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The central thalamus tracks attentional fluctuations in humans

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Article

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Abstract

Moment-to-moment fluctuations in sustained attention impair goal-directed behaviour. Although distributed cortical networks support attentional control, the contribution of subcortical electrophysiology remains poorly understood. As a key regulator of arousal and consciousness, the central thalamus is ideally positioned to support sustained attention, but direct evidence in humans remains scarce. Here we leveraged rare intracranial recordings from the centromedian (CM) nucleus of the thalamus in children with epilepsy, a population predisposed to attention deficits. During an attentional set-shifting task, we identified a robust CM event-related potential (ERP) following trial onset, arising temporally between two canonical scalp ERPs (N1 and P2) measured concurrently. Across all task conditions, larger thalamic ERP amplitudes predicted faster trial-by-trial reaction times, whereas ERP amplitudes progressively declined with time-on-task, paralleling behavioural slowing. Together, these findings demonstrate that central thalamic responses predict moment-to-moment behavioural performance, providing direct human evidence that the central thalamus contributes to the neural processes underlying fluctuations in sustained attention.

Introduction

Sustained attention describes the capacity to consistently engage with a particular task over prolonged periods of time.[1] As attentional systems become challenged, due to time-on-task, distractors, or task difficulty, sustained attention becomes more likely to lapse.[2] Momentary lapses in sustained attention are universal human experiences that can result in adverse consequences, particularly in high-risk contexts such as driving, flying or surgery.[3,4] Such lapses are also more prevalent and consequential in individuals with neurodevelopmental or neurological disorders such as attention-deficit hyperactivity disorder and epilepsy.[5,6] The development of novel means to modulate attentional lapses are limited by an incomplete mechanistic understanding of the cortical-subcortical interactions that sustain attention.

Sustained attention is classically conceptualised as a top-down cortical process serving to filter competing information and focus resources, primarily involving prefrontal cholinergic inputs.[2,7] In rodent models, reduced cholinergic transmission in the prefrontal cortex leads to impaired sustained attention, and increased sensitivity to distractors.[8–11] Human studies across multiple modalities consistently show involvement of prefrontal, anterior cingulate and parietal regions in sustained attention and attention lapses.[12–15] However, converging evidence suggests that nuclei of the central thalamus, including the centromedian (CM) nucleus, may also play a critical role in mediating sustained attention.[16–18] The central thalamus contributes to arousal regulation through cholinergic inputs from the brainstem,[16,19] maintains dense structural connectivity with much of the frontal lobe,[16,20] and functionally tracks fluctuations in sustained attention.[21,22] Despite this, direct evidence relating the central thalamus to sustained attention in humans remains scarce, primarily due to the challenge of measuring thalamic activity non-invasively with sufficient spatial and temporal resolution.

Previous intracranial work in humans has shown promising relationships between the central thalamus and aspects of attention. In auditory oddball tasks, event-related potentials (ERPs) and beta-band activity in the CM nucleus increase following target tones.[23,24] Moreover, in a visual perception task, greater central thalamic ERPs were associated with stimuli that were consciously perceived.[25] These studies support a role for the central thalamus in selectively propagating task-relevant sensory information, suggesting that top-down influences may bias thalamic gating functions. However, it remains unclear whether the central thalamus is involved in lapses in sustained attention, indexed by trial-wise variation in behaviour. This information is critical to exploring the central thalamus as a potential target for closed-loop neuromodulation of attention.[12,18]

Here, we leverage rare intracranial recordings of the CM thalamus in children with epilepsy performing an attentional set-shifting task. We identify a distinct event-related potential (ERP) in the CM nucleus, and characterize its temporal dynamics relative to concurrently recorded cortical activity. By relating trial-wise variability in thalamic ERP amplitude to behavioural performance, we demonstrate a role for the CM nucleus in mediating sustained attention in humans.

Results

Intracranial recordings from the human CM thalamus

Six youth with drug-resistant focal epilepsy (13-17 years old) underwent stereoelectroencephalography (sEEG) for presurgical evaluation. Intracranial recordings were obtained from distributed cortical regions, while a single research electrode targeted the CM of the thalamus (Fig. 1a, IRB#1000080202). Post-implantation localization confirmed that the deepest contact was positioned within the CM in all participants, while adjacent contacts sampled neighbouring sensorimotor thalamic nuclei, including the ventrolateral (VL) and ventral posterolateral (VPL) nuclei (Fig. 1). Concurrent scalp electroencephalography (EEG) was also recorded in five participants using the international 10-20 system.

