on a cue and then perform a perceptual judgment which determines the button to be pressed. Nonetheless, the separability of these control signals in the frequency domain suggests that multiple types of cognitive control can be engaged simultaneously so as not to interfere with each other. However, there may be serial processing and bottlenecks in decision-making processes at each control level, for example, in the posterior LPFC during response selection (Dux et al., 2006). Using fMRI, Dux and colleagues found that (i) the posterior LPFC is coactivated by tasks that share neither sensory nor output modalities, and further, they showed significant patterns of (ii) serial queuing under dual-task conditions and (iii) response selection activity in this region. These are three key criteria expected of a neural substrate of a central bottleneck of information processing, suggesting that the LPFC plays a key role in mediating multiple task demands. With a convergence of sensory signals and principal role in motor control, a

multiplexed system would facilitate the LPFC in processing multiple streams of information for multiple purposes.

The behavioral findings from others studies using tasks that depend on hierarchical rules support a parallel processing model of cognitive control. Human participants tend to exhibit predominantly parallel decision-making dynamics during hierarchical control. For example, Ranti and colleagues adopted a response deadline procedure to assess the accuracy and timing (speed of processing) of decisions made at each level of a hierarchy, independently from the other levels (Ranti et al., 2015). In this study, participants selected responses to stimuli using a complex structure of task rules, in which some rules were contingent on others, creating three levels of contingencies (or orders of policy abstraction). It was found that participants exhibit a decline in error rates across the levels of the hierarchy, which is for the most part simultaneous and happens at identical rates, showing only a tendency for completing the highest level of decision first. This pattern of behavioral findings provides evidence of primarily parallel rather than serial processing in hierarchical decision-making. We contend that a parallel processing model is also supported by our observation that distinct control signals are mediated by distinct oscillations (delta and theta) (Pagnotta et al., 2024). Such a form of multiplexing scheme, which consists of segregating signals by the frequency of oscillations, is called ‘frequency-division multiplexing’ (Akam & Kullmann, 2014). Frequency-division multiplexing could facilitate parallel operation of the frontoparietal processing systems, particularly in areas positioned in the intermediary functional zone (midlateral contextual zone). As previously discussed, the middle portion of the DLPFC likely constitutes the apex of the frontal control hierarchy (Badre & Nee, 2018; Nee & D’Esposito, 2016, 2017), exerting the most widespread influences throughout the frontal lobes (Nee, 2021; Pitts & Nee, 2022). Our findings that in the mid-LPFC there are delta and theta modulations in both oscillatory power and functional connectivity, which depend on the specific level of control (delta for contextual and theta for sensorimotor) (Pagnotta et al., 2024), support this model that the mid-LPFC integrates control signals at different levels of hierarchical processing, in parallel. Different populations of neurons in the mid-LPFC may process distinct streams of information for the different frontoparietal processing systems, for mediating multiple levels of control processing, by creating assembly behavior through delta and theta oscillations. The extent to which these signals are segregated between different neuronal populations and how these neurons organize functionally and anatomically are aspects that could be explored in the future with the use of intracranial and single-unit recordings.

One of the advantages of using both fMRI and EEG is that together they provide a more complete picture of the functional organization of cognitive control processes. The rationale of the multimodal approach was that fMRI was critical to spatially separate the different control networks and to determine the involvement of subcortical structures such as the basal ganglia and thalamus, which mediate the interactions between cortical areas in the frontoparietal networks (Choi et al., 2018; Hwang & D’Esposito, 2022; Shine, 2021; Shine et al., 2023). The oscillatory dynamics of different control processes are critical as well, and these were underspecified in previous hierarchical control models, which required the use of a method able to measure them, like EEG. Further, the use of methods like fMRI and EEG allows the capture of large-scale network dynamics at the whole-brain level, compared to, for example, intracranial iEEG recordings with limited spatial coverage, which are better suited for studying localized processes. With iEEG (i.e., stereo-EEG and ECoG), coverage is guided solely by clinical necessity. It is possible that with enough iEEG participants, a sufficient number will possess the appropriate pairing of spatially precise electrodes with high temporal resolution. For example, after establishing a model of multiplexed hierarchical control, future work using iEEG guided by our findings could provide an unprecedented access to the oscillatory interactions between cortical and subcortical structures, which cannot be assessed using noninvasive methods such as EEG.

