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PRESTIMULUS FRONTAL MIDLINE THETA REFLECTS INCREASED COGNITIVE CONTROL DURING SPONTANEOUS LAPSES OF ATTENTION

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PRESTIMULUS FRONTAL MIDLINE THETA REFLECTS INCREASED COGNITIVE CONTROL DURING SPONTANEOUS LAPSES OF ATTENTION[4]

Performance errors are well studied under conditions of increased demands for motor inhibition; within this framework, errors are considered to be manifestations of motor conflicts between mutually exclusive responses to stimuli presented. However, tasks that require prolonged exertion of sustained attention and complex stimulus-response mapping may involve somewhat different internal causes of performance errors related to fluctuation in cognitive control; this aspect has not been previously addressed in literature. Specifically, it has not been studied whether performance errors can result from conflicts with spontaneous internally generated task-unrelated processes.

In the present study, modulation of prestimulus brain activity in relation to spontaneous performance errors was studied during the auditory condensation task. Frontal midline theta (FMT) power, which is an indicator of cognitive control system activation, was found to be significantly higher before incorrect responses than before correct ones. Relative increase in FMT power before incorrect responses was positively correlated with Strength of excitation (STI questionnaire) and negatively correlated with the percentage of errors and with correct-to-error response time ratio. These findings allow us to suggest that the increase in the prestimulus FMT power before incorrect responses under the condensation task was at least partly related to the adjustment of the cognitive control system and conflict regulation. We speculate that the conflict may arise from interference between task-related and task-unrelated processes such as mind wandering.

JEL Classification: Z

Keywords: cognitive control, attentional lapses, performance errors, EEG, frontal midline theta, condensation task, mind wandering.

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Introduction

Cognitive control can be considered a set of processes that are responsible for goal-directed flexible behavior [Yeung, 2013]. These processes can be conceptually divided into two broad classes: one of them forms a system of exertion of cognitive control itself, and the other one forms a system of monitoring the need to increase the level of cognitive control [Ridderinkhof et al., 2004]. Exertion of cognitive control includes top-down attention to the task-relevant sensory information; retention of relevant information such as task rules and the history of the previous task course in the working memory; integration of task-relevant neural processes that represent the sensory information, context, retrieved long-term memories, reward expectations and motor programs [Womelsdorf, 2010b]; facilitation of representations of the task-relevant actions; inhibition of representations of incorrect automatic or prepotent actions. The monitoring system signals the demand for increasing the cognitive control level in the situations such as simultaneous activation of conflicting action representations; detection of erroneous response commissions; ambiguous task rules; change in the task rules; discrepancy between the actual and the predicted reward [Womelsdorf, 2010b].

The neural substrate of most aspects of cognitive control is represented by a number of structures in the anterior part of the frontal cortex, linked into a highly interconnected network. Although their functions overlap, it is possible to distinguish relative contributions of these structures into cognitive control processes. Particularly, the lateral prefrontal cortex (lPFC) is presumed to be largely involved in retention of task-relevant representations, and thus it participates in such functions as working memory, top-down attention and creation of the behavioral bias towards correct responses consistent with the current task rules [Yeung, 2013; Ridderinkhof et al., 2004]. The orbitofrontal cortex (OFC) is an important node in reward prediction and evaluation [Ridderinkhof et al., 2004]. The medial frontal cortex (MFC), and, more precisely, its part called the rostral cingulate zone (RCZ), is believed to be involved in such processes as monitoring the need for increasing cognitive control [Yeung, 2013, Ridderinkhof et al., 2004] and producing behavioral adjustments by signaling this need to other cortical structures [Yeung, 2013].

Several behavioral adjustment effects related to cognitive control were described in literature. Typically they can be manifested within such experimental paradigms as the Stroop task and the Simon task, which involve presentation of two basically different types of stimuli: incongruent stimuli with relevant and irrelevant features mapped onto opposing behavioral responses and thus leading to a motor conflict between two alternatives, and congruent stimuli with relevant and irrelevant features mapped onto one and the same behavioral response, thus involving no conflict. Some of such investigations also rely on tasks involving the need to voluntary suppress a prepotent learnt response and thus also creating a conflict between the learnt bias for a response and the instruction to refrain from it – examples are the sustained attention to response task (SART) and the Go/NoGo task [van Driel et al., 2012].

One of the well-studied behavioral adjustment effects related to cognitive control is the so-called post-error slowing – increase in response time on trials following error commission; post-error slowing is accompanied by increased performance accuracy [Botvinick et al, 2001]. On the contrary, erroneous response times are often shorter than correct ones; this effect is usually observed in tasks that involve the need to suppress incorrect prepotent responses while trying to respond as quickly as possible.

The second behavioral adjustment is the so-called Gratton effect [Gratton et al., 1992], which can be observed during trials that follow conflict situations; this effect leads to increased response times to congruent stimuli (which are normally relatively shorter) and to decreased response times to incongruent ones (which are normally relatively longer). This effect is supposedly caused by increased level of cognitive control after the conflict; increased level of cognitive control likely prevents interference of relevant stimulus features with the irrelevant ones [Egner, 2007].

Third, post-conflict slowing is an increase in response times on trials following the conflict. This effect is usually masked by the Gratton effect, but it still could be demonstrated experimentally in a study of Verguts et al. [2010], who used congruent and incongruent bivalent stimuli to control the level of conflict, and simple monovalent stimuli to probe for post-conflict adjustments without the influence of the Gratton effect. However, post-conflict slowing was accompanied by decreased performance, raising doubts whether this effect was related to the increase in cognitive control.

