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Unconscious learning of automatic inhibition is reflected in frontal theta and sensorimotor oscillations

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Abstract

The cognitive control of action is thought to be mediated by conscious effort as reflected by changes in frontal theta activity. We measured frontal theta during a response inhibition task in 16 healthy adults who implicitly learned repeated patterns of go/switch cues, resulting in unaware differences in cognitive demand for different cues. Learning was reflected by reduced reaction times (RT) to probable compared to unexpected switch cues. In the rare absence of behavioural (RT) differences, concurrent measures of pupil diameter revealed changes in effort with stimulus probability, while effort was accompanied by parametric increases in theta. Additionally, theta predicted pre-response sensorimotor gamma, suggesting interactions between frontal and sensorimotor cortex during cognitive control. These results provide further evidence for a functional role of theta in cognitive effort during response preparation, inhibition and execution, even in the absence of conscious awareness.

Keywords: implicit learning; motor learning; cognitive load; automaticity; pupillometry; MEG; theta; gamma

Introduction

Human behaviour is argued to be to be under both cognitive and automatic control, as articulated in dual-process theories (Evans and Stanovich 2013). Within this framework, cognitive processes have been defined as mental acts of which we are conscious, that we intend, that require effort, and that can be controlled (Logan and Cowan 1984). In contrast, automatic processes are rapid and autonomous, and are thought to yield default responses unless intervened on by cognitive processes. Both processes occur during inhibitory control, often employed in experiments using rapid response tasks that produce automatic responding requiring occasional intervention by cognitive processes, such as in Go/No-Go or Go/Switch tasks. In this case, Go trials quickly become automatic, whereas No-Go or Switch responses require infrequent, intermittent inhibition of the prepotent Go response in favour of the alternate (No-Go or Switch). These cognitive processes are often associated with activity in the frontal cortex, however neural mechanisms underlying these processes and especially how automatic processes may be interrupted by cognitive processes, remain unknown.

Although frontal theta (4-8Hz) is often associated with inhibitory control and has furthermore been hypothesized to be a mechanism for control (Cavanagh and Frank 2014), it is not yet clear whether theta plays a functional role in this process or is alternatively a generic alarm signaling only the need for control (ibid.). For the purposes of the current literature review, only theta oscillations and not event-related potentials will be considered as it has been demonstrated that most of the mid-frontal signal that is relevant for cognitive control is contained within ongoing theta oscillations, and not the evoked signal (Cohen and Donner 2013).

Frontal theta oscillations have been associated with a variety of different control tasks, including working memory (Jensen and Tesche 2002), as well as response preparation and post-error activity (Womelsdorf, Johnston et al. 2010). Theta is also related to behavioural outcomes, suggesting there is a relation between the motor cortex and the timing as well as amplitude of frontal theta (Cheyne, Ferrari et al. 2012). The relative ubiquity and sensitivity of frontal theta during cognitive processing suggests it has a functional and not epiphenomenal role in cognitive control.

In order to test whether frontal theta is involved in cognitive control (as per dual-process theories), and not merely signaling the need for control (as per Cavanagh and Frank 2014), two claims must be established. First, theta must be sensitive to variations in cognitive processing. Second, in order to have a functional role, theta activity must have an impact on behaviour. A logical route of action would be via the sensorimotor cortex. Importantly, there is as of yet no direct evidence to support the second claim of a relationship between frontal theta and the sensorimotor cortex.

