Title: Theta oscillations shift towards optimal frequency for cognitive control

Author list: Mehdi Senoussi[1]*, Pieter Verbeke[1], Kobe Desender[1,2,3], Esther De Loof[1], Durk Talsma[1], Tom Verguts[1]

Affiliations:

1. Department of Experimental Psychology, Ghent University, Belgium
2. Department of Neurophysiology and Pathophysiology, University Medical Center Hamburg-Eppendorf, Germany
3. Brain and Cognition, KU Leuven, Belgium

* corresponding author

Corresponding author:

Dr. Mehdi Senoussi
Department of Experimental Psychology, Ghent University
Henri Dunantlaan 2,
9000, Ghent, Belgium
E-mail: mehdi.senoussi@ugent.be

Abstract:

Cognitive control allows to flexibly guide behaviour in a complex and ever-changing environment. It is supported by theta band (4-7Hz) neural oscillations that coordinate distant neural populations. However, little is known about the precise neural mechanisms permitting such flexible control. Most research has focused on theta amplitude, showing that it increases when control is needed, but a second essential aspect of theta oscillations, their peak frequency, has mostly been overlooked. Here, using computational modelling, behavioural and electrophysiological recordings, in three independent datasets, we show that theta oscillations adaptively shift towards optimal frequency depending on task demands. We provide evidence that theta frequency balances reliable set up of task representation and gating of task-relevant sensory and motor information and that this frequency shift predicts behavioural performance. Our study presents a mechanism supporting flexible control and calls for a re-evaluation of the mechanistic role of theta oscillations in adaptive behaviour.

Introduction

Cognitive control permits adapting behaviour to task demands, crucial in an ever-changing environment. The flexibility of such a fundamental cognitive ability is at the core of intelligent behaviour. Cognitive control is supported by neural oscillations in the theta band (4-7Hz)[1,2] (also called frontal midline theta) that coordinate distant neural populations to create task-relevant functional networks through synchronization[3–7]. Medial frontal cortex (MFC) generates theta oscillations when cognitive control is needed, i.e. during conflict or in preparation of a difficult task[1]. Task rules and goals dictating behaviour are instead encoded in lateral frontal cortex (LFC)[8–10]. The coordination of these two areas through theta-rhythmic processes, has been shown to support successful task performance[11]. It has been proposed that task-relevant functional networks are established through top-down gating from these frontal areas, by synchronizing distant neural populations allowing efficient communication, i.e. communication-through-coherence[3,12].

Theta oscillations thus play a critical role in the implementation of cognitive control, but to be adaptive, theta oscillation characteristics must change with task demands. However, the exact neural mechanisms that support flexible control remain largely unknown. Most research has focused on theta amplitude, showing that it increases after conflicts and errors, causing subsequent neural adaptation leading to better task performance[1].

Critically, a second essential aspect of theta oscillations, their peak frequency within the 4-7Hz range, has occasionally been reported to vary across tasks and participants[13–15]. However, most studies report band-average theta power per condition which precludes observing changes in peak theta frequency across conditions. Moreover, estimating shifts in peak frequency from conventional representation of spectral data (e.g. power spectra or time-frequency maps) is non-trivial and must avoid confounding factors such as changes in the aperiodic component of the power spectra[16]. It therefore remains unclear whether reliable theta peak differences exist. Finally, this variability and its mechanistic consequences are commonly ignored and no theoretical account has considered its role in cognitive control. To address this gap, we draw from two prominent frameworks: biased competition (BC)[17] and communication-through-coherence (CTC)[12]. We built a computational model where theta oscillations orchestrate competition between task representations, which in turn guides CTC to set up task-relevant functional networks. Model simulations show that, depending on task demands, different theta frequencies are optimal for task performance. We tested model predictions on behavioural and electrophysiological data and confirmed that the frequency of theta oscillations adaptively shifts towards optimal frequency depending on task demands.

Results

Theta frequency controls reliable task implementation.

We designed a stimulus-action mapping task (Figure 1a) wherein on each trial, a different mapping (i.e. a rule, with variable difficulty) needs to be established. The task consists of reporting the tilt of one of two gratings, clock-wise (CW) or counter-CW from the vertical axis, using the index or middle finger of one of both hands. On each trial a two-letter cue instructed the rule: which was the target grating (Left (L) or Right (R), top-letter) and which hand to use (L or R, bottom-letter). We thus manipulated task difficulty: same-side cues (i.e. (top-letter – bottom-letter) RR and LL) were easier than different-side cues (LR and RL).

Our model consists of five units (Figure 1b): two control units (Lateral and Medial Frontal Cortex, respectively LFC and MFC), two processing units (Sensory and Action), and an Integrator unit. In LFC, cues activate instruction nodes, which themselves activate rule nodes. Rule nodes form a competitive accumulator network[18] that implements BC: In a Stroop-like manner, the connectivity between instruction nodes induces stronger competition between rule nodes for different-side than same-side rules. Importantly, rule node competition is orchestrated by theta oscillations generated by the MFC unit: competition is (re-)initiated when MFC theta exceeds a processing threshold (Figure 2a, b). Each rule node points to rule-relevant processing modules. Processing nodes oscillate at gamma frequency. Rule nodes gate communication between Sensory and Action units through CTC[12,19], thereby implementing the instructed mapping, by means of phase-resetting bursts emitted by MFC at theta oscillation peaks[3,19] (Figure 2b-d). The Integrator unit constitutes a competitive accumulator network[18] that accumulates information received from Action nodes, and triggers a response once one of the Integrator nodes reaches a threshold (Figure 2e).

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Crucially, with a fast theta frequency, e.g. 7Hz, rule nodes gate processing modules frequently, shortening “off”-periods in which rule-relevant processing nodes de-synchronize, at the cost of shorter competition windows. With a slow theta frequency, e.g. 4Hz, gating is imposed less frequently, but competition windows are longer. Due to BC, one rule will win the competition; but for difficult rules, resolving the competition will take more time, i.e. require longer competition windows. In our task different-side rules are more difficult, so the model achieves better performance at slower theta frequencies where competition is long enough for the correct rule node to win (Extended Data Figure 1a-b). In contrast, for easy rules, competition is won quickly, thus higher theta frequencies yield better performance as rule-relevant nodes are frequently gated, reducing “off”-periods. Hence, an optimal agent would shift theta frequency depending on task demands.

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Model simulations (Figure 3a) confirmed that for difficult rules the model achieves optimal accuracy at a slow theta frequency, whereas for easy rules, a fast theta is optimal ($W = 105.5$, $p < 0.001$, $r = 0.64$, 95% CI: (1.00, 2.00); Figure 3b). Fits from the drift diffusion model on model data (see Methods) showed that only drift rate exhibited this theta-frequency – rule-difficulty interaction (Extended Data Figure 2a), refuting a speed-accuracy trade-off (SATO) explanation. Theta amplitude alone could not explain this result as theta amplitude only negligibly affected competition window length relative to frequency (Extended Data Figure 1c-d).

Furthermore, theta-rhythmic gating of processing nodes should yield better model performance shortly after a burst, i.e. at theta oscillation peaks (Figure 3c). By varying the instruction-stimulus delay (ISD), to sample model performance at different phases of the theta-rhythmic process[20,21], we showed that model accuracy oscillates at a frequency closely matching MFC theta frequency (Figure 3d, Supplementary Figure 1).

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These simulations lead to two key behavioural and neural predictions. First, oscillations of accuracy-by-ISD should shift towards optimal theta frequency depending on task demands. Second, frontal theta oscillations should also exhibit this effect, and the degree to which theta frequency shifts according to task demands should be predictive of subsequent task performance.

Frequency shift in behavioural performance oscillations.

In an experiment on human participants (Dataset 1), we first confirmed that rules varied in difficulty (Figure 4a). There was a significant target-location – hand interaction in accuracy (RR and LL easier than LR and RL; $F(1, 33) = 27.82$, $p < 0.001$, $\eta^2 = 0.236$), and a main effect of hand ($F(1, 33) = 4.33$, $p = 0.045$, $\eta^2 = 0.012$). Consistent with model simulations, only drift rate exhibited this interaction (Extended Data Figure 2b); we therefore used accuracy as our dependent variable. To test model predictions on behavioural oscillations, we computed peak theta frequency of accuracy-by-ISD (see Methods, Supplementary Figure 2a). As predicted, we found a significant target-location – hand interaction ($F(1, 33) = 6.51$, $p = 0.015$, $\eta^2 = 0.047$), showing that accuracy oscillated at a slower theta frequency for difficult rules (LR, RL; Figure 4b), and no main effect.

Frequency shift in frontal theta predicts task performance.

Next, we investigated whether neural theta exhibited this frequency shift due to task demands. We extracted EEG theta peak frequency in a 1s pre-stimulus window from an electrode cluster exhibiting significantly higher theta power in correct than incorrect trials ($p < 0.001$; Figure 4c; see Methods). As predicted, peak theta frequency in correct trials significantly decreased from same-side to different-side rules ($F(1, 33) = 18.96$, $p < 0.001$, $\eta^2 = 0.107$; Figure 4d; see also individual participant spectra in Extended Data Figure 3). Although peak theta frequency differed numerically between different-side rules (i.e. LR and RL), this difference was not statistically significant ($W=211$, $p = 0.139$, $r = -0.29$, 95% CI: (-0.72, -0.14)). Furthermore, contrasting correct and incorrect trials revealed that higher theta frequency improved performance in same-side rules, whereas a lower theta frequency improved performances in different-side rules ($F(1, 33) = 4.62$, $p = 0.039$, $\eta^2 = 0.036$; Figure 4d). Finally, across participants, the degree to which theta frequency shifted from difficult to easy rules positively correlated with overall accuracy ($r(32) = 0.49$, p = 0.004, 95% CI: (0.17, 0.71); Figure 4e), indicating that a higher sensitivity of theta frequency to rule difficulty improved task performance. These analyses were carried out using the FOOOF toolbox[16] to estimate peak and power of theta oscillations. Additional control analyses revealed that our results were robust and observable without using this toolbox (i.e. by estimating theta peak frequency on raw spectra, see Methods and Supplementary Figure 7). These results cannot be explained by changes in theta power alone as both peak and power were estimated independently over the 1/f spectrum (Supplementary Figure 2b, see also the Control analyses section below).