So far we have established that there exists a functional hierarchy of frontoparietal networks supporting cognitive control (Badre & Nee, 2018; Choi et al., 2018; Nee, 2021; Nee & D’Esposito, 2016, 2017) and different oscillatory signals (delta and theta) have been shown to mediate the cortico-cortical connectivity in distinct frontoparietal networks, with a multiplexing of signals in the mid-DLPFC (Pagnotta et al., 2024). However, subcortical structures such as the thalamus may be an alternative source of these different oscillations. A recent study using stereo-EEG and electrical stimulation procedures showed delayed-onset slow oscillations following thalamic stimulations (Parvizi et al., 2024). Electrical stimulation of the cortex, in contrast, induced earlier activations in the thalamus, providing evidence for cortico-subcortical mechanisms by which different thalamic sites and cortical activity can influence one another. These findings provide causal evidence for the thalamus playing a key role in modulating global oscillatory dynamics in the brain (Shine, 2021; Shine et al., 2023). While future research is required to further understand these mechanisms and to determine the exact position of the thalamus in the control hierarchy, this stereo-EEG study is a prime example of the added value provided by brain stimulation techniques, which is discussed in more detail in the next section.

#### 4. The added value of brain stimulation techniques

The use of brain stimulation techniques allows for causal hypothesis testing of brain functions by targeting specific brain regions or networks (Romei et al., 2016). Since these techniques target one node of a network, they do not disrupt or modulate the activity of all the nodes of a network to an equal degree. Instead, they provide novel insights into the role of the node that is stimulated, but this needs to be disambiguated from the impact of stimulation on its functional network. Two primary techniques commonly used are transcranial magnetic stimulation (TMS) and transcranial alternating current stimulation (tACS). TMS is a noninvasive brain stimulation method based on the principle of electromagnetic induction of an electric current, which is created by delivering a brief high-intensity magnetic pulse through an electrified coil near the scalp (Rossi et al., 2009). TMS allows for spatial selectivity of stimulation on cortical activity in a focal area underneath the coil. The spatial resolution of TMS is on the order of centimeters and depends on the shape of the stimulating coil—i.e., approximately 0.5–1 cm using figure-eight coils (Bolognini & Ro, 2010; O’Shea & Walsh, 2007; Toschi et al., 2008). Technical developments have made it possible for TMS systems to deliver several pulses in rapid rhythmic sequences (‘trains’), which is called ‘repetitive TMS’ (rTMS) and allows for the investigation of the role brain oscillations at different frequencies (Kobayashi & Pascual-Leone, 2003; Rossini & Rossi, 2007; Thut & Miniussi, 2009). The use of EEG following the administration of rTMS pulses allows researchers to quantify the immediate impact on brain activity. Previous work often found spectral modulation of the low-frequency bands (delta/theta) after stimulation to LPFC, and on mid-frequency alpha/beta oscillations following sensory and motor cortex stimulation (Thut & Miniussi, 2009). By applying rhythmic TMS concurrent with EEG, previous work found that TMS transiently drives a targeted brain rhythm (Albouy et al., 2017; Hanslmayr et al., 2014; Riddle et al., 2024; Thut et al., 2011). In contrast to TMS, tACS is the application of weak electric current via electrodes placed on the head of the participant (Antal et al., 2008; Marshall et al., 2006). tACS provides an additional means of entraining specific frequencies of oscillations, but can also deliver arbitrary patterns of electrical activity using customizable waveforms (Fröhlich, 2014; Riddle & Fröhlich, 2021). However, the spatial specificity of this method is inferior to TMS, typically on the order of 10 cm. This is also due to the dimensions of the conductive electrodes, which are typically approximately 5-by-5 cm in size (Ahn et al., 2019; Riddle et al., 2021; Violante et al., 2017), although recent techniques using high-definition tACS use 1 cm<sup>2</sup> electrodes with electric fields on the order of a few cm (Alekseichuk et al., 2016; Reinhart & Nguyen, 2019). Both TMS and tACS provide novel insight into cognitive control



mechanisms by causally testing correlational findings.