Thus, the objective of the current study is to determine whether frontal theta has a functional role in cognitive control by testing the two claims described above. That is, *if* frontal theta is sensitive to cognitive processing load in a behavioural

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control task, *and* frontal theta is related to activity within the sensorimotor cortex, then it is likely to have a functional role in behavioural control, and not merely an alarm signaling the need for control. We hypothesize that theta amplitude would be sensitive to variations in cognitive load as determined by task-evoked pupillary response (TEPR, Beatty, 1982), and that it would correlate with pre-response high gamma (60-90 Hz) amplitude within the sensorimotor cortex. In order to establish variations in processing load in a behavioural control task, we used an implicit stimulus pattern learning Go/Switch task (Isabella, Urbain et al. 2019) paired with pupillometry which is an independent measure of cognitive effort (that is, the amount of effort one exerts to process a given load). Sixteen healthy adults performed this task during simultaneous pupillometric and magnetoencephalographic recordings in order to measure oscillatory neural activity from the frontal and sensorimotor cortices.

Methods

Subjects

Sixteen healthy right-handed adults (8 females, range 22-31 years) participated in this experiment. All subjects were recruited from the Toronto area and provided informed consent using protocols approved by Hospital for Sick Children Research Ethics Board. Subjects were compensated 60 CAD for their participation.

Go/Switch Task

The Go/Switch task employed in this study was similar to that by Isabella et al. (2019). All subjects were presented with a rapid stream of digits from "1" to "4", where each target had an equal 25% probability of occurrence. Each stimulus was displayed for a fixed duration of 0.4s, followed by a stimulus mask ("#") that was displayed for an additional 2s until the presentation of the next digit, for a total inter-trial interval of 2.4s. All stimuli and the mask were isoluminant. The subjects were informed that they were performing a go-switch task, for which the default movement to stimuli 1, 2, or 4 was a button press with the right index finger, with instructions to switch response hands to the left index finger when presented with the target "3" stimulus.

Subjects performed this task over 244 trials across each of 6 blocks. Each block began with 4 trials containing stimuli (digits 1-4) chosen at random. Subjects were uninformed that the remaining 240 stimuli were presented in 30 repeats of an 8-trial probabilistic sequence (3-1-4-3-2-4-1-2), known to induce pattern learning (Isabella, Urbain et al. 2019). Stimuli for 90% of trials followed the sequence order (Pattern), whereas for the remaining 10% of trials, the stimulus for the individual trial within the 8-trial sequence did not follow the sequence order (Deviant).

In order to assess whether the presence of the sequence of stimuli was explicitly learned, following the experiment, subjects were asked for general feedback on the task, and to write out a sample stream of stimuli from the experiment.

Recordings

Neuromagnetic activity was recorded using a whole head 151-channel CTF MEG system in a magnetically shielded room. T1-weighted structural MR images were obtained from each. Subjects sat upright in an adjustable chair and responses were collected using a nonmagnetic fiber optic response pad. Stimuli were presented using Presentation Software via a LCD projector on a back-projection screen.

Real-time TEPR was measured using an EyeLink 1000 system, recording at 600 Hz and synchronized with the neuromagnetic activity. Pupil diameter was measured in arbitrary units.

Analysis

i. Behavioural Analysis

Response Types Response types were defined as follows:

- Pattern Go (PGo): correct Go response (right index) to the Go stimulus (the digits 1, 2, or 4) matching the pattern.
- Pattern Switch (PSw): correct switch response (left index) to the Switch stimulus (the digit 3) matching the pattern.
- Deviant Go (DGo): correct go response (right index) to a Go stimulus (digit 1, 2, or 4) deviating from the repeated pattern, i.e. a Go stimulus where an expected "3" stimulus would have occurred.
- Deviant Switch (DSw): correct switch response (left index) to improbable switch "3" stimulus, deviating from the repeated sequence, i.e. where the expected Pattern stimulus would have required a Go response.

Importantly, all trial types as defined were preceded by a Go response. All trials following a "3" stimulus were not included in the analysis, as subjects quickly learned that the Switch stimulus "3" never occurred twice in succession and therefore could explicitly predict that a Go trial would follow a Switch trial. Therefore, every trial included in the analysis was preceded by a Go trial.