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Theta frequency shift generalizes to other tasks.

Having established a robust effect of task demands on theta frequency in our stimulus-action mapping task, we tested the generality of this mechanism, namely a decrease of theta frequency for difficult tasks, to other cognitive control tasks. First, we reanalysed previously published data[22] from an experiment in which seventeen participants performed an arithmetic task, preceded by a cue indicating whether the arithmetic operation was going to be easy or difficult (Dataset 2; Figure 5a). Different from our original experiment (i.e., Dataset 1), in Dataset 2, only two levels of difficulty were used, thus allowing us to test whether theta frequency is lower following a difficult compared to an easy cue. There was a significant effect of difficulty on error rates and on reaction times (see original article for details[22]). In order to use a comparable time window for the analysis of the EEG data (relative to Dataset 1), we selected a 1 second segment of EEG data in the post-cue interval. This segment was centered around the time point in which the difference in theta power between difficult and easy conditions was the highest (2,000ms post-cue onset, see Figure 4a in [22]). Thus, we considered EEG data in the 1,500 to 2,500ms segment post-cue onset. Furthermore, because of the low number of incorrect responses (error rates of 1% and 6% for the easy and difficult conditions respectively) we decided not to use the correct-incorrect contrast as in Dataset 1 (Figure 4c) and chose an a-priori electrode, FCz, based on prior findings in theta oscillations in cognitive control[1,23–25]. Due to the absence of identified theta oscillations using the FOOOF toolbox in the easy condition of three participants, we analysed 14 participants in total in Dataset 2. Confirming the model predictions and the observation from Dataset 1, we found a lower peak theta frequency in correct trials in the difficult compared to easy condition (W = 86, p = 0.017, r = 0.64, 95% CI: (0.01, 0.14); Figure 5b).

Second, we reanalysed another published dataset[26] from an experiment in which thirty-three participants performed an Go – No-Go task, where each trial was preceded by a cue indicating whether the upcoming stimulus was a certain-go (i.e. a Go stimulus with 100% certainty) or a maybe-go (i.e. a No-Go stimulus with 25% certainty; Dataset 3; Figure 5c). There was a significant effect of cue type on error rates (see original article for details[26]). We tested whether theta frequency is lower following a maybe-go cue compared to a certain-go cue (followed by a No-Go stimulus). As for Datasets 1 and 2, we estimated peak theta frequency in a 1s segment preceding stimulus onset. Similar to Dataset 2, the number of incorrect responses was low (1.7% error rates in the certain-go condition), we thus used electrode FCz. Again, confirming our findings from model and Datasets 1 and 2, we found a higher peak theta frequency following certain-go cues compared to maybe-go cues (W = 358, p = 0.039, r = 0.36, 95% CI: (-0.01, 0.08); Figure 5d)).

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Control analyses.

We showed that peak theta frequency decreases with task difficulty. A recent study has demonstrated that, in the case of posterior alpha oscillations, amplitude and frequency are intrinsically related[27] due to the thalamo-cortical circuits thought to generate alpha oscillations[28]. One concern could be that such a relationship also exists in the case of midfrontal theta oscillations, thereby confounding frequency and power. We thus verified whether peak theta amplitude exhibited the same pattern of decrease with task difficulty. We carried out the same analysis procedure that was used for peak theta frequency on peak theta amplitude (Figure 6) and showed that there was no statistically significant difference in peak theta amplitude between easy and difficult conditions in any of the three Datasets (all ps > 0.078, uncorrected for multiple comparisons). This result shows that peak theta amplitude could not account for the decrease in peak theta frequency across conditions.

Additionally, we tested whether the shift in peak theta frequency could be confounded by amplitude or frequency of nearby frequency bands. For both the delta and alpha frequency bands, we followed the same procedure as for the main results on the theta band but instead we analyzed peaks in the 1-3Hz range (delta) or 8-12Hz range (alpha band). No statistically significant decrease with task difficulty was found for the delta or alpha band, neither in peak frequency (all ps > 0.091, uncorrected for multiple comparisons, Extended Data Figure 3a, c, e, g, i, k) nor in peak amplitude (all ps > 0.200, uncorrected for multiple comparisons, Extended Data Figure 3b, d, f, h, j, l).

These control analyses therefore suggest that the shift of peak theta frequency with task difficulty happens independently of changes in theta amplitude or changes in nearby frequency bands.

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Discussion

In this study, we have identified an adaptive mechanism allowing flexible cognitive control. We propose a computational model, test its predictions in behavioural and electrophysiological data, and show that theta oscillations lawfully adapt to task demands by shifting towards optimal frequency for task performance. Moreover, we replicate this finding in two independent datasets implementing entirely different tasks (arithmetic operations and response inhibition) and show that the shift of theta frequency according to task demands is a general mechanism involved in a wide range of cognitive processes. Finally, we controlled for possible confounding factors such as amplitude modulations and changes in nearby frequency bands and showed that the shift in theta peak frequency took place independently from other changes in oscillatory activity.

These findings are in line with evidence that frequency of neural oscillations adapts to external demands, e.g. perceptual demands in alpha band[29,30], and is related to short-term memory capacity in theta band[31]. Our study complements and extends our understanding of how neural oscillations support cognitive processes by providing a mechanistic account allowing to simulate and test further hypotheses. An exciting avenue for future research lies in characterizing how adaptive shifts in theta frequency relate to cross-frequency coupling dynamics[32], e.g. between theta and gamma oscillations.

A related body of work has investigated the role of theta peak frequency in working memory processes. Indeed, theta oscillations originating from medial temporal lobe and basal forebrain structures (e.g. hippocampus, septum) have been hypothesized to support the maintenance of ordinal information in an item sequence in working memory[31]. According to this theory, the phase of theta oscillations structures the (re-)activation of distinct neural populations oscillating at gamma frequency, each representing an item of the maintained sequence. This theory thus predicts that a slower theta frequency, leading to longer periods in which items could be nested, would increase working memory capacity (see also [33] for a discussion of oscillatory frequency and cognitive resources). Some studies have confirmed this prediction empirically by showing that higher working memory loads led to a reduction of theta frequency[34,35]. Moreover, a recent study causally tested this prediction using tACS[36] and showed that stimulating a fronto-parietal network at a slow (i.e. 4 Hz) versus fast (i.e. 7 Hz) theta frequency led to increase in working memory capacity. Although theta oscillations that support working memory and cognitive control serve different purported roles (i.e. structuring maintained information in working memory versus synchronizing for communication in cognitive control), and have distinct neural origins (hippocampus/septum in working memory versus medial frontal cortex in cognitive control), both views on theta oscillations highlight the importance of peak oscillatory frequency. One exciting avenue of research concerns the interplay between theta oscillations supporting cognitive control and supporting working memory. Indeed, the control over memorized items in a working memory task, for instance after retro-cuing a subset of maintained items or during manipulation of a memorized sequence of items, has been shown to depend on midfrontal theta oscillations[37,38], which are plausibly homologous to the ones observed in the current experiment and in cognitive control more generally[1,39]. Finally, some studies have demonstrated that midfrontal and hippocampal theta oscillations can phase-lock or exhibit coherence to each other in certain contexts[39,40], suggesting that the two theta-generating systems can interact. For now, more studies are needed, for instance using intracranial recordings in humans, to better understand the relationship between midfrontal and hippocampal theta oscillations.

In our model, the MFC unit generates theta oscillations when a rule is instructed. These oscillations orchestrate rule node competition and generate bursts synchronizing rule-relevant sensory and action nodes. This mechanism based on theta oscillations is coherent with an energizing, or more generally modulatory, role of the dorsal Anterior Cingulate Cortex (dACC), in line with the Expected Value of Control (EVC) theory[41,42]. According to the EVC theory, the dACC specifies the intensity of the control signal. This has also been described as a motivational function of the dACC, in line with the observation that lesion of dACC can lead to deficits in motivated behaviour[43]. However, these accounts do not discuss the specific role or importance of theta oscillations. Another line of work demonstrated that the exertion of cognitive control critically relies on theta oscillations[1,2] to create task-relevant functional networks[3,4]. Most of these studies showed that the amplitude of theta oscillations generated in the dACC, increases after conflicts and errors, and that it predicts improvement in task performance[1]. Our study thus extends our knowledge on the energizing role of dACC by showing that, in addition to theta amplitude, another dimension of theta oscillations is crucial for optimal control of task representations: theta frequency. This generalization of the energizing role to a modulatory one, allows for an extra degree of freedom in control. Specifically, it posits that two separate aspects of this control signal can be independently manipulated (by the dACC): the intensity of the control signal through theta amplitude, and the time window of the control signal's effect on the task representations through theta frequency. Previous studies have shown that adaptive changes in theta amplitude (i.e. the intensity of the control signal) are critical for cognitive control, e.g. in conflict adaptation[44,45]. On the other hand, adaptively changing the processing time window through theta frequency allows to adjust a trade-off in the orchestration of task representations by theta oscillations. In easy task rules, a faster theta frequency is optimal as these representations are set up quickly and reliably, whereas a slower theta frequency is necessary for difficult rules. This observation opens new avenues for research to understand the functional role of both theta amplitude and frequency in dACC.