One type of TMS protocol, called ‘continuous theta burst stimulation’ (cTBS), produces a reversible ‘virtual lesion’ in the targeted area (Pascual-Leone et al., 1999; Walsh & Rushworth, 1999). In cTBS, short bursts of 3 pulses at 50 Hz rTMS are applied at a rate in the theta range (5 Hz), typically for either 20 or 40 seconds (300 or 600 stimuli in total, respectively), which was shown to produce relatively long-lasting effects on the stimulated portion of cortex, for approximately 50 minutes (Huang et al., 2005). Another TMS protocol, called ‘intermittent theta burst stimulation’ (iTBS), consists of 2-second trains of 3 pulses at 50 Hz, repeated every 10 seconds for a total of 190 seconds (600 pulses in total) (Huang et al., 2005; Rossi et al., 2009). The iTBS protocol was shown to produce excitatory effects on the central somatosensory pathway, suggesting that this protocol may be useful to induce synaptic plasticity changes resembling long-term potentiation (Di Lazzaro et al., 2008; Katayama & Rothwell, 2007). Thus, the use of iTBS and cTBS in combination could evoke either facilitating or inhibiting effects, respectively, allowing for greater inferential power than the use of either method alone, although this framing of TBS as excitation or inhibition may be an oversimplification (see (Hermlinger, 2024)).

TMS not only alters the function of the stimulated area but also changes activity in remote regions that display functional connectivity with the site of stimulation. For example, previous research has shown that TMS allows the assessment of remote cortical network effects of the stimulation (Lee & D’Esposito, 2012; Lorenc et al., 2015; Miller et al., 2011), as well as the remote effects on deep-brain areas of the medial temporal lobe (Hermlinger et al., 2020) and subcortical structures in the basal ganglia (Riddle et al., 2022), which are not directly accessible using noninvasive stimulation methods.

TMS protocols can be performed ‘offline’, followed by recording with other methods such as fMRI, EEG, and magnetoencephalography (MEG). In this way, it is possible to quantify the effect of alteration of a given brain region on behavior and neural function (Ruff et al., 2009). For example, previous studies of cognitive control combining offline cTBS with fMRI have found that disruption of LPFC function decreases category-specific neural tuning of the extrastriate cortex to stimulus categories, impairing working memory performance (Lee & D’Esposito, 2012; Miller et al., 2011), as well as producing a reduction in the fidelity of the goal relevance code in a distributed set of brain regions in frontal, parietal (including the intraparietal sulcus–IPS), and occipital cortices (Lorenc et al., 2015). The findings of these combined cTBS and fMRI studies establish that the LPFC is a source of control signals to distributed cortical areas. In this context, the use of TMS provides causal evidence for the role of the LPFC in cognitive control processes, as well as the consequences of its stimulation on the fMRI activity in other regions of the brain. This cannot be achieved by simply using a combination of two correlational methods, such as fMRI and EEG.