Finally, slowing of responses to incongruent stimuli themselves can be partially explained by competition between motor programs associated with the relevant and irrelevant features of stimulus, as well as by a quick increase in the motor threshold that prevents commission of premature erroneous responses [Wiecki, Frank, 2013; Zavala et al., 2014].

Theta rhythm, i.e. oscillations of the brain electrical potential within 4 - 8 Hz frequency range, is a frequently studied electrophysiological correlate of active cognitive processes [Mitchell et al., 2008]. With the use of local field potential (LFP) recording, theta band oscillations can be found in a wide variety of cortical and subcortical areas [Womelsdorf et al., 2010a]. Within the electroencephalographic (EEG) signal, cognition-related theta rhythm is most prominent at frontal midline sites, thus it is often referred to as frontal midline theta (FMT) [Mitchell et al., 2008].

Theta power can be modulated at long and short time scales. Relatively long periods of increased FMT (composed of theta bursts) can be observed during such cognitively demanding tasks as retention of objects in working memory [Sauseng et al., 2004], arithmetic operations [Iramina et al., 1996], or spatial navigation in virtual space [Ekstrom et al., 2005]. This activity can be modulated by the task complexity, e.g. by the number of objects to be memorized [Hsieh, Ranganath, 2013]. Short theta bursts emerge at a single-trial timescale and presumably reflect activation and integration of decision-related processes [Womelsdorf et al., 2010]. Paradoxically, FMT can also appear during drowsiness, at stage 1 of non-REM sleep, and during REM sleep [Inanaga, 1998; Takahashi et al., 1997]. Some authors speculate that FMT activity during sleep is related to mental activity such as production of dream images [Inanaga, 1998], while the others consider this type of FMT as a correlate of blocking the external information [Mitchell et al., 2008]. Alternatively, sleep-related FMT can share no common functional properties with cognition-related FMT. Increased FMT activity during drowsiness probably reflects increased subjective difficulty of staying on-task under this state [Barwick et al., 2012].

It is most likely that FMT does not reflect a single specific aspect of cognitive activity, but rather manifests itself as a hallmark of activation or synchronization of certain neural circuits, so its functional properties depend on the specific type of computations that are currently performed by these circuits [Cohen, 2014; Mitchell et al., 2008]. In most cases, FMT is not phase-locked to the beginning of the task, stimulus onset or commission of a response; however, part of FMT power can be related not as much to the theta oscillatory process per se as to the event-related potential components such as N2, ERN or FRN [Cohen, Donner, 2013; Cohen, 2014]. Thus, theta-activity can be considered to reflect an internal process, which is modulated by external events.

The bursts of FMT power that occur around the presentation of stimuli and commission of responses are modulated by the conditions characterized by increased cognitive demands such as errors, conflict, reward omissions and task switching [Cavanagh, Frank, 2014; Womelsdorf et al., 2010a]. On this basis, theta activity is considered to be related to cognitive control, and, more specifically, to the process of monitoring the need in the increased level of control. This view is supported by a number of studies that localize the source of FMT in the MFC areas, including ACC [Asada et al., 1999; Gevins et al., 1997]. Moreover, phasic FMT power is related to some behavioral effects associated with the control-demanding situations or with the exertion of control itself. For example, FMT power within the time interval preceding the response was shown to be correlated with the response time, this correlation being stronger under high-conflict situations [Cohen, Cavanagh, 2011]. Furthermore, the power of FMT in the time interval following erroneous responses is known to be correlated with the degree of post-error slowing [Cavanagh et al., 2009].

FMT activity related to cognitive control is most often studied in the time window following the stimulus presentation or around a response. However, there is some evidence that task-selective theta activity can occur before the actual presentation of a stimulus. For example, Womelsdorf et al. [2010a] discovered neuronal populations in the monkey ACC that generated theta activity selectively related to the current task rule (prosaccade vs. antisaccade) beginning 400 to 200 ms before stimulus onset. Importantly, this activity commenced earlier before correct trials following errors compared with correct trials following correct ones, and was absent before erroneous trials. These results clearly suggest that theta activity reflects activation of the cognitive control system.

In many cases, detection of the need to increase the level of cognitive control is related to some explicit event such as a conflicting stimulus, error commission, unpredicted behavioral outcome or specific instruction. As mentioned above, those events are associated with activation of the monitoring system represented by an increase in MFC activity and in the FMT power. However, increased control could be needed in the face of any processes that interfere with the task performance. These processes may be of external or internal nature and may be spontaneous (intrusions) or volitional (diversions) [Mishra et al., 2013]. Particularly, spontaneous internal processes that interfere with the main task are often referred to as mind wandering (MW).

The relation between MW and cognitive control is not straightforward. On the one hand, MW, which can potentially interfere with main task, may lead to an increase in cognitive control; this increase may be aimed either at preventing diversion of attention from the main task to MW, or, alternatively, at supporting multitasking (i.e. simultaneous occurrence of MW and the processes related to the main overt task) [Christoff et al., 2009]. On the other hand, the actual transition from the main task to MW may be a consequence of a failure in cognitive control. Indeed, it has been shown that occurrence of MW is negatively correlated with the level of cognitive control: it occurs more frequently during simple or automatic tasks requiring little cognitive control; moreover, subjects with low working memory capacity (working memory being a hallmark of cognitive control) as well as subjects with cognitive impairments such as attention deficit hyperactivity disorder (ADHD) are more prone to MW [Kane et al., 2007; Shaw, Giambra, 1993]. Finally, MW itself can encompass controlled processing of important personal goals [Smallwood, Schooler, 2006], and thus it can involve thoughts laden with internal conflicts leading to the increase in the level of cognitive control [Christoff et al., 2009].