Prior models have ascribed some aspects of rule or action representations to the dACC (e.g. [46,47]), and it has been shown empirically that dACC represents certain aspects of task sets[41,48–51]. It could thus be argued that our MFC unit should represent some aspects of actions or task sets. Here, we would like to underline that our anatomical labelling (e.g. LFC, MFC) was rather broad, in part because the functional architecture is not fully known, especially with respect to the division of labour between lateral and medial prefrontal cortices. Thus, the two theories are not necessarily in contradiction, and may simply highlight different functional roles of lateral and medial frontal cortex. We believe that it will be critically important for future modelling studies to investigate how the modulation of task representations can be implemented through targeted theta oscillations, and that future experimental work should aim at disentangling how dACC and LFC modulate and represent and task information.

Theta oscillations have also been shown to support attention in a several previous studies (e.g. [20,52–56]). Many studies showed that the amplitude of theta oscillations increases when attention is endogenously oriented (sometimes referred to as sustained attention[52,55]), or when it needs to be re-oriented[20,53]. These studies report changes of amplitude in neural oscillations in the theta frequency band or theta band fluctuations in behavioural performance[55–58] (see also [21] for a review). It has been proposed that theta oscillations supporting attentional processes reflect rhythmic sampling of visual information at the attended location and across the visual field. These theta oscillations are thought to be supported by a network comprising the lateral intraparietal cortex, the pulvinar nucleus of the thalamus and the frontal eye fields[59,60] (but see also evidence that interaction between local receptive fields in V4 can induce theta oscillations[61]). But to date, none of these studies reported a shift in theta frequency across conditions. One possibility is that such shifts have been overlooked due to averaging of spectral amplitude across frequencies in the theta frequency band that is commonly performed to test for difference in amplitude of theta band oscillations, or contamination of peak frequency by other factors (e.g. the aperiodic component of the spectrum).

However, it seems unlikely that differences in attentional demands underlie our findings. In Dataset 1, the difficulty between same-side and different-side instructions (which induced the theta frequency shift) was situated at the stimulus-action mapping level, in contrast with attentional demand manipulations of stimulus discriminability or identity (e.g. simple feature versus feature conjunction searches in [57], or the number of stimuli to track in [58]). Indeed, the tilt of grating stimuli in Dataset 1 was determined in a separate block before the main experiment and kept constant throughout the main experiment blocks. Furthermore, there was no difference in the validity of rule instructions relative to target location (i.e., all instructions were 100% valid) and thus, no uncertainty in stimuli location that would differentially affect sampling of visual information by attentional processes. Similarly, no differences specific to attentional orientation or attentional sampling demands distinguished the conditions in Datasets 2 and 3. Thus, differences in attentional demands alone cannot explain the shift in theta frequency we observed here. Nevertheless, it is possible that different theta oscillation-generating systems co-exist and interact to support attention and cognitive control. In fact, in our model, the activity of rule-relevant Sensory nodes oscillates at theta frequency due to the bursts sent from the MFC unit. It would therefore be interesting in future studies to investigate how midfrontal theta oscillations supporting cognitive control interact with other generators of theta oscillations shown to support attentional processes[62].

Our study also provides a potential explanation for the discrepancy in reported oscillatory frequencies contributing to top-down cognitive processes[63]. Indeed, several studies have reported the involvement of different low-frequency bands[14,64–67] during top-down control processes (e.g. decision making, working memory, hierarchical task implementation). The intrinsic frequency range of theta oscillations poses limits on the processes that they can orchestrate. Therefore, based on the overwhelming evidence that theta oscillations support task rule implementation and action monitoring[1,68,69], it would seem that such processes must take place within a theta cycle. In our model, we chose to use the canonical 4-7 Hz limits of theta oscillations, thus a task rule that would require a longer build-up time than the slowest theta frequency (4Hz, period of 250ms) could not be reliably instantiated. However, several recent studies have shown that the implementation of complex task rules (e.g. multiple simultaneous novel rules, nested task rules) elicit frontal midline slow oscillations in the delta range (1-3Hz; e.g. [65,66]). Although we have not found such a spread into lower or higher frequency bands in our own Datasets (see Extended Data Figure 3), these results potentially question the conventional frequency limits of oscillations supporting cognitive control (usually attributed to the theta band). More abstract task rules (e.g. [65,70]) recruit a larger extent of frontal areas[71] and more rostral frontal areas, in line with accounts of a hierarchical organization of the frontal cortex [70,72]. This larger network of areas might thus require longer periods to build up stable task representations and necessitate slower oscillations (in the low theta or delta bands) to efficiently and reliably implement such abstract task rules.

It would therefore be of interest to further test whether a gradual increase in task complexity or abstractness could elicit a slowing of neural oscillations generated by the medial frontal cortex towards the delta range. For instance, based on the stimulus-action mapping task we developed for our model and

Dataset 1, it would be interesting for future research to see whether we observe further slowing of midfrontal theta oscillations (i.e. into the delta frequency band) if we increase the number of response options from two (i.e. clockwise, counter-clockwise) to three or four (i.e. different angles of grating rotation relative to the vertical). Another possibility to study the effect of gradual increase in task complexity would be to use multi-step tasks, such as hierarchical and/or temporally-extended tasks[73,74]. Such studies would inform our understanding of the interaction between task complexity and the flexibility of the temporal scale of neural operations.

Our model predicts that a decrease in MFC theta frequency from easy to difficult tasks is beneficial for behavioural performance. Several studies have tested the causal role of theta oscillations in cognitive control using transcranial alternating current stimulation (tACS) in the theta frequency band[75–77]. In these studies, a fixed theta frequency (e.g. 6 Hz) is used across participants and conditions. It would therefore be interesting to test this prediction from our model by varying tACS frequency across the theta frequency range.

The Integrator unit in our model aggregates inputs from the Action unit, which is itself activated by the Sensory unit; the Integrator unit commits to a response when the activity of any node in this unit reaches a (collapsing) threshold (see Methods). The slope of the information accumulation of the correct node (for a particular trial) thus reflects the strength of the sensory signal or the difficulty of the instructed rule; or, more generally, the task difficulty. This relationship with task difficulty is consistent with the relationship observed empirically between the P3b ERP component (also referred to as Centro-Parietal Positivity, CPP) and the difficulty of perceptual decisions[78]. Indeed, the Integrator unit of our model constitutes a leaky competing accumulator network[18], which is thought to capture essential dynamics of perceptual decision making as studied in[78]. One interesting avenue for future research is the observation that our model accumulation in the Integrator node associated with the correct response, is locked to gamma oscillations that modulated the activity of rate code neurons in each neural triplet. It has been previously shown that evidence accumulation is subject to slow-rhythmic fluctuations in the delta frequency band[79]. It would therefore be interesting to test whether additional fast-rhythmic dynamics exist in the upslope of the P3b component, which could have been hidden in previous studies. Indeed, if these gamma oscillations were not phase-locked across trials, the ERP averaging procedure would average out such fluctuations.

We observed a large interindividual variability in peak theta frequency across conditions (see individual spectra in Supplementary Figures 3-6). Although interindividual variability of the absolute theta peak (in Hertz) can be partly attributed to non-functional sources of variance such as skull conductivity and thickness[80,81], variations in individual peak frequency correlate with cognitive performance in the alpha band[82–84] and this variability is related to properties of cortico-thalamic white matter projections[85]. This suggests that individual peak frequencies, in different frequency bands can be a stable neurophysiological trait[86] and that this variability of peak theta frequency, in itself, would be an interesting topic of investigation for future studies. For instance, investigating the causes and consequences of individual peak theta frequency could have an important impact on the development of personalized neurostimulation interventions using TMS or tACS[77]. Indeed, targeting peak theta frequency could allow to optimally modulate functional connectivity which has been shown to be dysregulated in Alzheimer’s disease[87–89]. Moreover, significant response variability exists in repetitive TMS treatment using intermittent Theta Burst Stimulation (iTBS) for treatment of major depressive disorder[90]. It would thus be interesting to test whether individualized iTBS frequency, estimated in a separate experimental procedure (e.g. [91]), could, at least partly, reduce this response variability.

Despite the robust and replicable association of theta oscillations and cognitive control, the neurobiological underpinnings of theta generation and modulation remain unclear. Microcircuit models of theta generation in anterior cingulate cortex (ACC) have been proposed[92], and although the relevance of peak frequency fluctuations has been mentioned, no clear mechanism driving such fluctuations was proposed yet. One candidate mechanism could be a reinforcement-learning system based on ACC-brainstem structures involving the locus coeruleus (LC) and noradrenergic neuromodulation of ACC circuits[93]. Indeed, the LC heavily innervates medial frontal cortex, has been shown to modulate cortical oscillations, and its activity increases with task demands[94]. It would thus be interesting to test whether noradrenergic pathways modulate the frequency of ACC-generated theta oscillations in response to task demands. Future studies investigating these candidate neurobiological mechanisms allowing adaptive cognitive control will be crucial to better understand pathogenesis of several psychiatric disorders, e.g. attention-deficit/hyperactivity disorder[93,95].

Neural oscillations may address the fundamental binding problem in cognition by gating information flow in the brain to support cognitive flexibility [33,96]. Our results provide critical insights into the adaptive nature of theta oscillations supporting cognitive control, and call for a more systematic evaluation of theta characteristics, at computational, behavioural, and neurophysiological levels.

Methods

Model

Overview

The model implements biased competition (BC) and communication-through-coherence (CTC) and consists of five units: two control units (lateral and medial frontal cortex, LFC and MFC respectively), two processing units (Sensory and Action units), and an Integrator unit accumulating evidence from the Action unit, and producing a response. We will first briefly describe how BC and CTC are implemented in the model, and then proceed to a detailed description of each unit, and the nodes composing them.