Reaction Times (RT) were measured as the difference in time between stimulus onset and the button press within 1.5s of each trial. Efficiency is defined as accuracy / reaction time and reveals the overall speed-accuracy strategy utilized by each subject across trial types.

ii. Pupil Diameter

Continuously recorded pupil diameter data was segmented into epochs and time-locked to stimulus onset. Eyeblinks were linearly interpolated using a custom Matlab script. Data was low pass filtered at 10Hz, and z-transformed within-participant to minimize inter-subject variability (Smallwood, Brown et al. 2011).

Pre-stimulus pupil diameter was measured as the mean z-scored pupil diameter for the 0.4s preceding stimulus onset, which was then subtracted from the entire trial. TEPR was measured as the mean z-scored pupil diameter for 2s following stimulus onset (until the subsequent pre-stimulus time period).

iii. MEG Analysis

MEG analysis proceeded in a similar manner to previously published studies (i.e. Isabella, Ferrari et al. 2015). Briefly, continuously-recorded MEG data were segmented into epochs centered upon the button response (response-locked) for each of the four response types described above. Localization of brain activity was carried out using frequency-based beamformer algorithms implemented in the BrainWave Matlab toolbox (Jobst, Ferrari et al. 2018).

In order to account for different trial numbers in each response type, PGo was used as a covariance dataset to calculate the beamformer weights, creating common weights for all trial types. Mean power was then calculated for each subject over the time window of interest, for each trial type and time-frequency representation (TFR).

iv. Statistical Analyses

RT was log-transformed to normalize its distribution. To examine differences between trial types across performance measures, TEPR, and mean oscillatory power, 2-by-2 within-subject repeated measures ANOVAs were conducted (factors: Switch and pattern), and partial eta squared (η_p^2) was used to calculate effect sizes. Given that there were 2 levels per factor, sphericity was not violated. Post-hoc comparisons were conducted using t-tests with Bonferroni corrections.

In order to investigate relationships between frontal theta and the other outcome measures of interest (TEPR, gamma), a multiple regression approach was used in order to control for possible interactions of task variables (Switch and pattern). Relationships between measures were determined using the sum of squares from a repeated measures ANOVA between variables according to $r = \sqrt{(SSpvs/(SSpvs + SSr))}$ where SS*pvs* is the sum of squares for the predictor variables (as determined by the multiple regression), SS*r* is the sum of squares for the residual, and *r* is the correlation coefficient (Bland and Altman 1995). All statistical tests were performed using R (Team 2017).

In order to test the implications of these correlations, we sought to determine whether a relationship between frontal theta and behaviour was mediated by sensorimotor gamma activity. This was tested using causal mediation analysis (Tingley, Yamamoto et al., 2014), and significance was tested using bootstrapping procedures.

Results

i. Behavioural Results

All 16 subjects complied with task instructions, completed a minimum of 6 blocks and provided feedback on the task. None of the subjects were able to replicate the stimulus sequence at the end of the experiment and failed to provide any evidence of explicit knowledge of the stimulus sequences. Error trials were not analyzed for this study. Mean number of trials (within subject) included in the analysis were (mean ± standard error): PGo = 666.7 ± 3.1, DGo = 35.4 ± 0.3, PSw = 280.8 ± 3.1, DSw = 30.6 ± 1.2.

Reaction Times To determine the effects of task (switch = Go/Sw and pattern = Pattern/Deviant) on responses, reaction times were measured as the duration between stimulus onset and the button press response for the four trial types of interest, in order of decreasing probability: PGo, DGo, PSw, and DSw. Mean RT was greater for Sw responses over Go, and greater for Deviant over Pattern trials (mean PGo = 0.347s, DGo = 0.349s, PSw = 0.370s, DSw = 0.380s, **Figure 1A**). To determine the effects of task parameters on reaction times, an ANOVA was conducted on log-transformed averaged reaction times, revealing a main effect of Switch ($F(1,15) = 16.85$, $p < 0.001$, $\eta_p^2 = 0.53$) and of pattern ($F(1,15) = 8.64$, $p = 0.01$, $\eta_p^2 = 0.37$). Post-hoc comparisons revealed significant differences between PGo and PSw, as well as PSw and DSw (all $p < 0.003$), but not PGo and DGo ($p = 0.30$). Switch responses of all types were delayed, but Deviant trials were delayed only for Sw trials and not Go trials (i.e. DGo). These results demonstrate an inverse relationship between response duration and variations in stimulus probability for all trial types except for DGo. The overall pattern of results replicates previous findings (Isabella, Urbain et al. 2019), with differences between Pattern and Deviant trials that were evident from the first block, demonstrating rapid learning of the stimulus pattern.