The complex relations between MW and cognitive control are reflected in a number of psychophysiological studies. There is a vast fMRI literature that refers to the so-called default mode network (DMN), which is activated at resting state and deactivated during task performance. DMN activation is associated with decreased task performance, and it has been shown that increased DMN activation can predict performance errors as early as 30 seconds before their actual commission [Eichele et al., 2008]. DMN activity is increased during MW episodes, and the frequency of MW episodes is positively correlated with DMN activity during cognitive tasks [Christoff et al., 2009]. In some studies, DMN activation was shown to be anticorrelated with activation of frontal networks related to cognitive operations and sustained attention [Eichele et al., 2008]; these observations could support the view that MW reflects a decline in cognitive control. However, in other studies MW was accompanied by simultaneous activation of the DMN and the executive network including dorsal ACC and lPFC, which can be a hallmark either of multitasking, or of an attempt to return the attention to the main task, or of conflicting thoughts occurring during MW [Christoff et al., 2009]. The authors claim that the last interpretation is correct, because more strong activation of both networks was observed during MW without meta-awareness. However, it is still possible, that conflict monitoring is somewhat automatic and does not require meta-awareness, so the executive network is stronger activated during MW without meta-awareness just because its interference with task-unrelated activity is stronger in this situation, leading to a state of stronger conflict.

The relation between MW and FMT is also not straightforward. First, a number of studies have demonstrated negative correlation between FMT power and BOLD-signal in the DMN at rest [Scheeringa et al., 2008] as well as during working memory tasks [Michels et al., 2010] or episodic memory tasks [White et al., 2012]; these observations can reflect the opposite relations of these phenomena to the cognitive effort [Hsieh, Ranganath, 2013]. Second, there are iEEG studies that have shown that some nodes of DMN (e.g. posteromedial cortex) can generate theta activity themselves during the resting state [Foster, Parvizi, 2012], but it is not clear whether this activity is positively or negatively correlated with BOLD signal and whether it makes any contribution to the FMT-signal. Third, the increase in FMT power has been observed during self-reported episodes of MW in the task of breath cycles counting [Braboszcz, Delorme, 2011]. However, this effect can be related to the MW process itself as well as to the increased cognitive control associated with self-awareness and the need to perform the report, as well as to increased drowsiness leading to the attentional drift. It should be also noted, that FMT oscillations associated with MW, in addition to the conveying of the conflict signal (task-related or task-unrelated), could potentially reflect such processes as retrieval of task-unrelated episodic memories [Qin, Perdoni, 2011], or production of emotions [Sasaki et al., 1996]. The situation is further complicated by the fact that some medial frontal nodes of the executive network (presumably involved in the generation of FMT) can be activated in certain conditions that are not related to the cognitive control per se, such as a negative affect [Cavanagh, Shackman, 2014].

As mentioned above, subjects differ both in the level of cognitive control they can maintain and in their predisposition to mind wandering [Smallwood, Schooler, 2006]. The extreme cases of impaired cognitive control can be seen in patients with such neurological disorders as ADHD or frontal injuries. At the same time, FMT power is known to be correlated with some personality traits such as neuroticism and extraversion [Mizuki et al., 1984] and some neurochemical measures such as monoamine oxidase platelet activity [Hashimoto et al., 1998], as well as with individual performance level in cognitive tasks [Klimesch, 1999].

Thus, most of the information available concerning the relation between neural activity interfering with task performance and FMT power comes from cognitive control studies based on direct manipulations of task difficulty. At the same time, error-related FMT signal occurs mostly after the actual response, presumably reflecting error detection process rather than the mental state leading to error commission. The relation between FMT and spontaneous changes in the background state, such as during MW, is poorly studied, and the existing empirical data are often controversial. Such lack of knowledge results from the complexity of interactions between the DMN and the executive network of the brain, which are not fully understood.

The main goal of the present study was to investigate the relation between the prestimulus FMT activity and error commissions, and, more specifically, to determine whether this activity is more strongly related to the cognitive control or to the processes that interfere with the performance of the task. We focused our analysis on the prestimulus (i.e. background) time interval in order to investigate the effect of spontaneous fluctuations in subject’s cognitive state on the processing of the incoming stimulus.

We hypothesize that prestimulus FMT will be increased before errors indicating that errors are related to conflicts stemming from interference between the task performance and spontaneous internally generated task-unrelated processes.

For this purpose we used the auditory condensation task [Garner, 1975], which is based on feature binding and binary response selection; this task produces high attentional load, and participants' performance is involves a substantial number of incorrect responses [Osokina, Chernysheva, Chernyshev, 2012].

Methods

Participants

The present study was performed in 80 volunteers aged 18-29 years (M ± SD = 20.0 ± 1.7 years) (57 females and 23 males, including 71 right-handed and 9 left-handed persons). All participants had normal hearing, normal or corrected to normal vision and reported no history of auditory, neurological or mental illness. An informed consent was signed by all participants before the experiment, and they were asked to fill a short questionnaire concerning their current state of mood and arousal level. Only those participants who reported no apparent drowsiness were admitted to the experiment. Experiments were conducted with the approval of the ethics committee of the National Research University Higher School of Economics and in accordance with the Declaration of Helsinki and its amendments.