BC proposes that task representations compete, biased by top-down input. We implemented BC in the LFC unit, which was composed of rule nodes that pointed to specific processing nodes. Each rule node pointed to processing modules composing the rule. This allows a rule node to gate task representations (encoded via an input-output matrix), relevant for that particular rule. For instance, a rule node could implement the rule “report sensory feature 1 using action set 2” (see this example in Figure 1b). We used location (Left (L) or Right (R)) as a sensory feature. We used two action sets, namely Left (L) and Right (R) hand (see Action unit in Figure 1b). Rule nodes were interconnected to create a competitive accumulator network. Each rule node also received a biasing input throughout a trial from instructions in the form of two letters presented simultaneously and modelled as a top letter instructing which stimulus feature was the target (L or R) and bottom letter instructing which action set to use (L or R). We refer to these instructions, or rules, in this manner: RL for “Right-Left”, in which the first letter refers to the top instruction letter, instructing the target stimulus feature (Right grating), and the second letter refer to the bottom instruction letter, instructing the action set to use (Left hand). Each rule in the task (i.e. RR, LL, LR, RL) activated a unique set of instruction nodes (see in Figure 1b, LFC unit). Two nodes represented the top letter of an instruction, and two others the bottom letter. This network of instruction nodes created a congruency effect between instruction letters: top and bottom “Left” nodes were connected, thereby activating each other, and similarly for “Right” nodes. In a Stroop-like manner, the connectivity in instruction nodes induced a stronger input to rule nodes for same-side (LL, RR) than for different-side (LR, RL) rules. Furthermore, different-side rules also activated non-instructed instruction nodes more than same-side rules due to the lateral excitation in instruction nodes, thereby making the BC between rule nodes more difficult for different-side rules to win.

The top-down bias signal from control units was implemented through CTC. The MFC unit generated theta oscillations. During a temporal window whose size depended on the specific theta frequency (i.e. the slower theta, the longer the temporal window), a competition was initiated between rule nodes. During this competition window, MFC unit sent bursts of activity[11,19,97]. The most active rule node (i.e. the one "winning" the competition) amplified the burst and sent it to Sensory and Action nodes it points to. All Sensory and Action nodes oscillated at gamma frequency. These bursts reset the phase of Sensory and Action nodes selected by the LFC unit, and increased synchrony between them, allowing for efficient communication, i.e. gating. Through this selective routing of bursts to Sensory and Action nodes, the model implements CTC by creating functional networks to implement a rule.

As a result of the BC, one rule (typically, the correct one) will win the competition; but in cases in which the competition is stronger, it will require a longer competition window for the correct rule to win the competition. The latter are difficult rules. In the model, rule difficulty was implemented through conflicting instructions that activated more rule nodes than easy instructions, making the competition more balanced between the instructed and the other rule nodes. The consequence is that for difficult rules, the model will achieve better performance at a slower theta oscillation frequency because longer competition will permit rule nodes to win the competition and thus gate the rule-relevant processing nodes. In contrast, for easy rules, performance increases with a higher theta frequency because rule nodes quickly win the competition and the faster theta frequency allows to more frequently gate rule-relevant processing nodes. Hence, an adaptive agent would shift theta frequency depending on task demands.

Oscillatory nodes: a neuronal triplet

In the MFC unit and processing units, each node i implements a cortical column simplified as a triplet of neurons, as used in previous models[19,45,97]: a rate code neuron (x_i) and two phase neurons (one excitatory (E_i) and one inhibitory (I_i) neuron), see Figure 1b-c and Figure 2b, c-d. Phase neurons, i.e. the E-I pair, generate oscillations with a frequency defined by the E-I pair's coupling parameter (C). This E-I architecture uses the same basic principles as the pyramidal-interneuron network gamma (PING) model, which is commonly used to model gamma frequency generation[98–100] but has also been used to simulate neural oscillations in other frequency bands (e.g. [101,102]). The activity of each phase neuron is defined by a system of stochastic difference equations, following previous work[19,97], for E neurons:

$$E_i(t + \Delta t) = E_i + \Delta t(-CI_i(t) - Damp\mathrm{J}(r > r_{\min})E_i(t) + \ B_i(t)) \tag{1}$$

and for I neurons:

$$I_i(t + \Delta t) = I_i + \ \Delta t(CE_i(t) - Damp\mathrm{J}(r > r_{\min})I_i(t)) \tag{2}$$

In which $E_i(t)$ and $I_i(t)$ denote the activity of the excitatory and inhibitory neurons of node i at time t and model data were simulated at 500Hz, so Δt=0.005s. The radius r of oscillation ($r = E^2 + I^2$) of an E-I pair, which corresponds to its oscillatory amplitude, is constrained to a radius $r_{\min}$ = 1 (except for simulations in which we varied MFC theta amplitude, see Extended Data Figure 1c-d). To implement this constraint, we use an indicator function $\mathrm{J}(.)$, which returns 1 when its argument is true (i.e., when $r > r_{\min}$), and 0 otherwise. The parameter *Damp* represents the strength of the attraction towards $r_{\min}$ and prevents the activity of the E-I pair from growing too large (i.e., it dampens activity of the E and I neurons). In more neurophysiologically realistic models (e.g. [103]), such dampening of the E-I pair oscillatory amplitude would be implemented via a projection between the E-I pair and a pool of inhibitory neurons that in turn can inhibit the E and I neurons. For convenience, we here implemented the simpler, approximate implementation via the indicator function J and the *Damp* parameter, in line with previous models[19,45,97]. The parameter $Damp$ was set to 0.3 for processing nodes. For the MFC node, $Damp$ was set to 0.005**theta_frequency* to scale with the speed of the E-I pair theta oscillations and maintain an equal amplitude across time for all theta frequencies. The term B_i denotes the burst that processing nodes could receive depending on the trial instructions (see Medial Frontal Cortex unit and Lateral Frontal Cortex unit for details). The MFC node did not receive bursts, thus B_{MFC} was set to 0.

The frequency of oscillations generated by the E-I pair was defined by the coupling parameter C, and its relation to frequency in Hertz is given by the following equation:

$$C = f2\pi \tag{3}$$

In which *f* denotes the frequency in Hertz and C the coupling parameter in the E-I pair.

Rate neurons receive, process, and transmit information to other nodes. Their activity (x_i) is determined by the input to the node (in_i). For instance, in a Sensory node, the input in_i to a rate neuron is either zero (if its preferred stimulus feature is not presented) or 0.02 (if its preferred stimulus is presented; see Processing units for more details). This input is then modulated by its excitatory phase neuron (E_i). Thus, rate neuron activity is updated by:

$$x_i(t + \Delta t) = x_i(t) + \Delta t(-x_i(t) + in_i F\big(E_i(t)\big)) \qquad 4$$

with $F(.)$ being a logistic function of E_i:

$$F(E_i) = \frac{1}{1 + e^{-5(E_i(t) - \theta_E)}} \qquad 5$$

Processing units

The processing units are a Sensory unit and an Action unit. Each unit is composed of nodes representing cortical columns (see Oscillatory nodes: a neuronal triplet section).

In all nodes of Sensory and Action units, the coupling parameter C was set to generate gamma oscillations. The gamma oscillations were set to 30 Hz by using a coupling parameter of $C = 188.5$, which, in the computational implementation of the model, was set to 0.377 to account for the sampling rate at 500Hz ($C/500 = 0.377$). We used low gamma-band oscillations around 30 Hz as this sub-band of gamma has been shown to be critically important for visual processes[104,105] and to be modulated by theta-band oscillations following task cues[11]. To test model stability, we also ran simulations using a higher gamma frequency of 50 Hz and found similar results.

To further show model stability and induce noise in processing nodes' oscillatory phase, we modified the neural triplet dynamics used in prior implementations[19] in which noise was introduced by independently varying the oscillatory frequency of each neural triplet across trials, while fixing it across time for each single trial. For that purpose, we added random slow fluctuations in the coupling parameter of nodes oscillating at gamma frequency, thereby mimicking noise in ongoing gamma oscillations as observed in empirical studies[106]. We generated random numbers from a normal distribution with parameters $\mu = 1$, $\sigma = 1$, for each trial and each processing unit (i.e. Sensory and Action). A low-pass filter was then applied to these coupling fluctuations time courses, i.e. Gaussian convolution with $\sigma = 1$ (in seconds). Finally, the coupling parameter (i.e. $C = 0.377$, for 30Hz oscillations) was multiplied by the value of these low-frequency coupling fluctuations. The result of this manipulation was slow random fluctuations of gamma frequencies in phase neurons of processing units. For example, for one trial, Sensory nodes were oscillating at 32Hz at a certain time t, then gradually shifting to 27Hz, then to 35Hz, etc. This slow fluctuation was generated independently for Sensory and Action units.

Rate neurons of the Action unit receive input from rate neurons of Sensory nodes in order to implement the two-alternative orientation discrimination task on gratings. The main task was to report whether the target grating was tilted clock-wise (CW) or counter-CW (CCW) from the vertical axis. To report the tilt the rule was to use the index and middle fingers of either the left or right hand, indicated by the instructions. The left middle finger and right index finger should be used to report a grating tilted CW, and the left index finger and the right middle finger should be used to report a grating tilted CCW. Therefore, the connectivity between Sensory and Action nodes' rate neurons implemented this rule.

Integrator unit

The Integrator unit accumulates information for each response, and triggers the model response once one of the Integrator nodes reaches a threshold. There is thus one Integrator node for each Action node. The Integrator nodes constitute a competitive accumulator network (as implemented in prior work, e.g. [18]) and followed the following update:

$$\boldsymbol{y}_{Integ}(t + \Delta t) = \boldsymbol{y}_{Integ}(t) + \Delta t(\boldsymbol{W}_{Integ}\boldsymbol{x}_A + \boldsymbol{W}_{lat,Integ}\boldsymbol{y}_{Integ}(t)) + \sigma_{Integ}\boldsymbol{N}(t) \qquad 6$$

In which $\boldsymbol{y}_{Integ}(t)$ is a vector collecting the activity of all Integrator nodes at time t, $\boldsymbol{W}_{Integ}$ denotes the weight matrix between Action nodes and Integrator nodes, $\boldsymbol{x}_A$ denotes input from Action nodes to Integrator nodes. $\boldsymbol{W}_{lat,Integ}$ denotes the update matrix of Integrator nodes in which off diagonal cells are set to -0.10 to implement lateral inhibition, and diagonal cells, representing the update rate of the competitive accumulator network, are set to 1. Finally, noise was added for each of the four variable Integrator nodes with $\sigma_{Integ} = 0.05$ multiplying a vector $\boldsymbol{N}(t)$ of four random values drawn from a standard-normal Gaussian distribution.