Efficiency Mean efficiency was greatest for PGo and DGo trials, while it decreased for PSw and DSw trials (mean PGo = 2.83 correct/s, DGo = 2.85 correct/s, PSw = 2.31 correct/s, DSw = 2.15 correct/s; **Figure 1B**). To determine the effects of task parameters on efficiency, a 2-way ANOVA was conducted on averaged efficiency rates, revealing a statistical main effect of Switch ($F(1,15) = 23.35$, $p = 0.0002$, $\eta_p^2 = 0.61$) but not of pattern ($F(1,15) = 1.98$, $p = 0.18$). Post-hoc comparisons revealed significant differences between PGo and PSw ($p < 0.001$), as well as PSw and DSw ($p < 0.05$), but not PGo and DGo ($p = 0.30$). Effects of task parameters on efficiency rates were similar to effects on RT, demonstrating that subjects did not change their speed-accuracy strategies across trial types. Subjects maintained consistent performance across P and DGo trials, with longer RT and efficiency for PSw and DSw, respectively.

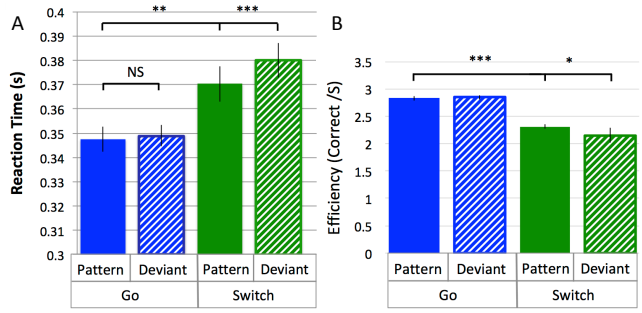

Figure 1: Mean RTs (A) and mean efficiency (B) with standard errors for response types Pattern and Deviant Go, Pattern and Deviant Switch.

ii. Pupil Responses

Pupil dilation is a well-established covert measure of quantifying cognitive control (Kahneman and Beatty 1966). In the current study, TEPR followed a typical time course, beginning at a minimum prior to stimulus onset, and dilating to a maximum diameter within 0.5 to 1.5 seconds (**Figure 2**). Diameters generally returned to approximately pre-stimulus levels following PGo trials ahead of the next trial at 2.4s. Mean TEPR was calculated as the mean baselined z-scored pupil diameter for 2s following stimulus onset, and was smallest for PGo trials, and increased for each of DGo, PSw and DSw trials (mean PGo = 0.25 ± 0.03z, DGo = 0.43 ± 0.03z, PSw = 0.46 ± 0.03z, DSw = 0.57 ± 0.03z). In order to determine the effects of the task parameters on TEPR, a 2-way ANOVA was conducted, revealing a main effect of Switch ($F(1,15) = 186.9$, $p<0.001$, $\eta_p^2 = 0.93$) and of pattern ($F(1,15) = 88.7$, $p<0.001$, $\eta_p^2 = 0.86$). Post-hoc comparisons revealed significant differences between PGo and PSw, PGo and DGo, and Pattern and Deviant Sw (all $p< 0.001$). These results reveal a parametric increase in TEPR with decreasing stimulus probability, and contrasted with RT results, are consistent with previous findings that TEPR and RT index different processes within cognitive control (Isabella, Urbain et al. 2019).