After the experiment, participants filled the STI questionnaire [Strelau et al., 1990], which assessed Strength of excitation and Strength of inhibition dimensions, and 41 of them also passed a post-experimental interview that included questions related to their tiredness and episodes of mind wandering.

Materials

The experiments were performed in a sound-attenuated chamber with standard ceiling lighting. Participants were comfortably seated in an encephalographic chair with adjustable headrest and armrests. A 19” LCD monitor was in front of them at chest level.

Experimental settings. Electroencephalogram was recorded with NVX-52 system (Medical Computer Systems, Russia) and NeoCortex Pro software (Neurobotics, Russia) from 27 electrodes according to 10-10% international system and 1 electrooculographic electrode referred to linked earlobes, with ground electrode located on forehead. Impedance was kept lower than 10 kΩ. The hardware bandpass filtering in a range between 0.5 and 200 Hz was applied.

Auditory stimulation and recording of behavioral responses. Auditory stimuli were presented to the participants using E-Prime software (Psychology Software Tools, Inc., U.S.A.) through a high-quality stereo headset with in-ear design, which additionally reduced ambient sounds. Four pre-recorded auditory tones were presented. Each tone was a sinusoidal signal of either 500 Hz (‘low’) or 2000 Hz (‘high’), either a pure tone (‘pure’) or the same tone with broadband noise added to the signal (‘noised’); root mean square amplitude of noise was 4.9

times smaller than root mean square amplitude of pure tones, or approximately -14 dB relative to pure tones. The four stimuli were named in the instruction presented to the participants as (1) ‘low pure’, (2) ‘low noised’, (3) ‘high pure’, and (4) ‘high noised’. The duration of all stimuli was 40 ms, with rise and fall time 10 ms each; sound pressure level was 95 dB. The stimuli were easily discriminated by all participants in a pre-task test and in control blocks (see below).

Behavioral responses were obtained from the participants with the help of a handheld gamepad.

Instruction

Participants were instructed before the experiment to hold the gamepad in their dominant hand and to press one or the other of the two buttons in response to the stimuli. The participants were also instructed that if he/she would press the correct button, a ‘smiley’ would be briefly presented on a LCD screen in front of them.

The participants were offered to familiarize themselves with the following table (Table), which was given to them printed in a large typeface on a sheet of paper for free viewing and then removed from the chamber before the start of actual EEG recording. Table specifies the conjunction contingencies between the two stimulus features (‘high’ / ’low’ and ‘pure’ / ‘noised’) comprising the set of the four stimuli, and the response required to the left and right buttons of the gamepad. Though the rules are very simple, the task cannot be solved at above chance level via processing any single feature but it rather requires a mental conjunction of both features.

Before the experimental blocks all of the participants were familiarized with the stimuli (the experimenter manually played them to the participants and named them orally (‘low pure’, ‘low noised’ etc.), and then the participants were blind tested with the stimuli. During this test,

Table. Response contingencies in the experimental task: this table was read as well as handed in printed form to the participants immediately before the experiment.

	High	Low
Pure	Left button	Right button
Noised	Right button	Left button

all of the participants easily named all of the stimuli correctly, and all of them stated confidently that they could clearly feel the difference between all of the stimuli and knew which button corresponded to each stimulus.

Additional control procedure was performed after the main experiment in 30 participants: during two additional blocks, they were asked to choose the response based on one single feature (pitch in one block and presence of noise in the other block). The results of these control procedures demonstrated that in easy condition of simple stimulus-response mapping, which did not require feature binding, the percentage of correct responses was at least 97% or higher in all participants tested. Thus, the main cause of errors and omissions was not related to sensory limitations such as inability to discern the pitch of a tone or the addition of the noise to a pure tone.

Experimental procedure

The experiment involved six experimental blocks; after each block the participants were asked how they were feeling, and recommended to relax and / or move their head and limbs a little within the armchair.

Each block included 100 stimuli of four types (see above) intermixed in a random order with equal probability ratio. Although all four stimuli were presented with equal probability, in most block stimuli percentages were not exactly equal to 25%: overall M ± SD for the 4 stimuli were 24.9 ± 3.8, 25.3 ± 4.1, 25.1 ± 4.1, and 24.8 ± 4.1, the difference between them being non-significant (F(3, 648) = 0.46, ns). Due to random algorithm used, the participants were definitely unable to predict the order of the stimuli. The stimuli were presented with random stimulus onset asynchrony (SOA) of 2500 ± 500 ms (flat distribution). Visual feedback was given during the experiment: correct responses within the time interval of 300-1700 ms after stimulus onset were reinforced by a ‘smiley’ (a schematic smiling face depicted by eyes and mouth in a ring filled with yellow on a neutral grey background), which was presented for 500 ms immediately after correct responses in the center of the screen. The screen was neutral grey between the presentations of the feedback.

The time interval from the moment of a key pressing until the next auditory stimulus onset was kept to no less than 500 ms by prolonging the particular SOA when needed. The resulting SOA throughout the experiment was 2657 ± 321 ms (M ± SD), with minimum and maximum 2063 and 5010 ms correspondingly.

The instruction only informed the participants that they had to press one of the two buttons according to the rule specified, but it did not tell them that they had to react as fast as possible, nor did it compel them to make a random choice if they were uncertain. In other words, the trials were not ‘forced’ and participants were implicitly allowed to omit responses.

The participants stated after the experiment that the task required a significant effort on their part to maintain good quality of responding. During the experiment most of the participants found it difficult to respond in a continuous manner – notwithstanding the fact that inter-trial intervals were relatively long (2-3 s). The real difficulty of the task probably lies in choosing an appropriate response based on feature conjunction.