As stated before, the Integrator unit produces a response when a threshold is reached by one of the Integrator nodes. To model a speeded task constraint, we modified the classic competitive accumulator network[18] to implement a collapsing threshold, equivalent to a collapsing bound in the drift diffusion model, which has been shown to adequately model the dynamics of response threshold in speeded tasks[107]. The threshold θ_y therefore decreased exponentially from stimulus presentation to response deadline following this equation:

$$\theta_y(t) = 4 - \left(1 - e^{\left(-\frac{t}{0.35}\right)^2}\right)\frac{a}{2} \qquad 7$$

In which $\theta_y(t)$ denotes the threshold of the Integrator unit at time t, and a denotes the initial starting point of θ_y. In all simulations a was set to 4. Once one of the four Integrator nodes reached the threshold, we recorded the accuracy, depending on instruction, stimuli and the Integrator node which reach the threshold, and the time elapsed from stimuli onset, which provided reaction time for this response (see Figure 2e).

Medial Frontal Cortex unit

The MFC unit generates theta oscillations that 1) generate bursts that phase-reset the processing units, as in prior work[19,45,97], and 2) that additionally initiate a competition window in LFC nodes (see Figure 2a-b).

The MFC unit is composed of one single node in which the E-I pair generates theta oscillations, whose frequency depends on the coupling parameter between the E-I pair. The rate neuron of the MFC node follows a Bernoulli process (Be) with a probability defined by the activity of the node's E neuron:

$$MFC_x(t) = Be\left(\frac{1}{1 + \mathrm{e}^{-5(E_{MFC}(\mathrm{t}) - \theta_{burst})}}\right) \qquad 8$$

In which *Be* denotes the Bernoulli process, E_{MFC} denotes the activity of the MFC E neuron, and θ_{burst} (set to -1) denotes the offset of the relation between E_{MFC} and p (probability to trigger a burst). *Be*(*p*) is 1 with probability *p*, it will thus typically be 1 when $E_{MFC}(t)$ oscillation is near its peak. When $MFC_x = 1$, a fixed amplitude burst = 0.5 is emitted to the LFC unit. The purpose of this burst is to synchronize processing nodes selected by the LFC, by phase reset of their E neuron (see Processing units for the burst's effect, and Lateral Frontal Cortex unit for the selection of the processing nodes receiving the burst).

In addition to the burst-emitting function of the MFC proposed in earlier work[3,19], the MFC in the present model opens a competition window between rule nodes in the LFC at each cycle of its theta oscillations. At each cycle of theta oscillations in E_{MFC} activity, a competition window is opened in which LFC rules compete; this competition starts when $E_{MFC} > \theta_{comp}$, with $\theta_{comp} = 0.1$. The competition window lasts a fixed temporal interval across cycles defined by (as just defined) θ_{comp} and the crucial C_{MFC} parameter, which determines the theta frequency. To simulate different theta frequencies in the MFC, we varied the MFC coupling parameter (C_{MFC}) from 0.050 (for 4Hz theta), to 0.087 (for 7Hz theta), see equation (3) in the section Oscillatory nodes: a neuronal triplet.

Lateral Frontal Cortex unit

In order to implement biased competition in rule implementation, we extended previous models simulating task rules. We considered rule nodes as pointers to processing nodes constituting components of the rule (e.g. [41,108]). Such pointers permit to bias processing units according to task rules and to create bindings between task-relevant components (e.g. [109]). In recent computational accounts incorporating oscillations and synchrony, the Lateral Frontal Cortex (LFC) has been hypothesized to contain such pointers which route MFC bursts to processing nodes[3,19,45,97]. However, in these latter models no competition occurs between rule nodes. In the current model, LFC is composed of rule nodes, where each such node consisted of one rate code neuron only. Together, they form a competitive accumulator network[18], thereby implementing competition between rules. Each rule node receives a constant input throughout a trial from instruction nodes, which themselves are activated by the two instruction letters. Two instruction nodes represent the top letter of an instruction, and two other instruction nodes the bottom letter. This network of instruction nodes implements a congruency effect between instruction letters: top and bottom “Left” nodes were connected with a positive weight, thereby activating each other, and similarly for “Right” nodes (see instruction nodes in Figure 1b). Instructions are represented as a vector of binary values (zeros and ones) in which the first two indices represented a top L and R, respectively, and the two last indices represented the presence of a bottom L and R, respectively. For instance, the rule RL was represented as $\boldsymbol{instructions} = [0, 1, 1, 0]$. This was the input to the instruction nodes, which then projected to rule nodes through the following equation:

$$\boldsymbol{in}_{rule} = \boldsymbol{W}_{instruction}\,\boldsymbol{instructions} \quad (9)$$

In which in_{rule} denotes the input to rule nodes (i.e. from instruction nodes). Matrix $\boldsymbol{W}_{instruction}$ represents the connectivity between instruction nodes implementing the lateral excitation, i.e. instruction letter congruency effect. The diagonal of $\boldsymbol{W}_{instruction}$ was set to 1, and the cells representing the positive weight implementing the lateral excitation were set to 0.5.

The activity of rule nodes is updated through the following equation:

$$\boldsymbol{y}_{rule}(t+\Delta t) = \boldsymbol{y}_{rule}(t) + \Delta t(\boldsymbol{W}_{in}\boldsymbol{in}_{rule} + \boldsymbol{W}_{lat,rule}\boldsymbol{y}_{rule}(t)) + \sigma_{rule}\boldsymbol{N}(t) \qquad 10$$

In which $\boldsymbol{y}_{rule}(t)$ denotes the activity of all rule nodes at time t, $\boldsymbol{in}_{rule}$ denotes the input to rule nodes (i.e., instructions) and $\boldsymbol{W}_{in}$ denotes the weight matrix between instruction nodes and rule nodes in which weights between an instruction node of a particular letter and rules containing this letter was set at 0.5. For example, instruction nodes “top R” and “bottom L” projected to the rule node “RL” with weight 0.5 (see connectivity between instruction and rule nodes in Figure 1b). $\boldsymbol{W}_{lat,rule}$ denotes the update matrix of rule nodes in which off-diagonal cells are set to -0.1 to implement lateral inhibition; the diagonal cells, representing the update rate of the competitive accumulator network, are set at 0.13. Finally, noise was added for each of the four rule nodes with $\sigma_{rule} = 0.075$, multiplying a vector $\boldsymbol{N}(t)$ of four random values drawn from a standard-normal Gaussian distribution.

This architecture from instruction nodes to rule nodes allowed to manipulate task difficulty. For instance, the same-side rule LL, modelled as $\boldsymbol{instructions} = [1, 0, 1, 0]$, provided strong input to the LL rule node, and a small input to the LR and RL rule nodes as they each share the bottom and top letter, respectively, with the instruction LL. Thus, for $\boldsymbol{instructions} = [1, 0, 1, 0]$, $\boldsymbol{in}_{rule} = [0, 1.4, 0.7, 0.7]$, in which the $\boldsymbol{in}_{rule}$ indices represent, in this order, RR, LL, LR and RL. On the other hand, a different-side rule like RL, modeled as $\boldsymbol{instructions} = [0, 1, 1, 0]$, provided a relatively strong input to the RL rule node, and a small input to LL, RR and LR nodes. Thus, for $\boldsymbol{instructions} = [0, 1, 1, 0]$, $\boldsymbol{in}_{rule} = [0.7, 0.7, 0.4, 1]$, creating a stronger competition between the instructed rule (RL) and the other rules (RR, LL and LR), see Figure 2a.

Finally, the most activated rule node at each time t, amplified and routed the burst emitted at time t by the MFC ($MFC_x(t)$) to the processing nodes it points to:

$$\boldsymbol{B}(t) = \boldsymbol{LFC}_{pointers}\left[\boldsymbol{y}_{rule}(t) \circ \mathrm{J}\big(\boldsymbol{y}_{rule}(t) = \max\big(\boldsymbol{y}_{rule}(t)\big)\ \big)\right] MFC_x(t) \qquad 11$$

In which $\boldsymbol{B}(t)$ is a vector of burst values arriving at each processing node's E neuron (to reset its phase). $\boldsymbol{y}_{rule}(t)$ is the activity of rule nodes at time t and $\circ$ represents point-wise product. $\mathrm{J}(.)$ is an indicator function that returns an array of 0 and 1, with 1 only for the most activated rule node at time t. $\boldsymbol{LFC}_{pointers}$ is a matrix containing the processing nodes each rule node is pointing to. $MFC_x(t)$ is the activity of the MFC rate neuron at time *t*. This could be 0 or 0.5 (activity values were fixed), depending on whether the MFC is emitting a burst or not at that particular time point. Critically, equation (11) shows that only processing nodes corresponding to the most activated rule node received the burst, while all other processing nodes did not. For instance, if the instructed rule is RR and the most activated rule node at time t is RR, the Sensory module "Right grating" and the Action module "Right hand" received the burst, thereby synchronizing their gamma oscillations.