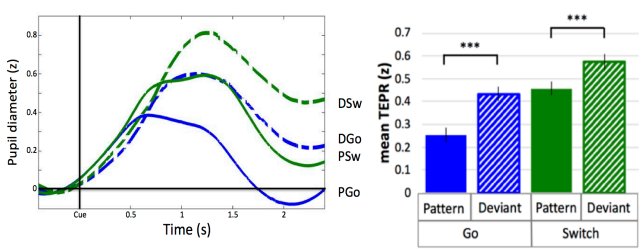

Figure 2: Mean TEPR (in z-scores) and standard errors from cue onset until 2 s for all response types.

iii. Neuromagnetic measures

Frontal Theta The relationship between variations in cognitive control and frontal theta oscillations was of critical interest in the current study. Beamformer analysis revealed consistent theta band (4-8 Hz) oscillatory activity in the right middle frontal cortex (mean Talairach coordinates: x = 26, y = 59, z = 21, BA 10) for correct pattern and deviant trials, (**Figure 3**; baseline = -1.1 to -0.6 s).

Theta power followed a typical time course, increasing to a maximum just prior to the response. Mean theta power was calculated as the mean percent change in power from 0.4 s prior to until 0.2 s after the button press response, relative to the pre-stimulus baseline. Theta power was smallest for PGo trials, and increased for each of PSw, DGo and DSw trials (mean PGo = 10.08 ± 2.16%, DGo = 23.39 ± 2.31%, PSw = 23.01 ± 2.35%, DSw = 36.64 ± 4.48%). In order to determine the effects of varied cognitive control on frontal theta oscillations, a 2-way ANOVA was conducted on mean power, revealing a main effect of pattern ($F(1,15) = 14.6$, $p = 0.002$, $\eta_p^2 = 0.49$), and also an effect of Switch ($F(1,15) = 21.9$, $p < 0.001$, $\eta_p^2 = 0.59$). Post-hoc comparisons revealed a difference between PGo and PSw ($p = 0.002$), between PGo and DGo ($p< 0.001$), and PSw and DSw, ($p < 0.019$). Interestingly, these results reveal theta has a similar relationship to task parameters as TEPR, revealing a strong difference between PGo and DGo in the absence of any behavioural differences. This result supports our hypothesis that frontal theta is sensitive to parametric increases in cognitive control.

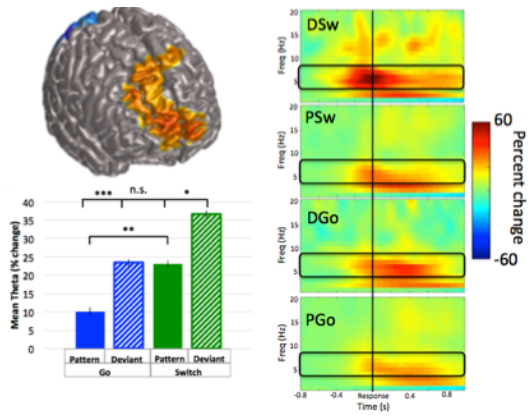

Figure 3: Mean theta for all response types, calculated from 0.4s prior to 0.2s after the button press response.

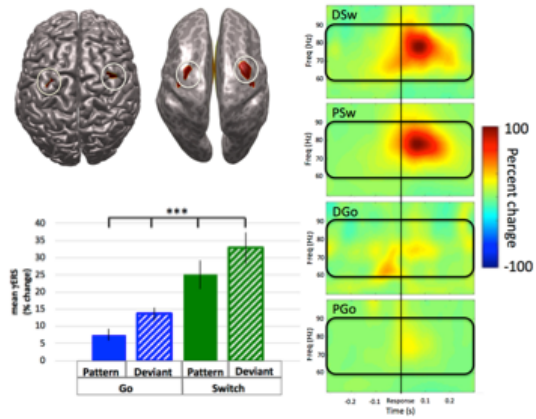

Figure 4: Mean gamma for all response types, calculated from onset until button response.