Data extraction and analysis

Performance. Behavioral outcome of each trial could be one of the following: a correct response (pressing the correct button), an error (pressing the wrong button), and a response omission (failure to press any button). It should be noted that any response committed after 1700 ms since the last stimulus was considered the omission. Proportions of each of these outcomes were calculated as well as mean response latencies for correct responses and errors.

EEG. EEG was analyzed within MATLAB and EEGLAB [Delorme, Makeig, 2004] software. Movement artifacts were manually rejected from the EEG data, and electrooculographic artifacts were corrected with the use of regression analysis implemented in EEGLAB.

In order to obtain the prestimulus FMT power, a window Fourier transformation with Hanning tapering was applied to the signal recorded at Fz electrode in the time interval from -1000 ms to 0 ms for each epoch, and the absolute values of complex amplitudes were taken as the estimations of frequency power. The Fourier transformation was performed using EEGLAB toolbox. FMT power was calculated as a sum of frequency powers in the range from 4 to 7 Hz at 1 Hz steps. Absolute pre-stimulus FMT power was calculated for each condition independently (correct responses, errors, omissions, errors + omissions) by averaging power values over all corresponding trials. The relative differences in FMT power between errors (or errors and omissions pooled together) and the correct responses were calculated as the differences of the corresponding absolute powers normalized by the sums of these powers. This normalization was performed in order to exclude possible multiplicative effect of between-subject difference in the absolute FMT power, which can be related, for example, to the variations in the anatomy of the skull.

Statistical analysis

We performed a number of statistical procedures in order to explore the relations between pre-stimulus FMT power, behavior and personality traits.

First, we compared the percentage of correct responses that were committed by participants with the percentage of errors and omissions. This was done by using one-way ANOVA with repeated measures; two levels of factor ‘response’ were used in each comparison: ‘correct’ vs. ‘error’, and ‘correct’ vs. ‘omission’.

Second, we compared the mean latencies of correct responses and errors committed by participants. For this purpose, we also used one-way ANOVA with repeated measures; two levels of factor ‘response’ (‘correct’ vs. ‘error’) were used.

Next, we estimated a group-level significance of between-condition difference of FMT power. In this analysis, correct responses were compared with errors as well as with errors and omissions pooled together. For this purpose, we performed one-way ANOVA with repeated measures on the vectors composed of the FMT power logarithms obtained for each subject in each of two compared conditions: factor ‘response’ (‘correct’ vs. ‘error’ or ‘correct’ vs. ‘error and omissions’). In addition, we estimated the within-subject individual statistical significance of FMT difference between conditions. To do this, for each pair of conditions under consideration we compared two corresponding sets of trials with one-way ANOVA with repeated measures.

We also performed a correlational analysis in which we compared spectral variables with behavior and individual traits. We used individual relative FMT differences between conditions as the first variables in the correlational analysis. The second variable was one of the following dimensions: percentage of errors, ratio of average response time of correct responses to average response time of erroneous ones (correct-to-error RT ratio), Strength of excitation, and Strength of inhibition (STI). For each of 8 pairs of variables the Pearson correlation coefficient was calculated. In order to correct for multiple comparisons we have repeated this analysis on the permuted data in which the values of second variable were randomly shuffled over the participants. For each of 1000 permutation steps we selected the minimal and maximal correlation coefficients over all 8 comparisons and constructed two distributions (of permuted minimal and maximal coefficients correspondingly). Then we compared the negative non-permuted coefficient with “minimal” distribution and the positive coefficients with “maximal” distribution, and so we obtained a permutational p-value for the result of each comparison.

We have also performed the correlational analysis similar to that described above in order to estimate the relation between the percentage of errors and the correct-to-error RT ratio. For this analysis, we calculated p-value as the probability that the correlation coefficient is significantly greater than zero.

The participants were included in the group-level and correlational analysis according to the following conditions. First, we excluded 4 participants who had less than 64% of correct responses (which corresponds to 2 standard deviations from the group mean performance). Second, each participant was included in the analysis of every spectral variable only if he/she had no less than 20 trials of each of the corresponding conditions. For example, the participant was included in the analysis of correlation between the task performance and the relative FMT power difference between errors and the correct responses only if he committed no less than 20 errors during the experiment. During the permutation, these rules were applied at the each permutation step.

Results

Behaviour

Participants committed 11.3±0.8% errors, 5.1±0.4% omissions and 83.6±1.0% correct responses (Fig 1A). The percentage of correct responses was significantly higher than the percentage of errors (factor ‘response’, F(1,79)=1575.90, p<.0001). The percentage of errors was significantly higher than the percentage of omissions (factor ‘response’, F(1,79)=49.06, p<.0001).

Average response times for correct and erroneous responses were, correspondingly, 890±9 and 1029±18 ms (Fig. 1B). Average correct response time was significantly lower than the average response time of errors (factor ‘response’, F(1,79)=116.02, p<.0001).

The correct-to-error RT ratio was positively correlated with the percentage of errors (r=.41, p=.0002, N=76) (Fig 1C).

FMT power

At the group level, we have found no difference in logarithms of FMT power calculated before errors and before correct responses (factor ‘response’, F(1,64)=.62, ns). At the same time, logarithm of FMT power before errors and omissions pooled together was significantly larger than before correct responses (factor ‘response’, F(1,74) = 6.49, p=.01) (Fig 2A).