As a result of the congruency in instruction letters and BC between rule nodes, the instructed rule will win the competition more quickly for same-letter rules, i.e. easy rules, than for different-letter rules, i.e. difficult rules (Extended Data Figure 1a-b). Therefore, same-side rules will succeed to synchronize rule-relevant processing nodes more quickly. One consequence is that, for difficult rules, the model will achieve better performance at a slower theta oscillation frequency when competition lasts longer. In contrast, for easy rules, model performance increases with a slightly higher theta frequency. Hence, an optimal agent would shift theta frequency depending on task demands.

Simulations

We ran simulations of the model on the task depicted in Figure 1a. Instructions are shown for 200ms (two letters), then a variable ISD between 1,700 to 2,200ms, in 11 steps of 50ms, allows to prepare the instructed mapping, and subsequently two gratings are shown for 50ms. There were four possible instructions: RR, LL, LR and RL.

The presentation of each possible stimulus was modelled as constant input set to a value of 0.02 to the corresponding Sensory node. There were four possible stimulus configurations because each of the two gratings could be tilted either CW or CCW. For each combination of task parameters, we ran 100 repetitions, which amounts to: (11 ISD + 4 instructions + 4 stimuli configurations) * 100 = 17600 trials. We then grouped repetitions into 34 groups of ~500 trials each, each representing one participant.

Effect of amplitude on competition window

To verify that high and low theta frequencies are optimal for easy and difficult tasks, respectively, we independently varied MFC theta amplitude and frequency, and computed the competition window lengths for each combination (Extended Data Figure 1c). Higher theta amplitudes increased the competition window length but quickly reached a ceiling (around an amplitude of 3). Theta frequency on the other hand produced larger increases in competition window, indicating that effects of theta frequency on model performance cannot be explained by theta amplitude alone. Furthermore, we replicated our main simulation at different MFC theta amplitudes and obtained similar results (i.e. the difference in optimal frequency for easy and difficult rules, see Extended Data Figure 1d).

Stimulus-action mapping experiment (Dataset 1)

Participants

Thirty-nine human participants were recruited for this experiment (M ± STD = 23.7 ± 4.5 years old, range: 18-41 years old; 27 females). All participants had normal or corrected-to-normal vision and no history of neurological problems. All participants provided written informed consent and received monetary compensation for their participation. Five participants were excluded from the analysis: two completed less than 5 blocks, one had less than 200 trials after trial rejection based on eye-tracking data, one had poor overall behavioural performances (i.e. less than 50% overall accuracy), and one participant was left handed. The experiment was approved by the local ethics committee (Faculty of Psychology and Educational Sciences, Ghent University). Sample size was not computed a priori: we aimed for more than 30 participants. First, we recruited 35 participants to reach a total number of more than 30 participants after drop-out, considering a ~10% drop-out rate due to noise-corrupted data or other issues related to participants' task performance. The sample size after exclusions dropped at 30 participants, we thus tested 4 more participants, which were all included, bringing the sample size to 34 participants. Assuming a medium effect size and aiming for a power of 0.8 in a within-subject repeated measures ANOVA analysis, the study would require a sample of 32 participants. Data collection and analysis were not performed blind to the conditions of the experiments.

Apparatus and stimuli

Participants sat in a dimly lit room, 60 cm from a 24in LCD monitor (refresh rate: 60 Hz; resolution: 1280 × 1080 pixels). A chinrest was used to stabilize head position and distance from the screen. The experiment was implemented using Python 2.7 and the PsychoPy toolbox[110].

Experimental design

Participants were instructed to perform a 2-alternative forced choice (2-AFC) orientation discrimination task on two sinusoidal gratings presented simultaneously on each side of a central fixation cross, as depicted in Figure 1a. Each grating was randomly tilted either CW or CCW relative to the vertical axis. The stimuli were sinusoidal gratings windowed by a raised cosine (size: 5° of visual angle, 10% contrast, 3 cycles per degree, at 5° eccentricity, on a gray background). The tilt angle was calculated for each participant using a staircase procedure (see below) to avoid ceiling accuracy. Participants were instructed at the beginning of every trial to perform the 2-AFC task on the right or left grating, and respond using their right or left hand (index and middle finger respectively for CW and CCW tilt).

Instructions letters were presented for 200ms with a size of 0.75° of visual angle, and positioned above and below the central fixation cross (vertical eccentricity: 1° of visual angle). The letter above the fixation cross instructed which grating was the target, i.e. on which grating the discrimination should be performed, and the letter below the fixation cross instructed which hand to use to respond. After instructions a preparation interval followed to allow participants to process instructions and prepare the stimulus-action mapping to perform the task. We used a dense behavioural sampling paradigm with multiple, densely distributed, instruction-stimulus delays (ISD)[20]: the duration of the ISD, between instructions and stimuli, was randomly chosen on each trial from 11 possible durations going from 1,700 to 2,200ms in 11 steps of 50ms. The variation in ISD was introduced to measure oscillations in behavioural performance and test predictions of the model (see Figure 3c).

A trial time course consisted of a 1000ms baseline period, followed by instruction presentation for 200ms, then the ISD, and finally the stimuli presentation for 50ms. After stimuli onset, the fixation cross turned blue, indicating the beginning of the 700ms response window. If a correct response was given, the fixation cross turned green; if an incorrect response was given, the fixation cross turned red. If no response was given during the response window, a message indicated that the participant was too slow and the experiment was paused, prompting the participant to take a break if needed, and press “Space” to resume the experiment. Every trial that was missed, i.e. not responded to, was added to the trial queue, and presented again at the end of the block. Participants performed one training block to familiarize them with the experimental design, one staircase block to compute the participant’s grating tilt angle, and between 5 and 8 blocks of the task depending on the number of missed trials (i.e. participants who missed more response deadlines had longer blocks because trials were queued at the end of the block). The practice block consisted of 80 trials, the stimulus was shown for 100ms and the response window lasted 1000ms to make the practice task easier.

Following the practice block, participants completed a block implementing a staircase procedure on the tilts of the gratings. The staircase was done across all instructions and all ISDs to find a tilt level that would avoid ceiling performance and thus allow for variability across ISDs. We used a one-up two-down staircase procedure consisting of 80 trials. The event timings and stimulus properties were the same as in the main task. Only the tilt of the gratings varied throughout the trials. Initially, a wide tilt (7°) was set. The procedure started with a step size of 3°, which was divided by 2 every other reversal starting at the second reversal. The reversal corresponded to switches in participants’ response accuracy, i.e. from a sequence of correct responses to an incorrect response or the other way around. When a participant switched from a correct response to an incorrect response, the difficulty of the task decreased by increasing the tilt of the gratings. Conversely, when a participant responded correctly after a sequence of errors, the difficulty of the task increased, i.e. the tilt of the gratings decreased. The minimum tilt step size was set at 0.1°, the maximum final tilt of the gratings was 30° and the minimum was 0.5°. The final tilt was the average of the last 10 tilts.

After the staircase block, participants completed between 5 and 8 blocks of the main task depending on the number of trials missed, i.e. participants who missed the response deadline more often, had longer blocks (because of queued trials), and therefore completed less blocks. In total the experiment lasted ~3 hours from explanation of the task to removing the EEG cap.

Eye-tracking acquisition and processing

We recorded eye movements using a SMI eye-tracker with a sampling rate of 250Hz (RED250 mobile system; SensoMotoric Instruments, Teltow, Germany). The eye-tracker camera using infrared optics was attached to the bottom of the computer screen. We used the PyGaze Python toolbox[111] to control the eye-tracker through the experiment's script. Each block of the experiment started with a calibration procedure in which participants had to follow a moving red dot with their eyes to nine locations on a grey background, the success of which was validated before continuing. Gaze position was epoched from instructions onset to stimulus presentation. To epoch gaze position data and align them with EEG data, we aligned the trial onset (instructions presentation) using the trial onset trigger in eye-tracking data and the trial onset trigger in EEG data. We then calculated the distance from the fixation cross in degrees of visual angle at each time point in the epoch. Any trial in which the gaze was outside a 1.5° radius centered on the fixation cross at any moment in the ISD, was rejected in the behavioural and EEG data.

Behavioural data analysis

As described above, trials in which gaze position distance from the fixation cross exceeded 1.5° of visual angle were discarded. Trials were grouped by instruction and by ISD. Model simulations showed a theta-frequency – rule-difficulty interaction in accuracy but not in reaction times (Figure 3a and Extended Data Figure 2a). We therefore used accuracy as our dependent variable.

To compute spectra of behavioural accuracy oscillations across ISDs we first average-padded accuracy values (Supplementary Figure 2a). Average-padding was performed for each participant and for each instruction independently to increase frequency resolution to 1Hz[20]. To pad the data, values corresponding to average accuracy across ISDs (by instructions) were added on either side of the empirical data points. Specifically, the 11 time points, spanning 500ms, were padded to get a 1,000ms segment, thus adding 5 data points before the first data point and 5 after the last one.

Then we computed a fast Fourier transform (FFT) to obtain frequency spectra of each accuracy-by-ISD time course for each participant and each instruction. FFT allows to decompose the behavioural data from the time domain into frequency components to estimate an amplitude spectrum, i.e., the amplitude of oscillations at each frequency present in the original data. We then extracted peak theta frequency by selecting the frequency with the largest amplitude. Finally, we z-scored the peak frequency value across rules, separately for each participant, to discard any difference in offset or range of theta peak frequencies across participants. This procedure was carried out to specifically test the model prediction that theta peak frequency decreases with task difficulty, thus inter-individual differences in theta peak frequency for each instruction were not of interest in this specific analysis. The raw peak frequencies for behavioural oscillations are also available in Supplementary Figure 7a (left panel).