Sensorimotor Gamma Movement-related gamma activity has only recently been shown to vary with task parameters and may be related to resolving response conflict. Beamformer analysis revealed consistent gamma activity the sensorimotor cortex contralateral to the response (mean Talairach coordinates left: x = -34, y = -17, z = 43; right: x = 30, y = -10, z = 43) for correct trials of all types, commencing approximately 200 ms prior to response (**Figure 4**; baseline = -0.6 to –0.4 s). No significant gamma activity found in the ipsilateral motor cortex. We calculated mean gamma power in the contralateral motor cortex from activity onset until response. Gamma showed a similar pattern of effects as theta, with the least power for PGo trials, and increasing for DGo, PSw, and DSw, respectively (mean PGo = 7.5 ± 1.8%, DGo = 13.7 ± 1.8%, PSw = 25.1 ± 4.2%, DSw = 32.9 ± 4.5%).

In order to determine effects of task parameters on pre-response gamma activity, an ANOVA was conducted on mean power in the contralateral motor cortex, with significant effects of Switch ($F(1,15) = 19.6$, $p < 0.001$, $\eta_p^2 = 0.57$) and pattern ($F(1,15) = 19.9$, $p < 0.001$, $\eta_p^2 = 0.57$). Post-hoc comparisons revealed differences between PGo and PSw ($p < 0.001$), between PGo and DGo ($p < 0.009$), and PSw and DSw, ($p = 0.003$). Like frontal theta, that sensorimotor gamma parametrically increases with decreasing stimulus probability is in line with previous findings (Isabella, Ferrari et al. 2015), and suggests that sensorimotor gamma is sensitive to cognitive control. Given the similarity to frontal theta, sensorimotor gamma may be involved in integrating cognitive control signals into the motor cortex.

iv. Regression and Mediation Analyses

In order to investigate the relationship between frontal theta and the variety of measures in this study related to cognitive and motor control, we performed a multiple regression and analyzed the sum of squares to determine the strength and significance between the measures and within subjects. Controlling for effects of pattern and Sw, there was a significant relationship between frontal theta and RT ($r = 0.77$, $p < 0.001$, $\eta_p^2 = 0.61$), efficiency ($r = -0.73$, $p = 0.002$, $\eta_p^2 = 0.53$), TEPR ($r = 0.91$, $p < 0.001$, $\eta_p^2 = 0.97$), and pre-response gamma ($r = 0.78$, $p < 0.001$, $\eta_p^2 = 0.41$; **Figure 5**).

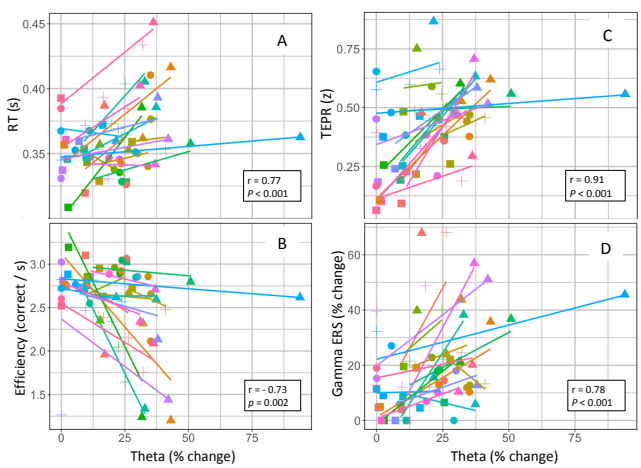

Figure 5: Theta values were regressed within-subject against RT, Efficiency, TEPR, and gamma.