Behavioural fluctuations during an attentional set-shifting task

Participants performed an attentional set-shifting task designed to probe flexible reorientation of attention.[13,26] During each trial (Fig. 2a), stimuli were matched according to either colour or shape. Some trials contained unannounced changes in the relevant feature dimension, requiring participants to shift their attention. Shifts were classified as either implicit (within-dimension, colour-to-colour or shape-to-shape) or explicit (between-dimension, colour-to-shape or shape-to-colour). While behavioural and neural effects of implicit or explicit shifts are associated with attentional flexibility,[27] fluctuations *within* any particular task condition more closely reflect levels of sustained attention.[2,28]

Across prolonged recording sessions (approximately 20-30 minutes), the task elicited spontaneous trial-to-trial fluctuations in attention, quantified behaviourally using reaction time (Fig. 2b). Explicit – but not

implicit - attention shifts were associated with significantly prolonged reaction times ($p < 0.001$, linear mixed effects regression [LMER], Fig. 2c), consistent with increased cognitive demand when switching attention between different features. Matching shapes also elicited longer reaction times ($p < 0.001$, LMER, Fig. 2d), suggesting that colour may be a more salient feature compared to shape in this task. From early (< 100 trials) to middle (< 200 trials) phases of the task, reaction speeds increased ($p < 0.05$, LMER, Fig. 2e), suggesting an initial learning phase. From middle to late (> 200 trials) phases, there was a slowing of reaction speeds ($p < 0.001$, LMER, Fig. 2e), suggesting lapsing sustained attention due to time-on-task. Participants were trained before recording sessions and maintained high task accuracy (94 - 99 %).

Electrophysiological dynamics of the CM thalamus

Across the recording period, power spectral density (PSD) within the CM thalamus differed markedly from concurrently recorded cortical activity (Fig. 3a). Whereas cortical signals exhibited prominent oscillatory structure, particularly within the theta-alpha range (4 – 12 Hz), CM recordings were notably devoid of strong periodic activity. Log-scale PSD profiles additionally demonstrated distinct power-law scaling characteristics within the CM relative to cortex.[29]

Following trial onset, the CM exhibited a robust ERP characterized by an early component occurring approximately 160 ms after stimulus presentation (range:140-190 ms, Fig. 3b), followed by a broader late component between approximately 300 – 500 ms. In the frequency domain, this response was associated with increased low-frequency (2 – 7 Hz) power relative to pre-stimulus baseline activity (Fig. 3c). Concurrent scalp EEG recordings revealed widespread cortical ERPs following stimulus presentation (Fig. 3d), including an early (~110 – 130 ms) and later (~170 – 210 ms) component, each with maximal amplitude over occipital cortex (O2 electrode). Notably, the CM ERP emerged temporally between these early and late cortical ERP components (Fig. 3e).

CM thalamic activity tracks sustained attention

Trial-wise variability in CM thalamic activity tracked behavioural performance, with greater ERP amplitudes associated with faster reaction times ($p_{FDR} < 0.05$, LMER, Fig. 4a). Both the early (~ 160 ms) and later (300 – 500 ms) thalamic ERP components were enhanced during faster-response trials. Notably, these amplitude modulations occurred following stimulus onset but preceding typical behavioural responses, consistent with a relationship to attentional engagement rather than motor execution. Trial count also significantly reduced the early component of the thalamic ERP ($p_{FDR} < 0.05$, LMER, Fig. 4b), consistent with lapsing sustained attention due to time-on-task. Attention shifts (explicit shift compared to non-shift, Fig. 4c) and rule (shape compared to colour, Fig. 4d) also significantly influenced the thalamic ERP, whereby conditions associated with prolonged reaction times (explicit shifts, shape rule, Fig. 2) led to elongation of the later ERP component.