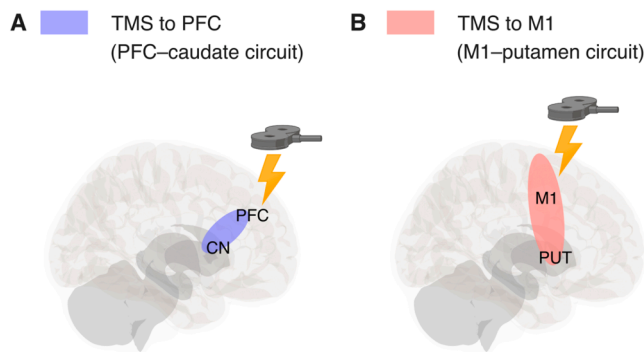
Other studies investigated the different types of control signals that might emanate from the LPFC. Zanto and colleagues used fMRI to guide 1-Hz rTMS (applied for 10 minutes) to disrupt the function of the right inferior frontal junction (IFJ) during the performance of a working memory task (Zanto et al., 2011). This study showed that disruption of IFJ function with rTMS affects pre-stimulus alpha-band phase coherence between frontal and posterior regions, which was predictive of a subsequent reduction in working memory accuracy, suggesting that long-distance top-down modulation by PFC in posterior cortical regions is mediated by alpha synchronization. Combining offline cTBS (guided by fMRI) with EEG/MEG, one study investigated the role of frontal eye fields (FEF) on the top-down control of alpha and gamma oscillations, during a cued visuospatial attention task (Marshall et al., 2015). A site-specific disruption of anticipatory alpha power modulation in the hemisphere contralateral to FEF stimulation showed that only right FEF cTBS enhanced gamma modulation in the left visual cortex.

TMS can also be performed concurrently with fMRI or EEG. In particular, concurrent TMS-fMRI presents more technical and methodological challenges compared to offline approaches, and less than 100

experimental studies have used this approach (Mizutani-Tiebel et al., 2022; Riddle et al., 2022). However, this method enables the quantification of the remote effects of cortical TMS on the neural activity of distant cortical and subcortical structures. For example, one study delivered theta-burst pattern (TBS: 50 Hz triplet pulses delivered at 5 Hz) over a duration of 2 seconds, during concurrent fMRI data acquisition, by targeting a cortical region of the hippocampal network in the lateral posterior parietal cortex, while human participants were performing a long-term memory task (Hermlinger et al., 2020). TMS increased activity in the anterior hippocampus during the encoding of visual scenes into long-term memory, which significantly improved the subsequent recollection of scenes during memory recall, demonstrating that TMS effects were immediate and trial-specific.

Concurrent TMS-EEG studies also investigated the mechanisms by which oscillations underlie cognitive control. For example, one study showed that the exogenous entrainment of beta oscillations in the inferior frontal gyrus (IFG) impaired memory encoding, an effect that was not observed at other frequencies. It was further demonstrated that there was a sustained oscillatory ‘echo’ in the left IFG following completion of the TMS train, specifically in the beta-band, demonstrating the frequency-specificity of rTMS on cortical oscillations (Hanslmayr et al., 2014). In another study, theta-band rTMS to the left IPS produced a selective entrainment of endogenous theta oscillations in the dorsal auditory stream, which improved auditory working memory performance and increased theta synchronization (as measured by the phase-locking value) over left frontal-parietal and right parietal regions (Albouy et al., 2017). A similar protocol combining EEG with online TMS demonstrated that posterior high-frequency activity (gamma) is nested into slow frontal-midline theta oscillations (4–7 Hz) during a visuospatial working memory task (Berger et al., 2019). Finally, a recent study demonstrated that theta-frequency TMS increased theta-frequency oscillatory power when applied to LPFC (Riddle et al., 2024). Theta TMS to LPFC also increased theta-frequency functional connectivity between LPFC and posterior parietal cortex and improved working memory capacity in a retrospective cued visual working memory task.