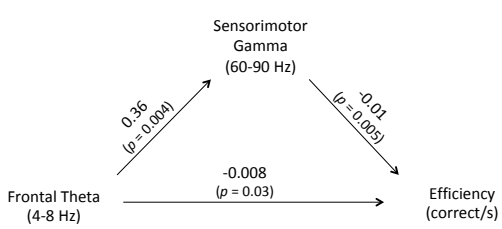

Figure 6: Effects of frontal theta on efficiency were fully mediated by sensorimotor gamma activity.

To interpret whether frontal theta affects behaviour via the sensorimotor cortex, we performed a causal mediation analysis between frontal theta and reaction times as well as frontal theta and efficiency, both mediated by sensorimotor gamma. Although sensorimotor gamma did not mediate the effect of frontal theta on reaction times ($p = 0.7$), the effect of frontal theta on efficiency was fully mediated by sensorimotor gamma ($p = 0.01$; **Figure 6**). The indirect effect was $(0.36)*(-0.01) = -0.004$ with an estimated proportion mediated of 0.47 ($p = 0.03$).

Discussion

We sought to test whether frontal theta is likely to have a functional role in cognitive control by testing two claims: if frontal theta is sensitive to cognitive load in a behavioural task and is related to activity within the sensorimotor cortex, then it is unlikely to be epiphenomenal but rather is involved in coordinating behavior during cognitive control. We manipulated cognitive control using a combined Go/Switch pattern learning task, without explicit awareness of the presence of a stimulus pattern. No relationship was evident between trial numbers and effect sizes across trial types for each outcome measure, and therefore was not analyzed further. Task effects of Go/Switch and pattern/deviant led to increased RT, indicating pattern learning, and TEPR confirming parametric variations in cognitive control. Frontal theta was sensitive to variations in cognitive control, and correlated with behavioural, pupillometric, and motor cortical activity. Correlations held for all trial types, including the unconsciously learned pattern, demonstrating that frontal control of behaviour may proceed without conscious awareness. Implications are discussed below.

RT is insufficient for capturing cognitive control

Differences between RT and TEPR are congruent with previous findings for this task (Isabella, Urbain et al. 2019). Increased TEPR has been associated with increased cognitive control (Kahneman and Beatty 1966), however, without a corresponding increase in RT or decrease in performance efficiency, we interpret this finding as increased cognitive effort without corresponding detectable behavioral effects. In particular, when comparing PGo and DGo, subjects increased cognitive effort to process the unexpected stimulus and response for DGo responses in the same amount of time as PGo responses. This finding has important implications for commonly used behavioral measures such as RT or efficiency in interpreting task difficulty or cognitive control, given that increasing cognitive effort need not produce detectable behavioral outcomes. We propose that TEPR is a more sensitive and direct measure of cognitive control than RT or performance efficiency.

Frontal theta is related to behavioural output via motor cortical signals

Increased cognitive effort to maintain consistent RT across

the two types of Go responses was likely driven by frontal theta activity, which correlated with RT (inversely) and motor cortical activity. A relation between theta and RT is in agreement with a study showing that frontal theta power had reduced amplitude on faster Sw trials (Cheyne, Ferrari et al. 2012), indicating that frontal theta increases are sensitive to the need for control processes. In the current study, frontal theta power was proportional to the amount of effort put into response inhibition and preparation, and this translated to behaviour in terms of performance efficiency that was mediated by sensorimotor gamma activity.

Sensorimotor gamma and frontal theta increased parametrically with cognitive control, and significant correlations were found between the two, suggesting a possibility for the gamma signal to integrate theta activity into the motor cortex. Furthermore, the information content of theta activity is likely related to updating the motor plan to the alternate response within the motor cortex prior to execution. This interpretation is congruent with previous findings for sensorimotor gamma when delayed gamma predicted error responses (Isabella, Ferrari et al. 2015). When competing responses are not sufficiently resolved in order to update the motor plan prior to responding, an error may occur. This interpretation is supported by evidence in clinical populations. Kurz et al. (2014) demonstrated decreased gamma in children with cerebral palsy who had difficulty anticipating grip forces, possibly related to deficits in motor planning. Given the current findings, we speculate that such impaired motor planning may be related to deficits in signaling from the frontal cortex, or inefficient integration into the sensorimotor cortex via gamma activity. However, further exploration into the mechanism of interaction between frontal theta and sensorimotor gamma are warranted to confirm the small but significant effect found here.