Discussion

The central thalamus is thought to mediate higher order functions such as sustained attention by gating information within subcortical and cortical circuits, yet direct evidence of this role in humans remains limited due to the difficulty in measuring deep brain activity with high temporal and spatial resolution. Here, we leveraged rare intracranial recordings of the human CM thalamus during an attentional set-shift task to directly examine its role in trial-by-trial behavioural fluctuations. We identified a distinct thalamic ERP that emerged temporally between early and late cortical ERP components and whose amplitude decreased with lapses in behaviour and time-on-task. Together, these findings support a role for the human CM thalamus in mediating sustained attention.

Our findings complement prior studies of central thalamic electrophysiology. In primates performing a simple visuomotor reaction time task, firing rate was greater in trials that were correctly responded to, which may also reflect fluctuation in sustained attention.[22] In humans performing an auditory oddball task, while reaction times were not studied, subjects who were instructed to count the number of deviant tones exhibited greater amplitude responses in the CM, reflecting states of greater attentional engagement.[23] Similarly, humans performing a visual perception task exhibited greater amplitude central thalamic ERPs following stimuli that were consciously perceived, which may also reflect states of greater sustained attention.[25] Our study provides direct insight into central thalamic modulation of trial-by-trial behaviour, occurring irrespective of task condition, thus relating more closely to internally-driven fluctuations in sustained attention.

The ERP in the CM thalamus was characterized by an initial peak at 160 ms after stimulus presentation, temporally intermediate to two canonical scalp ERP components occurring at approximately 110 ms and 200 ms, commonly referred to as the N1 and P2, respectively. [30–34] The N1 is generally associated with early sensory processing and feature discrimination, whereas the P2 has been linked to higher order attentional and executive processes, including attentional allocation and inhibition control, depending on task demands.[30–34] The temporal relationship between the CM thalamus ERP and these cortical components suggests that central thalamic activity may participate in coordinating information flow between early sensory processing and later-stage attentional control networks. Amplitude of the CM ERP may reflect the level of gain within this process, with greater amplitude ERPs supporting states of greater sustained attention, serving to selectively amplify relevant information.

In addition to the task-related dynamics, we identified marked differences in the intrinsic spectral organization of the CM thalamus, relative to cortex. Whereas cortical activity exhibited prominent rhythmic (oscillatory) structure, CM recordings were mostly devoid of strong periodic activity and demonstrated distinct power-law scaling characteristics. These findings suggest that electrophysiological dynamics within the central thalamus may differ fundamentally from those typically observed in cortical networks. Importantly, the relative absence of sustained oscillatory structure has implications for how CM signals are analysed and interpreted. In particular, connectivity approaches that rely on stable phase estimation may be less reliable when applied to non-periodic thalamic signals. More broadly, our findings highlight the need for frameworks specifically tailored to the unique dynamical

properties of human thalamic activity, which remain comparatively understudied relative to cortical electrophysiology.

The primary limitation of our study is the small sample size, reflecting the inherent difficulty of obtaining direct intracranial recordings from deep thalamic nuclei in humans. Nevertheless, the observed relationships between central thalamic activity and behavioural fluctuations were highly consistent across participants, with all six individuals demonstrating stronger thalamic ERP responses during faster-response trials. The robustness of the thalamic response and relationship to trial-wise behaviour places the CM as a potential target for closed-loop neuromodulation strategies,[12] which could serve to prevent or recover lapsing attention. Future studies incorporating larger cohorts, additional thalamic nuclei and diverse cognitive paradigms will be important for determining the generalizability of these findings and further defining the role of the human thalamus in mediating sustained attention.

Methods

Data Acquisition

Stereoelectroencephalography (sEEG) recordings were taken using AdTech electrodes at 2048 Hz. Concurrent scalp electroencephalography (EEG) was recorded in five out of six of the participants, using the standard 10-20 approach. During recording, both sEEG and EEG was referenced to a contact located in white matter.

Participants performed an attentional set-shifting task which has been used by several previous studies.[13,26,35,36] During each trial, participants were presented with a target symbol at the bottom of the screen, and two symbols above, each characterised by their colour and shape (e.g., yellow triangle). The participant was instructed to identify which of the two top symbols matched the target symbol in a single dimension, i.e., via either its colour or shape. Participants responded with a button box, using either the left or right button depending on which of the top symbols matched the target, using whichever finger was comfortable. Trials ended once the subject responded, or after 4 s had elapsed. The interstimulus interval was jittered between 800ms and 1200ms.