Only a few studies have used brain stimulation to explicitly test predictions about a putative control hierarchy. One study combined cTBS with fMRI dynamic causal modeling (DCM) to investigate the causal connection between LPFC dynamics facilitating cognitive control and the behavioral outcomes of different levels of control processing (Nee & D’Esposito, 2017). This study showed that cTBS to caudal-, mid-, and rostral-LPFC, respectively disrupted each level of control (sensorimotor, contextual, temporal), according to the predictions of the hierarchical model (Badre & Nee, 2018); however, cTBS to caudal-LPFC also disrupted the level of temporal control. This justified a revision of the model by including neural dynamics from caudal LPFC to mid-rostral LPFC, which posited the middle portion of LPFC as a critical nexus for cognitive control, providing causal evidence that the mid-LPFC forms an apex of the control hierarchy (Badre & Nee, 2018; Nee & D’Esposito, 2016). This formulation of the control hierarchy is also consistent with a previous fMRI and EEG study (discussed above) showing modulations of the functional connections through the mid-LPFC, within both levels of control processing (Pagnotta et al., 2024). A previous study used concurrent TMS-fMRI to administer rTMS at 10 Hz to either primary motor cortex (M1) or mid-LPFC and showed a hierarchical spread of activation both on frontal areas and frontostriatal loops (Fig. 4) (Riddle et al., 2022). M1 rTMS evoked a response in the putamen (i.e., its anatomically connected frontostriatal circuitry), which did not spread to rostral regions in LPFC; while stimulation of LPFC produced an increase in activity spreading to its anatomically connected striatal site in caudate nucleus and also to more caudal circuits of M1 and putamen. Although in this study the stimulation was administered during eyes-open resting-state, its findings highlight the potential for selectively influencing different levels of hierarchical control processing by noninvasively targeting different corticostriatal circuits. This possibility could be explored in future research.



**Fig. 4.** Causal evidence for a hierarchical organization of frontostriatal loops. Schematic representation of the key findings from (Riddle et al., 2022), providing causal evidence for a hierarchical organization of the cortico-subcortical loops with the striatum. **A** Stimulation to the PFC (10 Hz rTMS) is associated with increased activity in the caudate nucleus (CN), as well as in more caudal circuits (shown in B). **B** 10 Hz rTMS to the primary motor cortex (M1) is associated with increased activity in the putamen (PUT), with no spread to rostral circuits.

Another study employed EEG recordings in combination with cross-frequency tACS, providing causal evidence for the role of PFC in orchestrating different levels of hierarchical cognitive control through phase-amplitude coupling (Riddle et al., 2021). It was found that different components of control are mediated by two distinct cross-frequency coupling modalities (delta-beta or theta-gamma), which was derived from previous observations (Riddle et al., 2020) (see also above). The study showed that cross-frequency tACS successfully increased the targeted phase-amplitude coupling activity and modulated performance of the specific control component associated with the targeted phase-amplitude coupling activity, providing causal evidence for a specific nesting of oscillations within each level of control processing (Riddle et al., 2021). While this study did not directly test predictions about a hierarchy of cognitive control, the offline cTBS protocols with EEG/MEG and concurrent TMS-EEG studies (discussed above) together demonstrate that stimulation to areas that are in closer proximity to the sensorimotor cortex and more medially positioned typically produces modulations predominantly in theta, alpha, and gamma oscillations (Albouy et al., 2017; Berger et al., 2019; Marshall et al., 2015). On the other hand, stimulation of areas that are more distant from the sensorimotor cortex, such as the LPFC, tends to induce modulations primarily in beta oscillations (Hanslmayr et al., 2014). Stimulus-induced desynchronization of mid-frequency alpha and beta oscillations has been shown to be specifically associated with the levels of sensorimotor and contextual control, respectively (Pagnotta et al., 2024). Previous evidence suggests, in fact, that alpha and beta oscillations may provide inhibitory control signals that regulate access to representations stored in memory (Klimesch, 2012; Lundqvist et al., 2023; van Ede, 2018) and a disinhibition from these signals, as measured by desynchronization, would allow reading out relevant information from memory (Miller et al., 2018). Altogether these studies suggest that we can distinguish two main motifs in cognitive control tasks, between delta-beta oscillations on the one side (for contextual control) and theta-alpha-gamma oscillations on the other (for sensorimotor control).