EEG acquisition and preprocessing

EEG was recorded using a Brain Products actiChamp system with 64 active scalp electrodes positioned according to the standard international 10–20 system at a sampling rate of 512 Hz. Four electrooculographic (EOG) channels were used to record eye-movements and blinks: two were placed on the outer canthi of the eyes, and two were placed above and below the right eye. All preprocessing steps were carried out with the Python MNE toolbox v.0.21[112]. Raw EEG data were downsampled offline to 200Hz, re-referenced to the average reference and low-pass filtered at 48Hz using a FIR filter with a Hamming window. The analysis of the pre-stimulus interval was performed on epochs from -1000ms to 0ms relative to stimulus onset, yielding epochs of 1000ms. A linear detrend was performed on each epoch individually. After trial rejection based on eye-tracking data (see Eye-tracking acquisition and processing) raw EEG and EOG time courses were visually inspected on a trial-by-trial basis to reject visible artifacts, eye movements or blinks. The average percentage of rejected trials across participants was 26% ± 14 (mean ± standard deviation).

EEG spectral analysis

To estimate peak frequency of theta oscillations we first computed power spectral density over the 1000ms window using Welch's method provided in the Scipy toolbox v.1.3.1[113]. The Welch power density estimation was performed using a Hann window and zero-padding to obtain 400 time points of data in order to smoothen the spectra to improve estimation of peak frequency in the following analysis step. We then used a recent method that allows to parametrize neural spectra by fitting the 1/f pattern in electrophysiological recordings spectra (also called the aperiodic component), and subsequently identifies spectral peaks by fitting Gaussians on the flattened spectrum (i.e. after removing the aperiodic component). This method thereby provides a sensitive identification and estimation of oscillatory processes in neural activity (FOOOF toolbox, version 1.0.0[16]).

Indeed, this method permits to de-confound several factors that can mask shifts in peak theta frequency in grand average spectra (Supplementary Figure 3a). First and foremost, interindividual differences in the 1/f structure (also called aperiodic component) of the spectrum can mask shifts of peak theta frequency across conditions. More specifically, the offset and slope (also called exponent) of the aperiodic component have been shown to vary across participants[16,114–116], see Supplementary Figure 3b. This variability can therefore affect the apparent peak frequency in the grand average spectrum. Second, interindividual variability in the height of theta band peaks makes it more difficult to compare the grand average (as can be seen in the grand average spectra in Supplementary Figure 3a). And third, relatively large peaks in the alpha band (which can be as much as 6 times larger in power than the theta frequency peaks in some participants) vary in peak frequency and width across participants (see Supplementary Figure 3b (middle panel), individual participants' spectra in Extended Data Figure 3 and Supplementary Figure 5-6). These large peaks in the alpha band can alter the shape of the grand average spectra and mask changes in peak theta frequency. Together these confounding factors require the estimation of the aperiodic component of the spectrum and the independent estimation of oscillatory peaks over the aperiodic component, as is performed in the FOOOF toolbox[16] (but see below for control analyses in which we show that our main results are visible in raw power spectra, and robust and statistically significant when estimating theta peak frequency based on the raw power spectra, i.e. without the FOOOF toolbox).

This algorithm yields several measures, including the peak frequency and amplitude of oscillations detected over the 1/f pattern in the spectra (i.e. by reporting the mean and height of the Gaussian fitted to each identified spectral peak in the flattened spectrum, see Supplementary Figure 2b). Using this algorithm, we computed separately for every participant, trial and electrode, whether a peak was detected in the theta frequency range (i.e. higher than 3Hz, and lower than 8Hz) and we saved the estimated peak (in Hertz) and the amplitude of the peak (in $\mu V^2/Hz$). Settings for the FOOOF algorithm were set as follows. To obtain peak frequency and amplitude in the theta frequency range, the power spectra were parameterized across the frequency range 2 to 20Hz. The peak width limits were set between 0.5 and 2, to find peaks that were frequency-specific. The maximum number of peaks was set at 4, under the assumption that in the 2-20Hz frequency range there could be four meaningful peaks, i.e. one in each band (delta, theta, alpha and beta). No minimum peak height was set, peak threshold was set at 2 (default), and aperiodic mode was fixed (default).

To test model predictions in theta peak frequency we separated trials according to the instruction and accuracy for each participant and each electrode. As a sanity check, replication of previous findings on theta amplitude, and as an independent electrode selection procedure, we investigated the scalp distribution of theta oscillation power for correct versus incorrect trials for Dataset 1 (FCz was selected based on previous findings[1] for Datasets 2 and 3 since there were not enough incorrect trials, see Results). In order to perform this analysis, we extracted the power of peaks found in the theta band using the FOOOF toolbox, for each participant, for each electrode, for each instruction, and for each trial separately. We then z-scored these values across electrodes. This allowed to highlight the specific theta power topography elicited by proactive cognitive control, i.e. preparing to implement an instructed stimulus-action mapping. We performed a cluster-based permutation test[117] with 10,000 permutations on scalp topographies to test whether a cluster of electrodes showed relatively higher theta power in correct versus incorrect trials (across all instructions). This analysis revealed a significant cluster of electrodes in fronto-central sites (permutation cluster test: $p < 0.001$, Figure 4c). We then computed the average peak theta frequency (in Hertz), extracted using the FOOOF toolbox, in the selected cluster of electrodes (Figure 4c). In Dataset 1, we z-scored the peak frequency value across rules, separately for each participant, to discard any difference in offset or range of the EEG theta peak frequencies across participants. In Dataset 2 and 3, we centered the peak frequency value across conditions, separately for each participant, for the same reasons and because there were only two conditions. This procedure was carried out to specifically test the model prediction that theta peak frequency decreases with task difficulty, thus inter-individual differences in theta peak frequency for each instruction were not of interest in this specific analysis. The raw peak frequencies for EEG oscillations in all three Datasets are also available in Supplementary Figure 7a-c.

Because of the challenging nature of characterizing power spectra (see for instance [118]), we also carried out additional control analyses directly on the raw power spectra to test whether our main result was observable without using the FOOOF toolbox (i.e. no aperiodic component estimation nor Gaussian fitting). First, we sought to better illustrate the shift in theta peak frequency that can be confounded by interindividual differences and other factors (see Supplementary Figure 3a). To do so, we re-plotted the grand average spectra (from Supplementary Figure 3a) after aligning each participant spectra to its own peak in the most difficult rule (i.e. RL) and scaling each grand average spectrum between 0 and 1. This analysis, anchored in the raw spectra (without using the FOOOF toolbox) showed that a clear shift towards higher frequencies was visible for easier rules, confirming that our results are robust and observable at the group level.

Second, we showed that our main finding that frontal peak theta frequency decreases with rule difficulty is also present (both substantially and statistically) when estimating theta peak frequency directly in the raw amplitude spectra as the theta-band frequency exhibiting the highest power (in $\mu V^2/Hz$, see Supplementary Figure 8). More specifically, for each participant, condition and electrode in the identified fronto-central cluster, we extracted the theta-band frequency with the highest power, then averaged these peak frequencies across electrodes, resulting in a theta peak frequency per participant per condition. Moreover, to evaluate the presence of our predicted effect, i.e. a decrease in peak theta frequency from same-side to different-side rules, we computed the proportion of participants exhibiting a positive difference in peak theta frequency between same-side and different-side rules. We carried out this analysis in both peak frequencies obtained using the FOOOF toolbox, and peak frequencies obtained directly from the raw spectra. This analysis revealed that a majority of participants exhibited the predicted effect (see Supplementary Figure 8 and discussion thereof), showing once again that our results are replicated without the FOOOF toolbox, thereby alleviating any concern about the challenges in the estimation of the aperiodic component performed by the FOOOF toolbox (see [118]). However, we still believe that condition- and participant-wise estimation of the aperiodic component of the spectra, and frequency and power of peaks (as performed by the FOOOF toolbox) is necessary to avoid confounding factors that could mask the effect or result in spurious differences in peak frequency or power.

Finally, for the control analyses on theta amplitude (Figure 6) and nearby frequency bands (Extended Data Figure 4), we followed the same procedure as for the main analyses on theta frequency band (i.e. using the FOOOF toolbox). For the alpha frequency band, we followed the same procedure as for the main results on the theta band but instead we considered peaks in the 8-12Hz range. For the delta frequency band, we used frequency limit parameters equal to [0, 20] Hz in the parametrization of the power spectra, and considered peaks in the 1-3Hz range. For both delta and alpha frequency bands, we then followed the same procedure as for the main results on the theta frequency band.

Statistical analyses

To compute the optimal theta frequency per rule difficulty (same-side (RR, LL) versus different-side (LR, RL) rules) in the model we calculated the MFC theta frequency yielding the highest accuracy for each group of simulations (see Simulations). We then compared the two samples of optimal theta frequencies per rule difficulty using a two-sided Wilcoxon signed-rank test (Figure 3b). For this, and all other Wilcoxon signed-rank tests, we computed non-parametric confidence intervals using bootstrapping of the difference in medians between conditions. The reported effect size for Wilcoxon signed-rank tests is the matched pairs rank-biserial correlation (r)[119].

Reaction times and DDM parameters estimated on model data (Extended Data Figure 2a) were analyzed using a 2-by-7 repeated measure ANOVA with factors rule difficulty (two levels: same-side and different-side) and theta frequency (seven levels: from 4 to 7Hz in steps of 0.5Hz), using the StatsModels v0.10.1 (https://www.statsmodels.org/v0.10.1/) and the Pingouin v0.5.0[120] (https://pingouin-stats.org/) Python packages. Data distribution was assumed to be normal but this was not formally tested.

Participants' behavioural and EEG data from the stimulus-action mapping experiment (Dataset 1) were entered into two-way repeated measure ANOVAs with factors target-location (two levels: Left, Right) and hand (two levels: Left, Right) using the StatsModels and Pingouin Python packages. For behavioural data it consisted of accuracies, reaction times, and DDM parameters per rule (Figure 4a; Extended Data Figure 2a), and peak theta frequency (i.e. of accuracy-by-ISD) per rule (Figure 4b). For EEG data it consisted of the average peak theta frequency from the selected electrode cluster (see Methods) of correct trials per rule (Figure 4d; circles); and the difference between average peak theta frequency of correct and incorrect trials.