Behavioural Analysis

Using button-press trigger timings, the reaction time and accuracy (correct, incorrect) was calculated for each trial. Incorrect trials were excluded from all further analyses. We then used a linear mixed effects regression (LMER) to assess the effect of attention shifts (non-shift, implicit shift, explicit shift), rule (colour, shape), and trial count (early, middle, late) on reaction time, accounting for a random intercept per subject. Post-hoc pairwise comparisons were conducted using linear contrasts of fixed effects estimated from the LMER.

Data Preprocessing

Contacts within the centromedian (CM) nucleus of the thalamus were confirmed using Lead-DBS version 3.2. In brief, postoperative CTs were coregistered to preoperative 3D T1 MRIs using FSL FLIRT, then non-linearly normalized to Montreal Neurological Institute (MNI) space using FSL FNIRT.[37,38] After brain-shift correction, the CM electrodes were localised manually.[39] Lead-Group was used for 3D group visualization of CM electrodes using Probabilistic Thalamus Atlas.[40,41]

All signal processing was performed using MNE-python.[42] Both sEEG and EEG data were bandpass filtered between 1 and 45 Hz using a zero-phase finite impulse response filter. Each sEEG contact was re-referenced to the adjacent channel in the same lead. Bad scalp EEG channels were identified by visual inspection, and a grand average reference was calculated using the remaining channels and applied. To normalise signal amplitudes across subjects, a z-score was applied to both sEEG and EEG.

Power spectral density

To compare spectral composition of the CM thalamus to the cortex, power spectral density was calculated over the entire recording, using Welch's method with a 2 s window and 1 s overlap. For each participant, the "cortical" contact was the most superficial sEEG contact on the same lead as the CM contact, that was still within brain matter (including the adjacent reference). Across all subjects, the cortical contact fell within opercular or motor/pre-motor regions.

Event-related analysis

To assess ERPs in both the CM thalamus and scalp, data were taken around trial onsets, with epochs spanning -0.5 to 1.5 s, using a baseline between -0.5 and 0 s. Epochs with any signal exceeding a z-score of 10 were rejected. ERPs were found by averaging signal over all trials, while statistics were performed on single-trial data. The sign of thalamic data was corrected in some subjects to ensure consistent ERP polarity across subjects, as bipolar references in sEEG can cause sign flipping.

To assess time-frequency content, longer epochs spanning -1 to 2 s were taken to enable later clipping of epochs to remove ringing. A family of Morlet wavelets between 2 and 40 Hz were convolved with the data to assess spectral power dynamics. A percentage change was calculated from a pre-stimulus baseline spanning -0.5 to -0.1 s, and the resulting time-frequency responses were cropped between -0.5 and 1.5 s to remove ringing effects.

To perform trial-wise statistics on ERPs, we used LMERs at each timepoint. Trials with incorrect responses were omitted from these analyses, as participants were trained on the task and maintained high accuracy (94 – 99%). Each LMER tested fixed effects of attention shifts (explicit vs non-shift), matching rule (colour vs shape), reaction time (continuous) and trial count (continuous) on signal amplitude, with a random intercept per subject. Multiple comparisons across timepoints were accounted for by controlling the false discovery rate (FDR) at 5%. Timecourses contrasting each fixed effect were visualised separately. For visualising the effect of reaction time, the fastest and slowest third of trials

were taken. Similarly, for visualising the effect of trial count, the earliest and latest third of trials were taken.

Declarations

Declaration of Interests

The authors declare no competing interests.

Author Contributions

S.C.C – conceptualization, formal analysis, manuscript preparation; K.M. – conceptualization, manuscript editing; N.M.W – data collection, manuscript editing; S.W. – data collection; S.J. – formal analysis; manuscript editing; N.R. – manuscript editing; V.L. – manuscript editing; M.J.T. – conceptualization; G.M.I. – funding acquisition, supervision, conceptualization, manuscript preparation.

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Data Availability

Data will be shared subject to a formal agreement and any necessary institutional approvals, ensuring compliance with data use policies and confidentiality requirements.