A promising brain stimulation approach is the use of dual-site protocols, to probe inter-areal functional connectivity between the two sites of stimulation (Koch, 2020; Koch & Rothwell, 2009; Rothwell, 2011; Van Malderen et al., 2023). One study used direct cortical stimulation (DCS—that is, an invasive stimulation applied directly to the cortical surface) together with iEEG collected while three participants performed a Sternberg working memory task (Alagapan et al., 2019). Here, DCS was simultaneously applied to two nodes of the working memory network in frontal and parietal regions, which increased their oscillatory functional connectivity. In-phase periodic pulse stimulation produced

an improvement in working memory performance, by reducing the inter-regional phase lag relative to sham stimulation; while, anti-phase stimulation did not improve working memory performance and increased the inter-regional phase lag. In another study, iEEG was combined with invasive TBS stimulation to target two nodes of a network that exhibited functional selectivity for spatial compared to temporal memory-retrieval, which was identified using theta phase coherence as a measure of stronger coupling between nodes (Kim et al., 2018). TBS to the two nodes impaired the performance in spatial retrieval, by way of theta decoupling, while temporal retrieval remained unaffected. Although some differences in performance outcomes between studies may be explained by phase lag differences between stimulation types, and the effects of some stimulation parameters are still not well understood, these approaches have proven valuable to probe connectivity alterations and, thus, can offer unique insights into how neuronal communication is established.

Future studies using dual-site approaches could provide causal evidence for the functional role of specific inter-areal connections, within the multiplexed hierarchical control model (Pagnotta et al., 2024). For instance, delta-band periodic pulse stimulation (in-phase vs. anti-phase) could be simultaneously applied to sites in mid-LPFC and inferior parietal cortex, with the hypothesis that in-phase stimulation would produce an improvement in contextual control compared to anti-phase stimulation (or sham), having an effect only on higher levels of control abstraction but not low-level sensorimotor control. Also, dual-site TBS may be applied to the mid-LPFC and frontal midline areas (such as the superior frontal gyrus–SFG) or the supplementary motor area–SMA to test the effects of their interareal synchronization on sensorimotor control, which is hypothesized to have an effect across abstraction levels. This type of studies would test the hypothesis that the mid-LPFC is necessary for integrating signals at different levels of the control hierarchy.

In a similar way, another interesting avenue for future research is the use of concurrent TMS-EEG and TMS-fMRI to causally test predictions about the multiplexed hierarchical control model. Simultaneous TMS-EEG could be used to test the exogenous entrainment of oscillations (delta/theta) in the mid-LPFC and assess their effects on behavioral performance, in a hierarchical control experiment using response and dimension tasks (Badre et al., 2009; Badre & D'Esposito, 2007). This could be accomplished by using an online TMS approach with concurrent EEG, in which TMS trains of 4 biphasic pulses are delivered to the mid-LPFC in either 3 Hz (delta frequency), 6 Hz (theta frequency), or arrhythmic (control condition), during the execution of the dimension and response tasks. This online TMS approach has been successfully used in previous studies (but without simultaneous EEG recordings), showing that the behavioral impact of TMS critically depends on the match between the frequency of stimulation and the ongoing task-relevant neural oscillations (Riddle et al., 2019; Riddle, Scimeca, et al., 2020). In the context of the hierarchical control experiment, simultaneous TMS-EEG could allow us to assess whether or not the observed effects on behavior are specific for the associated control level (contextual for delta and sensorimotor for theta) and whether or not these are observed at other frequencies (e.g., alpha or beta). The same experiment and stimulation protocol could be used in a simultaneous TMS-fMRI study to quantify the remote network effects of cortical rhythmic TMS, in particular on the neural activity of subcortical structures in the striatum and thalamus. For a more comprehensive overview of the technical issues of these methods as well as methodological recommendations, we refer the reader to previous specialized reviews (Hernandez-Pavon et al., 2023; Mizutani-Tiebel et al., 2022; Riddle et al., 2022).

## 5. Conclusions

In her novel “Middlemarch”, Mary Ann Evans (a.k.a. George Eliot) wrote: “It is a narrow mind which cannot look at a subject from various points of view.” Multimodal imaging techniques and applications are