For Datasets 2 and 3 we reported the statistical results from their behavioural data analyses. For the analysis of their EEG data we followed the same procedure as for Dataset 1 and, because only two difficulty levels were available in these Datasets, we performed a one-sided Wilcoxon signed-rank test to test the hypothesis that theta frequency decreased from an easy to a difficult condition. For all control analyses, i.e.

effect of task difficulty on peak theta amplitude (Figure 6), and on peak frequency and amplitude in the delta and alpha frequency bands (Extended Data Figure 4), we performed two-sided Wilcoxon signed-rank tests.

To investigate inter-individual differences in the sensitivity of EEG peak theta frequency to rule difficulty in Dataset 1, we performed a linear regression of each participant's raw EEG peak frequency (in Hertz) in correct trials ordered by each rule's overall accuracy across participants (i.e. rule was treated as a linear predictor: RR = 79.16%, LL = 76.70%, LR = 71.87%, RL = 71.44%). In a second step, individual-participant slopes were correlated with overall accuracy, collapsed across rules (Figure 4e). We used a robust Spearman correlation (i.e. skipped correlation[121]) implemented in the Pingouin Python package, which identifies outliers based on the minimum covariance determinant. The effect was also significant using a simple Spearman correlation. For illustration purposes we computed a linear regression, excluding the identified outlier, to plot it as a regression line in Figure 4e.

Data availability:

Raw behavioural, eye-tracking and EEG data can be found at this Open Science Framework repository:
https://osf.io/nwh87/?view_only=b11ee1f860804da582c816fe8acdecad

Code availability:

Code of the model, the behavioural experiment and analysis scripts to reproduce all results and figures from the study can be found on this Github repository:
https://github.com/mehdisenoussi/theta_shift_cog_control

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Author contribution

M.S., D.T. and T.V. designed the study. M.S., P.V. and T.V. developed the model. M.S. and E.D.L. collected the data. M.S. analyzed model simulations, behavioural and EEG data. M.S. and T.V. wrote the manuscript. All of the authors discussed the results and commented on the manuscript.

Competing financial interests

The authors declare no competing interests.

Figure legends

Figure 1. Task and model structure. a Stimulus-action mapping task. Each trial starts with a cue instructing the mapping to use. In this example the rule is “LR” instructing to report the left grating’s tilt with the right hand. b Model architecture. c Each node of MFC and processing (Sensory and Action) units is a neural triplet composed of one excitatory (E), one inhibitory (I), and one rate neuron (x). The E-I pair generates oscillations (whose frequency depends on their coupling parameter). MFC Bursts are sent to E neurons. Rate neurons receive input from, and send output to, other nodes’ rate neurons. The activity (output) of a rate neuron is modulated by its E neuron.

Figure 2. Model dynamics. a The top two panels represent rhythmic BC in rule nodes at instructions onset (from two different trials): 3 cycles at a fast MFC theta frequency (7Hz) to illustrate difference in dynamics between easy and difficult rules. Top left panel (Easy rule): the rule node corresponding to the instructed rule in this trial (green curve) rapidly wins the competition over other rule nodes (grey curves). Top right panel (Difficult rule): the rule node corresponding to the instructed rule in this trial (orange curve) struggles to win the competition and often loses to other rule nodes (grey curves). Yellow areas represent competition window opened by MFC theta oscillations. Dashed yellow line represent MFC E neuron activity (see panel b). Each dot above curves represent a time point at which the instructed rule’s node was winning the competition. The bottom panel represents the biasing signal sent to the processing nodes. This corresponds to the burst sent by MFC (bottom plot in panel b) multiplied by the most activated rule node’s activity (note that the MFC theta frequency was set at 5Hz for this panel). b Activity of the MFC neural triplet at a theta frequency of 5Hz. Top panel represents activity of the E-I pair. The phase of both neurons is reset at instructions onset. c-d Time course of neural triplet activity of the rule-relevant Sensory (c) and Action (d) nodes around stimuli presentation with a MFC theta frequency of 5Hz. The yellow curve representing MFC theta oscillations is for illustration only, its activity is scaled to fit within these plots. e Time course of the four integrator nodes, representing each of the four possible responses to the task, around stimuli presentation. The green line represents the correct response in the simulated trial.

Figure 3. Model simulations. a Model accuracy by rule difficulty across theta frequencies. Data are presented as mean values, error bars represent standard deviation computed over n = 34 simulations per frequency. Green curve represent easy (same-side) rules, orange curve represent difficult (different-side) rules. b Violin plots representing optimal theta frequency, i.e. yielding highest model accuracy, per rule difficulty. For difficult rules the model achieves optimal accuracy at a slow theta frequency, whereas for easy rules, a fast theta is optimal (n = 34 simulations per theta frequency, two-sided Wilcoxon signed-rank test: W = 105.5, p < 0.001, r = 0.64, 95% CI = (1.00, 2.00)). Data are presented as violin plots, left- and right-most bars represent extrema, middle bar represent the median. Distribution density is represented by violin plot width. c Measuring theta oscillations in behaviour through densely-distributed Instruction-Stimuli Delays (ISD). d Accuracy-by-ISD by rule difficulty (left), and estimated peak frequency (right). Data are presented as mean values, error bars represent standard deviation computed over n = 34 simulations.

Figure 4. Testing model predictions in behaviour and EEG. a Overall accuracy: There was a significant target-location – hand interaction in accuracy (RR and LL easier than LR and RL; two-way repeated measure ANOVA: $F(1, 33) = 27.82$, $p < 0.001$, $\eta^2 = 0.236$), and a main effect of hand ($F(1, 33) = 4.33$, $p = 0.045$, $\eta^2 = 0.012$). b Peak frequency of oscillations in accuracy-by-ISD: there was a significant target-location – hand interaction (two-way repeated measure ANOVA: $F(1, 33) = 6.51$, $p = 0.015$, $\eta^2 = 0.047$). c Frontal cluster of electrodes with increased theta amplitude: significantly higher theta amplitude in correct than incorrect trials (cluster test, $p < 0.001$). d Theta peak frequency by rule in frontal electrodes cluster. Peak theta frequency in correct trials significantly decreased from same-side to different-side rules (two-way repeated measure ANOVA: $F(1, 33) = 18.96$, $p < 0.001$, $\eta^2 = 0.107$). Comparing correct and incorrect trials, we found that higher theta frequency improved performance in same-side rules, whereas a lower theta frequency improved performances in different-side rules (two-way repeated measure ANOVA: $F(1, 33) = 4.62$, $p = 0.039$, $\eta^2 = 0.036$). e Correlation between theta peak slope across rule difficulty and overall accuracy: the degree to which theta frequency shifted from difficult to easy rules positively correlated with overall accuracy (robust Spearman correlation: $r(32) = 0.49$, $p = 0.004$, 95% CI: (0.17 0.71)). Data are presented as

mean values, error bars represent s.e.m. computed over n = 34 participants. Smaller gray dots (and small colored dots in panel d) represent individual participants' data.

Figure 5. Testing model predictions in other datasets. a Experimental protocol in Dataset 2. In this study participants performed a cued serial mental calculation task in which a cue indicated whether the following calculations will be easy, i.e. only +1 additions were used, or difficult, i.e. addition or subtraction of different numbers. b Theta peak frequency at FCz for easy and difficult cues. Circles represent correct trials, triangles represent incorrect trials. Peak theta frequency was lower in correct trials in the easy compared to difficult condition (one-sided Wilcoxon sign-rank test: $W = 86$, $p = 0.018$, r = 0.63, 95% CI = (0.01, 0.14)). c Experimental protocol in Dataset 3. In this study participants reacted to an action signal (Stimulus; white square, circle or triangle). Each shape was randomly assigned towards one action (Go, No-Go, Switch-Go); only the Go and No-Go actions were analysed because Switch-go data were unavailable. On half of the trials, a *certain-go* cue (e.g. brown cross) indicated that the Stimulus was going to be a Go shape with 100% certainty. On 50% of the trials a *maybe-go* cue (e.g. blue cross) indicated that the Stimulus had a 25% chance of being a No-Go shape. d Theta peak frequency at FCz for *certain-go* and *maybe-go* cues. Circles represent correct trials, triangles represent incorrect trials. Peak theta frequency was lower in correct trials following *certain-go* cues compared to *maybe-go* cues (one-sided Wilcoxon sign-rank test: $W = 358$, $p = 0.039$, r = 0.35, 95% CI = (-0.01, 0.08)). The yellow framing around the Cue and Instruction stages in a and c represent the time window from which we extracted peak theta frequency. Data are presented as mean values, error bars represent s.e.m. computed over n = 14 participants in Dataset 2, and n = 33 participants in Dataset 3. Smaller gray dots represent individual participants' data.

Figure 6. Peak theta amplitude per condition in each Dataset. a Peak theta amplitude by condition for correct trials in Dataset 1. There was no significant main effect or interaction (n = 34 participants, two-way repeated measure ANOVA: all $Fs(1, 33) < 2.21$, all $ps > 0.146$). b Peak theta amplitude by condition for correct trials in Dataset 2. There was no statistically significant difference between conditions (n = 14 participants, two-sided Wilcoxon sign-rank test: $W = 24$, $p = 0.079$, r = 0.54, 95% CI = (-0.01, 0.03)). c Peak theta amplitude by condition for correct trials in Dataset 3. There was no significant difference between

conditions (n = 33 participants, two-sided Wilcoxon sign-rank test: $W = 257$, $p = 0.896$, r = -0.02, 95% CI = (-0.02, 0.02)). Data are presented as mean values, error bars represent s.e.m. Smaller gray dots represent individual participants' data.

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