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Figures

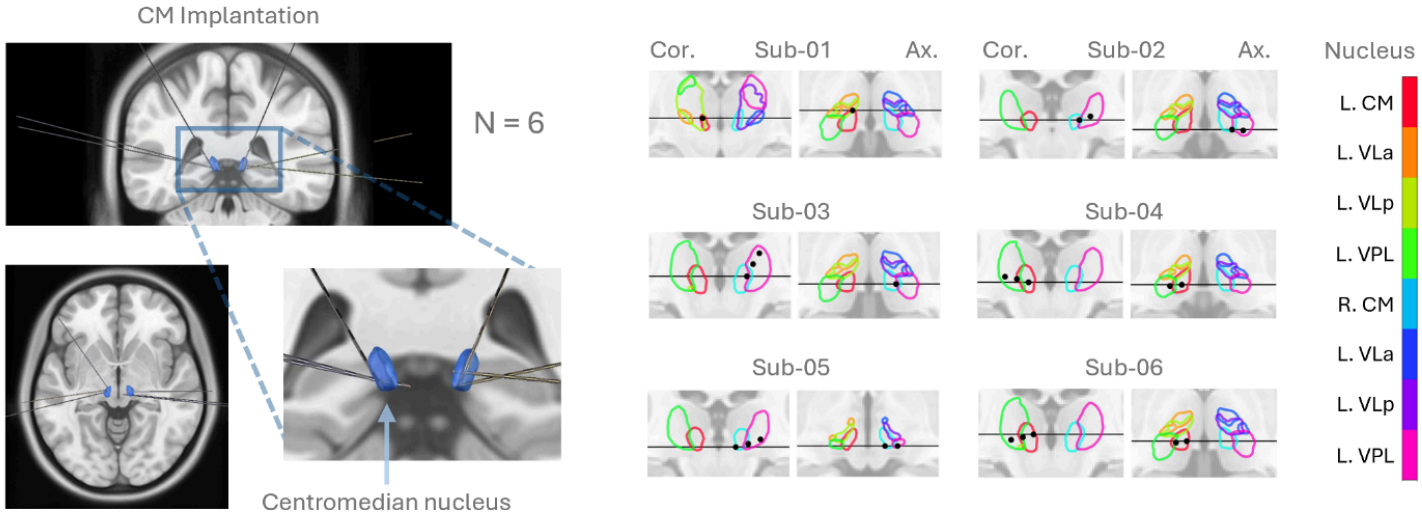


Figure 1

Thalamic implantation: In each participant, a single electrode was advanced into the CM nucleus of the thalamus. In all six participants, the deepest intracranial contact was located in the CM nucleus, while the next 1 – 2 contacts fell within sensorimotor domains of the thalamus, including the ventrolateral (VL – both anterior and posterior) nuclei and the ventral posterolateral (VPL) nucleus.