essential to characterize and understand the complex dynamics of cognitive control processing, as well as how this is mediated by distinct frontoparietal networks. Previous fMRI studies have demonstrated a hierarchical organization of control processing, supported by distinct frontoparietal association networks that subservise different levels of control along a functional hierarchy (the spatial facet of hierarchical control). Specifically, the frontal lobes are organized hierarchically from caudal areas, which are close to the sensorimotor cortex, to rostral areas, which are more distant from the sensorimotor cortex, depending on the level of abstraction of action representations and control. This hierarchical organization of functional units is mirrored in the posterior parietal cortices, extending from rostral to caudal-lateral areas, and further extends to subcortical structures, forming multiple hierarchically organized corticostriatal feedback loops through the thalamus. Previous EEG studies have shown that distinct oscillations in the delta and theta bands correspond to these different levels of control processing (the temporal facet of hierarchical control). In particular, delta oscillations are modulated by contextual control, which involves the control of action representations based on more abstract contextual information (higher in the hierarchy), within a network of frontoparietal areas distant from the sensorimotor cortex. In contrast, theta oscillations are associated with sensorimotor control, involving the control of stimulus-response associations and rules (lower in the hierarchy), within a network of frontoparietal areas closer to the sensorimotor cortex. Multimodal imaging has allowed us to reconcile these two facets of hierarchical cognitive control, revealing that low-frequency oscillations in the delta and theta bands serve as communication channels for the distinct frontoparietal networks involved in cognitive control, subserving contextual and sensorimotor control, respectively. This approach has also confirmed that each network and level of control processing is associated with increased cortico-subcortical functional connectivity with specific portions of the striatum (caudate nucleus and putamen for contextual and sensorimotor control, respectively). Neurostimulation techniques like tACS and simultaneous TMS-fMRI have provided causal evidence for the separation of control signals between delta and theta oscillations and a specific nesting of oscillations within each level of hierarchical control. They have also shown that it is possible to target different corticostriatal circuits (i.e., different levels of control processing) by stimulating different cortical areas along the frontal hierarchy. These findings are consistent with a multiplexing mechanism of hierarchical control mediated by distinct corticostriatal feedback loops, which provides a parallel and distributed processing organization.

Each method possesses unique strengths and limitations and can provide novel insights into different aspects of brain function. On the one hand, neuroimaging data obtained using fMRI allow the characterization of functional interactions among large-scale brain networks with high spatial resolution and facilitate the investigation of how cortical networks may be mediated by deep subcortical structures depending on cognitive demands. On the other hand, recordings obtained using EEG and MEG allow for the characterization of the cortical oscillatory dynamics underlying cognitive control processes with high temporal resolution. Combining these methods allows us to grasp a more comprehensive and holistic understanding of the neural basis of cognitive control, and we can probe and modulate these neural circuits with an additional set of tools. The use of noninvasive neurostimulation techniques, such as TMS and tACS, allows for causal hypothesis testing about specific cognitive control processes and functions. In particular, when combined with fMRI and EEG in either offline approaches or simultaneously, neurostimulation techniques provide causal evidence about the involvement of specific areas in control processes and oscillatory neural dynamics, as well as the functional role of specific inter-area connections. To complement these noninvasive multimodal approaches, invasive recordings obtained from patients with clinically implanted electrodes (iEEG) allow for the study of localized processes and the testing of specific hypotheses about brain functions, with high spatial specificity and high temporal resolution. In addition, invasive

stimulation techniques (such as direct cortical stimulation–DCS) in combination with iEEG can be used in dual-site protocols to probe inter-area functional connectivity between the two sites of stimulation. This method offers unique insights into how neuronal communication can be altered and possibly established. Altogether, such an integrative approach has the potential to advance our basic understanding of brain function as well as translate to clinical applications, which may allow us to improve treatment strategies for the large number of psychiatric and neurological disorders involving a selective dysfunction of frontoparietal networks.

#### CRediT authorship contribution statement

**Mattia F. Pagnotta:** Writing – review & editing, Writing – original draft, Conceptualization. **Mark D’Esposito:** Writing – review & editing, Writing – original draft, Conceptualization. **Justin Riddle:** Writing – review & editing, Writing – original draft, Conceptualization.

#### Declaration of Generative AI and AI-assisted technologies in the writing process

The authors did not use generative AI for preparation of this work.

#### Declaration of Competing Interest

The authors declare no competing interests.

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#### Data Availability

No data was used for the research described in the article.

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