Inhibitory control in the absence of awareness: role for frontal theta

Theta activity was localized to the right middle frontal cortex where it increased from approximately stimulus onset and peaked shortly prior to the response. As expected, theta power was sensitive to task parameters and distinguished trial types in a similar manner to TEPR, albeit on a shorter time scale. Results of the regression analysis revealed a very strong correlation between these two outcome measures ($r = 0.91$). Previous studies have linked TEPR with functional brain measures related to cognitive load and task difficulty, including alpha band power during a reading comprehension task (Scharinger, Kammerer et al. 2015) and theta power (evoked with oscillatory) during a combined flanker/n-back task (Scharinger, Soutschek et al. 2015). The current study identified a strong correlation between TEPR and oscillatory theta power and further demonstrated that these tracked parametric increases in cognitive control. Previous research has linked frontal theta with a variety of cognitive control processes, such as mental arithmetic (Gartner, Grimm et al. 2015), response preparation (Womelsdorf, Johnston et al. 2010), response switching (Cheyne, Ferrari et al. 2012) and response inhibition (Isabella, Ferrari et al. 2015). One study demonstrated the sensitivity of frontal theta to increasing load in a working memory task (Jensen and Tesche 2002). The current study supports the notion that frontal theta is sensitive to increasing load, and we extend those findings by demonstrating the relationship between theta and increasing cognitive effort using pupillometry, as well as behavioural outcomes.

Pupil diameter is tightly linked with activity in the locus coeruleus (LC) (Joshi, Li et al. 2016), and noradrenergic and cholinergic pathways (Jepma, Deinum et al. 2011, Reimer, McGinley et al. 2016). Task-related pupil responses during cognitive processing were related to the BOLD signal and LC activity (Murphy, O'Connell et al. 2014), and LC activity has been related to cognitive performance (Minzenberg, Watrous et al. 2008). Therefore, it is likely that the current TEPR findings are related to LC activity, and the tight correlation with frontal theta suggests the LC and frontal cortex are both engaged during focused task performance. The link between these two brain areas is currently unknown.

Although top-down control of action is generally thought to occur within the cortex, it has been suggested that conscious and unconscious processes are implemented by the same neural substrates performing the same neural computations, and the difference between the two might only be a matter of degree (Horga and Maia 2012). Others have gone further to suggest that there is no causal role for conscious processes in action control, and that automatic processes may underlie normal motor behavior that is generally attributed to top-down cognitive control (Hommel 2013, Jasinska 2013). Current understanding of implicit learning suggests that it is also automatically acquired and not under cognitive control. That subjects in the current study were not consciously aware of the existence of a pattern suggests that they were automatically increasing effort required to inhibit responses, either when predicted as in PSw or when unpredicted as in DSw. The association of frontal theta power with inhibitory control, in the current study as well as in others, suggests that both inhibitory control and processing of other parameters associated with cognitive effort such as response selection may all be under unconscious control.

Conclusions

Frontal theta has been lauded as the 'lingua franca' for cognitive control (Cavanagh and Frank 2014), however has lacked sufficient evidence to support this assertion, namely a link between behavioural and cognitive control. The current study provides a link between frontal theta and cognitive control (TEPR), as well as interactions with the sensorimotor cortex linking to behavioural output. This work supports frontal theta as a mechanism for frontal control of behaviour, via the motor cortex. In addition, that the stimulus pattern was learned and subjects were not able to consciously repeat the stimulus pattern reveals that control of behaviour occurred across all trial types via the same neural mechanisms, without conscious awareness.

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