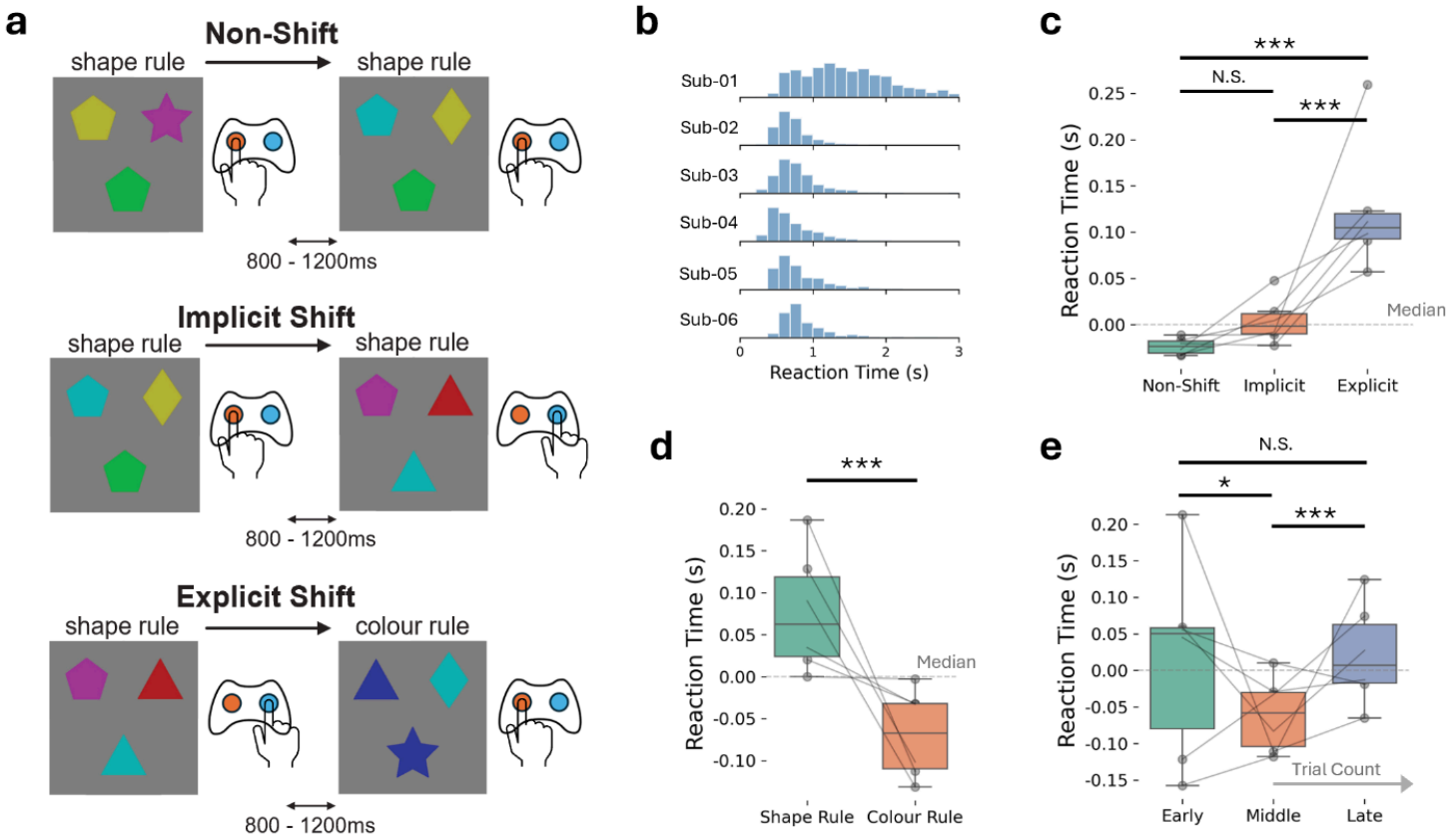


Figure 2

Attentional set-shifting task: a) A schematic of the attentional set-shifting task. Participants had to match the lower stimulus with either the left or right upper stimuli, based on either the colour or shape of the item. On set-shift trials, the rule would change from the previous trial. Shifts could either be implicit (within-dimension, e.g., yellow to green) or explicit (between-dimensions, e.g., yellow to triangle). **b**) The distribution of reaction times for each participant, used as a trial-by-trial measure of attentional engagement. **c**) Boxplots of reaction times separated by the degree of attention shift, relative to the median reaction time per participant. There was a significant slowing of reaction times due to explicit- but not implicit- attention shifts ($p < 0.001$, LMER) compared to non-shift trials. **d**) Boxplots of reaction times separated by the feature matching rule (colour or shape), relative to the median reaction time per participant. The shape matching rule elicited significantly longer reaction times ($p < 0.001$, LMER) compared to colour. **e**) Boxplots of reaction times separated by trial count – early (<100), middle (<200) and late (>200). There was a significant increase in reaction speed ($p < 0.05$, LMER) between early and middle phases, and a significant slowing ($p < 0.001$, LMER) from middle to late phases.