At the individual level, we have found that FMT power was significantly (p<.05) larger before errors compared to correct responses in 9 participants (although 3 of them made less than 20 errors), and significantly smaller in one participant. In addition, 10 participants had significant increase in FMT before errors and omissions pooled together compared to correct responses, and one participant had a significant decrease.

Correlations of FMT power with personality and behavioral measures

Relative difference in prestimulus FMT power between erroneous and correct trials was positively correlated with the Strength of excitation (r=.36, p=.008, N=62, Fig 2B) and negatively correlated with the correct-to-error RT ratio (r=-.26, p=.04, N=65, Fig. 2C). Relative difference in prestimulus FMT power between incorrect trials (errors and omissions pooled together) and the correct ones was negatively correlated with the correct-to-error RT ratio (r=-.27, p=.03, N=75, Fig. 2D), as well as with the percentage of errors (r=-.26, p=.04, N=75, Fig. 2E).

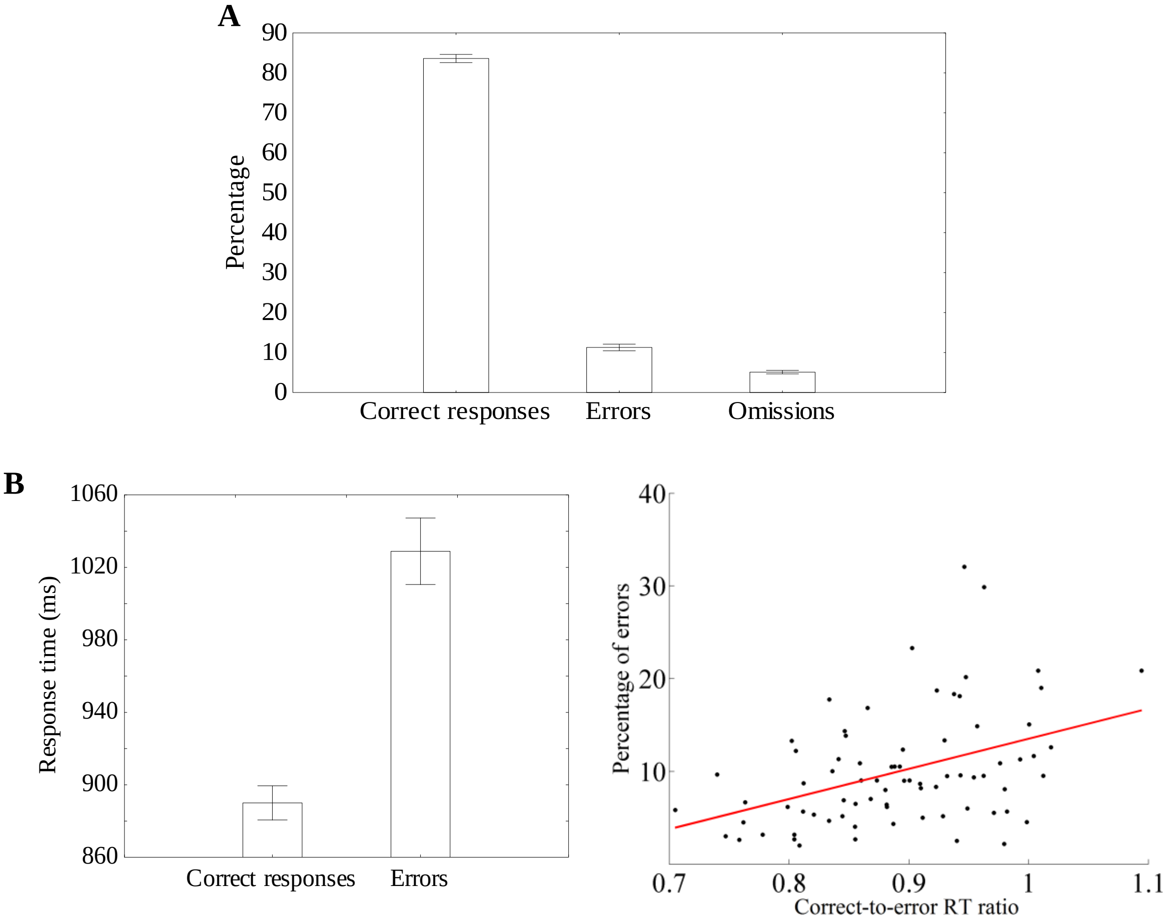

Fig. 1. Behavioral results. (A) Percentage of correct responses, errors and omissions for all participants (N=80); (B) Mean response time of correct responses and errors for all participants (N=80) (data are presented as M ± SEM); (C) Correlation between correct-to-error RT ratio and percentage of errors (r=.41, p=.0002, N=76).