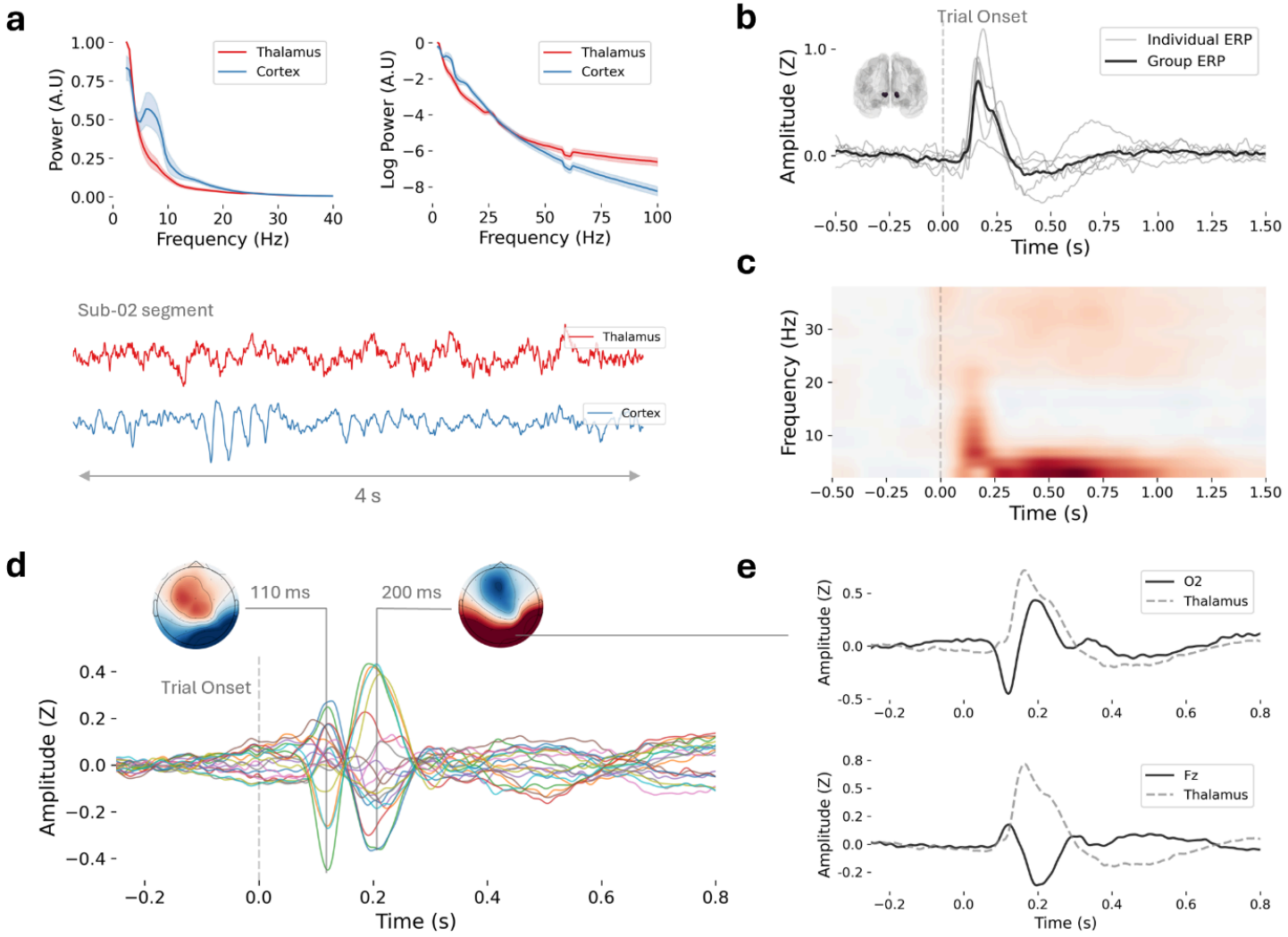


Figure 3

Thalamic task response: a) Over the entire recording, spectral content in the CM thalamus showed marked differences compared to superficial cortical contacts in the same sEEG lead, with the CM exhibiting very little periodic activity, and different power-law scaling. **b**) Following trial onset, the CM exhibited an ERP with an initial peak at approximately 160 ms (ranging 140 – 190 ms). **c**) In frequency space, the CM exhibited an increase in low (2 – 7 Hz) power compared to a pre-stimulus baseline (red = increase from baseline, blue = decrease from baseline). **d**) Concurrent scalp EEG recordings showed two distinct ERP peaks, the first at approximately 120 ms (ranging 110 – 130 ms) and the second at approximately 200 ms (ranging 170 – 210 ms) with peak amplitude over occipital regions (O2 electrode). **e**) The initial peak of the thalamic ERP occurred in between the two consecutive scalp ERPs.

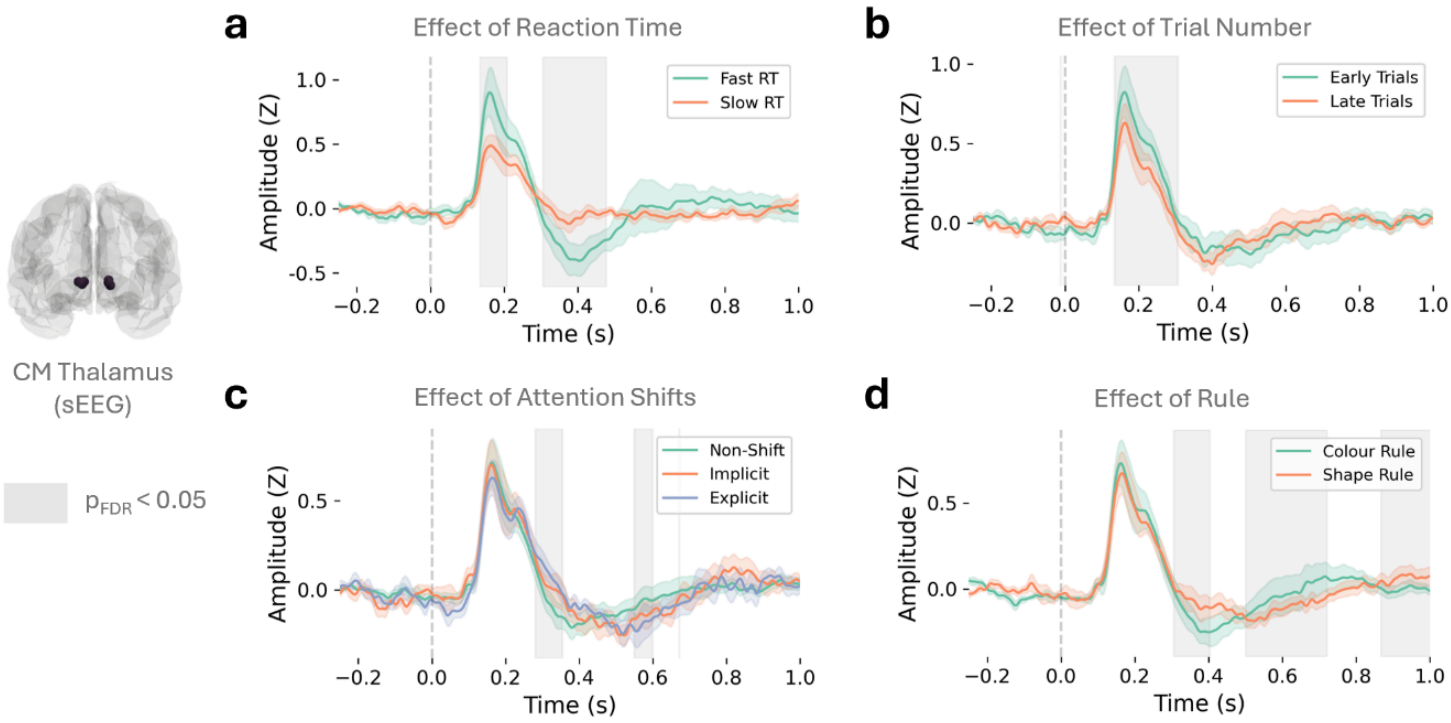


Figure 4

Thalamic activity and behaviour: LMERs were used to test the trial-wise fixed effects of reaction time (continuous), trial number (continuous), attention shifts (non-shift, implicit, explicit) and matching rule (colour, shape) on the CM thalamus ERP at each timepoint. **a**) There was a significant reduction in amplitude of the thalamic ERP with slower reaction times ($p_{FDR} < 0.05$, LMER), during both early (150 – 200 ms) and later (300 – 500 ms) phases. **b**) There was a significant reduction in the early phase of the thalamic ERP with trial count ($p_{FDR} < 0.05$, LMER). **c**) There was a significant effect of explicit attention-shifts on the thalamic ERP compared to non-shift trials ($p_{FDR} < 0.05$, LMER), but this appears to be elongation of later ERP components rather than amplitude differences. **d**) There was a significant effect of matching rule on the thalamic ERP ($p_{FDR} < 0.05$, LMER), which appears to be elongation of the later ERP component when matching based on shape.