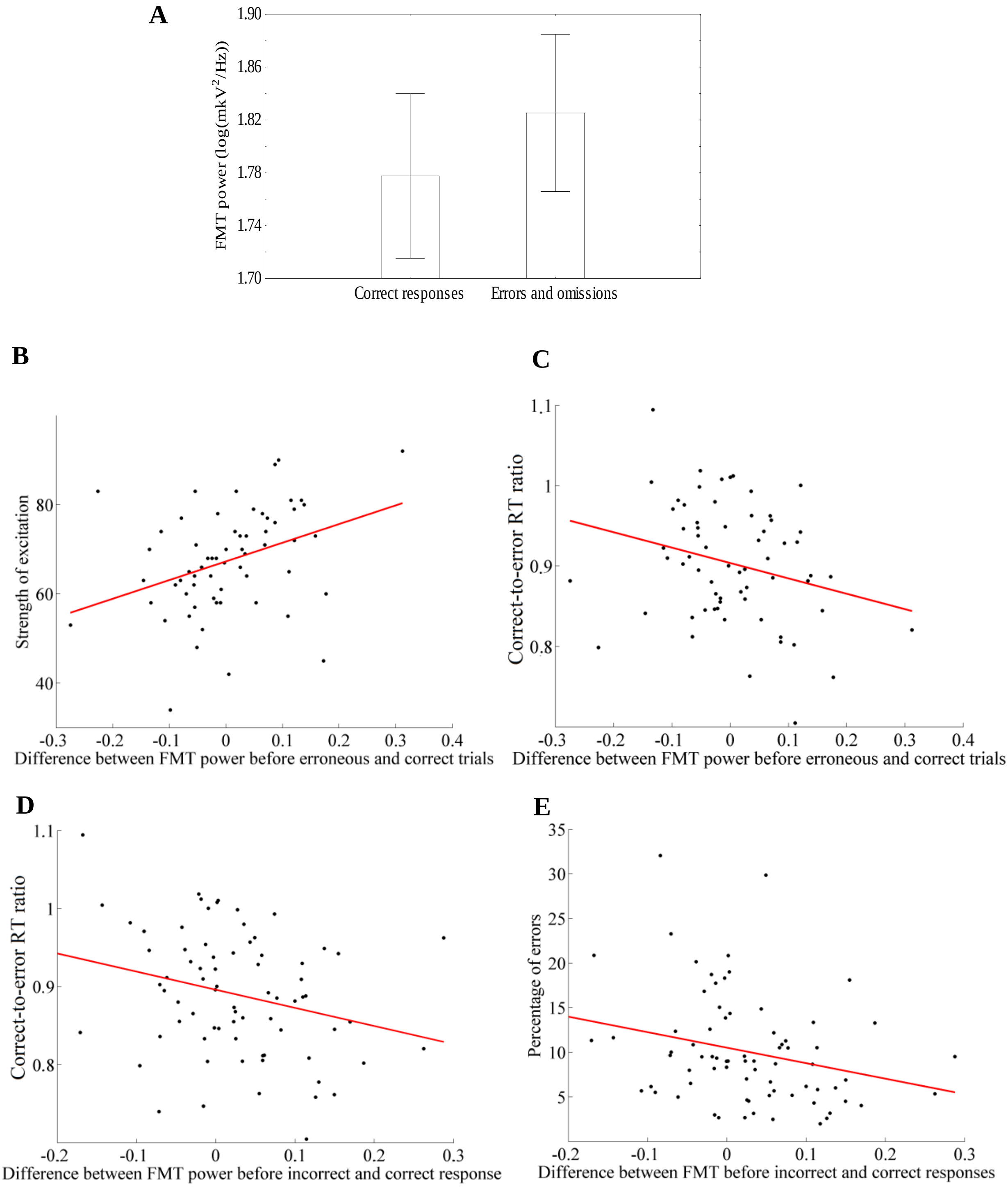

Fig. 2. FMT power. (A) Logarithms of FMT power before correct and incorrect (errors and omissions) responses (N=76); (B) Correlation between relative increase of FMT power before errors compared to correct responses and Strength of excitation (r=.36, p=.008, N=62); (C) Correlation between relative increase of FMT power before errors compared to correct responses and correct-to-error RT ratio (r=-.26, p=.04, N=65); (D) Correlation between relative increase of FMT power before incorrect responses (errors and omissions) compared to correct ones and response time ratio (r=-.27, p=.03, N=75); (E) Correlation between relative increase of FMT power before incorrect responses (errors and omissions) compared to correct ones and percentage of errors (r=-.26, p=.04, N=75).

Discussion

In the current study, participants committed a significant number of errors during the condensation task, and the latencies of erroneous responses were on average longer than the latencies of correct responses (Fig. 1). Tentatively, several different processes could possibly influence task performance in the experiment. First, the overall decrease in the vigilance level could cause the instability of task rule representations and impaired sensory processing that would lead to increased likelihood of error commission. Alternatively, impairment of task-related information processing may be a result of increased interference with some task-unrelated activity. This interference could be caused by spontaneous failures of the cognitive control monitoring system or by the increased level of task-unrelated activity itself.

Any substantial decrease in the arousal level and vigilance was unlikely during the experiment since all participants reported the absence of drowsiness at the beginning of experiment. In the post-experimental interview, only 12 out of 41 interviewed participants reported that they had been tired after the experiment, 18 participants reported that they had been moderately tired, while 11 participants reported that they had not been tired at all.

Spontaneous attentional drifts, which resulted in errors and omissions, may have been related to mind-wandering (i.e. attentional shift toward internally generated thoughts) as well as to the attention being redirected to some external task-unrelated sensory stimuli. We must note that the current data do not allow us to distinguish between these hypothetical situations. However, due to the constancy of the environment within the sound attenuated chamber where amount of the potential distractors was kept to minimum, it is more likely that MW was the main source of interference during the performance of the task. This hypothesis is further supported by the results of the post-experimental interview, during which 34 out of 41 participants reported that they had episodes of MW, while only 6 participants denied that.

Response times

At the group level of analysis, we found an overall increase in response latency for erroneous responses compared to correct ones (Fig. 1B). The increased rather than decreased latency of erroneous responses was likely observed due to the fact that the current task was highly demanding to cognitive resources and did not involve any predominant automated responses that would be committed with high probability in the situation of cognitive control failure (e.g. as in the Simon or SART tasks) [Botvinick et al., 2001].

The slowing of erroneous responses we have observed may be similar to the conflict effect in Simon or Stroop tasks, under which incongruent stimuli lead to increased response time and higher error probability. Although we do not know the level of conflict that was present during each particular trial, it is reasonable to suppose that a large part of errors was committed in the high-conflict state. This allows us to apply the same logic to the comparison of errors and correct responses as many authors do when comparing incongruent trials with the congruent ones in the classical cognitive control paradigms [Yeung, 2013; Cohen, 2014]. It is important to remind that correct responses in the current task required conjunction of two stimulus features: thus, each feature itself could potentially activate the representations of both responses. That means that, if the spontaneous attentional drifts (namely, MW) could somehow impair the feature binding process, then the stimuli presented during such a cognitive state would produce a response-level conflict. Such top-down disregulation may result in simultaneous activation of two opposite motor programs, and the consequences of this conflict would be manifested during the next trial.

Correlational analysis has shown that participants with more prominent increases in latency of erroneous responses compared to the correct ones demonstrated better task performance (Fig. 1C). This means that the increased latency of errors, at least in part, is related not to the cognitive interference itself but to activation of the cognitive control system aimed at keeping the optimal task performance. From this point of view, between-subject variation of error slowing reflects the difference in the ability to monitor conflict situations, which, in turn, leads to the difference in the overall task performance.

Prestimulus FMT

Prestimulus FMT power was on average higher before incorrect responses (errors and omissions) compared to the correct ones (Fig. 2A). Furthermore, higher relative difference of prestimulus FMT power between incorrect and correct responses was associated with stronger slowing of erroneous responses compared to correct ones (Fig. 2C and 2D). These results, again, point to the fact that the prestimulus FMT power is a hallmark of high-interference state, during which the task becomes more difficult to the participant. However, these results do not allow us to conclude whether FMT increase is related to the interfering process itself (e.g. episodic memory retrieval during MW) or to the adjustment of cognitive control system to the increased level of conflict.

The relative difference in prestimulus FMT power between incorrect and correct responses was also negatively correlated with the percentage of errors (Fig. 2E). That means that some part of prestimulus FMT power could be related to the activity of conflict monitoring subsystem of cognitive control, and that high FMT power reflects not just the level of conflict experienced by a participant but also the participant’s ability to resolve this conflict. This correlation is weaker than the correlation between FMT power difference and the error slowing. One possible explanation is that error percentage is associated only with the part of FMT power that is related to conflict resolution, while the response latency could be associated with the other processes potentially manifested in FMT increase as well. The correlation discussed above is also much weaker than the correlation between error slowing and percentage of errors. It can probably mean that the response slowing reflects the increase of cognitive control to a greater extent than the FMT power, and that FMT power is more strongly related to the fact of interference itself than the response slowing does.

We must note that there is one nuance in the above argumentation. It relates to the fact that the total number of trials on which participants experienced strong conflict is unknown, and we can only know the number of erroneous responses, which can be considered the situations of an unresolved conflict. However, the increase in cognitive control (and its correlates such as increased response latency and FMT power) should be related to all conflict situations rather than just to the unresolved ones. Let us consider two opposite marginal situations. First, let us hypothetically assume that all participant experience high conflict during the same percentage of trials and that they have the same increase in the variable of interest (response latency or FMT power) on these trials. In this case, participants with higher rate of successful conflict resolving will actually have smaller rather than larger difference in the variable of interest (response latency and FMT power) between erroneous and correct trials. That means that the observed negative correlation between the variable difference and the number of errors violates the hypothesis that all participants have the same increase in this variable during the conflict, and allows us to conclude that our interpretation is valid. However, the situation becomes opposite if we hypothetically assume that all participants have the same chance to resolve the conflict but some of them experience conflict more frequently than the others. In this case, participants with fewer errors will have larger difference in the variable of interest between conditions even if they have the same increase in this variable during the conflict. In other words, that will mean that the observed negative correlation between variable difference and the number of errors has purely mathematical but not physiological nature.

Strength of Excitation

Finally, we have a found positive correlation between the relative increase in FMT power before errors compared to correct responses with the Strength of excitation measured with STI questionnaire (Fig. 2B). The possible interpretation of this fact is that both of these variables are related to the ability of the participant to resist the distractions and to keep the optimal task performance. It should be noted that we have found no such correlation with the Strength of inhibition. This can be explained by the fact that our task does not involve the need to suppress automatic responses (as the Stroop task does), so the activity of the cognitive control system was aimed mainly at retention of task rules and the maintenance of task-directed attention rather than to motor inhibition.

Conclusions

In summary, erroneous responses are more likely to be committed during a cognitive state that is presumably caused by the interference between task-related and task-unrelated activity such as mind wandering. Our results suggest that this state is often associated with increased FMT power and increased response latencies. The degree of such increase is positively correlated with task performance, the fact that allows us to conclude that these effects are partly related to the adjustment of cognitive control system; however, the contribution of other mental processes (such as thoughts containing inner conflict) cannot be completely excluded. Between-subject difference in the degree of the effects discussed could be associated with the variations in individual ability to maintain goal-directed behavior in the face of spontaneous attentional drifts. This point of view is further supported by the positive correlation of FMT power increase before errors compared to correct responses with the Strength of excitation, which is defined as the ability to endure arousing environmental influences and to perform the work in stressful conditions [Strelau et al., 1990].

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