NATIONAL RESEARCH UNIVERSITY
HIGHER SCHOOL OF ECONOMICS

Boris V. Chernyshev, Vladimir A. Medvedev

EVENT-RELATED POTENTIAL STUDY OF P2 AND N2 COMPONENTS ON FAST AND SLOW RESPONSES IN THE AUDITORY CONDENSATION TASK

BASIC RESEARCH PROGRAM

WORKING PAPERS

SERIES: PSYCHOLOGY
WP BRP 70/PSY/2016

SERIES: *PSYCHOLOGY*

Boris V. Chernyshev[1], Vladimir A. Medvedev[2]

EVENT-RELATED POTENTIAL STUDY OF P2 AND N2 COMPONENTS ON FAST AND SLOW RESPONSES IN THE AUDITORY CONDENSATION TASK[3]

In tasks involving response choice based on certain stimulus-to-response mappings, at least two stages of information processing may be involved: (1) formation of sensory stimulus object representations leading to stimulus identification, and (2) application of stimulus-to-response mappings (i.e. “task rules”) to these representations leading to response selection. Most of the research done in this area involved simple reflex-like stimulus-to-response mappings, thus addressing mostly the perceptual aspect of decision making. Here we used the condensation task, which involves more complex stimulus-to-response mappings. Within each subject, we divided participants’ responses into four conditions depending upon performance speed and accuracy: fast correct, fast erroneous, slow correct and slow erroneous responses. We compared event-related potentials between these conditions. We found that P2 amplitude was related to performance accuracy, the effect being evident for fast but not for slow responses. N2 amplitude was increased for slow responses – both correct and erroneous. We suggest that fast errors result mostly from erroneous sensory representations that immediately become translated into actions in conditions of low motor threshold. On the contrary, slow responses happen in conditions of low executive attention, through reevaluation of sensory representations and invocation of cognitive control process via the mechanisms of response conflict detection.

JEL Classification: Z

Keywords: auditory perception, cognitive control, attention, response time, event-related potentials, P2, N2.

---

[1] National Research University Higher School of Economics, Laboratory of Cognitive Psychophysiology: Laboratory Head; National Research University Higher School of Economics, Department of Psychophysiology, assistant professor and department head. E-mail: bchernyshev@hse.ru

[2] National Research University Higher School of Economics, Laboratory of Cognitive Psychophysiology: analyst. E-mail: vamedvedev@hse.ru

[3] The study was implemented in the framework of the Basic Research Program at the National Research University Higher School of Economics (HSE) in 2016.

Introduction

Processes that support flexible goal-directed behavior by representing task-relevant information and guiding thought action are collectively termed cognitive control [Botvinick et al., 2001; Yeung, 2014]. Cognitive control is dealing with the balance of two complementary yet opposing mechanisms: maintenance of task-specific attention and maintenance of non-specific motor threshold [Cohen, 2014; Danielmeier and Ullsperger, 2011; Dudschig and Jentzsch, 2009; King et al., 2010; Ridderinkhof, 2002]. Solid experimental evidence suggests that performance errors may be of two different kinds: too low motor threshold may allow commission of premature responses leading to errors that have faster RTs compared with correct responses, while failures of attention lead to a different kind of errors, which have slower RTs compared with correct responses [van Driel et al., 2012]. Correct responses may also involve different mechanisms with slower responses involving reevaluation of the decision [Cohen and van Gaal, 2014].

Performance in many tasks depends upon several consecutive events, involving (1) encoding of sensory information, and (2) application of stimulus-to-response mappings (“task rules”) to these representations leading to response selection. Most of the studies in this field explicitly or implicitly studied decision making as a perceptual decision and thus either focused on perceptual factors (e.g. [Pailing and Segalowitz, 2004; Ratcliff and McKoon, 2008; Shadlen and Newsome, 2001]) or made no distinction between the two stages of information processing (e.g. [Dudschig and Jentzsch, 2009; Ridderinkhof, 2002; Ridderinkhof et al., 2004; van Driel et al., 2012]). Apparently, the tasks used in reports studying cognitive control – such as Simon task, flanker task and sustained-attention-to-response task (SART) – involved simple reflex-like stimulus-to-response mappings, thus indeed putting weight on the perceptual stage; in such tasks implementation of “tasks rules” to the sensory representations did not involve any complex operation to be done over the sensory representations. Thus, little is yet known what is the relative role of the two stages of decision making in the framework of the cognitive control paradigm.

The aim of this study was to distinguish the two stages of decision – formation of sensory representations, and implementation of “task rules”. In order to achieve this aim, we used the condensation task, which is attentionally demanding [Gottwald and Garner, 1975; Posner, 1964]. Most tasks used in cognitive control studies – such as Simon task, flanker task and SART – require overriding or inhibiting a prepotent response, making these tasks very sensitive to the level of motor inhibition [Dudschig and Jentzsch, 2009; Ridderinkhof, 2002; Ridderinkhof et al., 2004; van Driel et al., 2012]; although SART bears the attribute “attentional”, it is related to non-specific vigilance or alertness [O'Connell et al., 2009] rather than to specific forms of attention per se.

Errors in such tasks are mostly failures to inhibit fast automatic responses. Under attentional tasks, at least some errors are committed by the participants as a result of attentional lapses [van Driel et al., 2012; Weissman et al., 2006]. Thus, by using an attentional task we intended to avoid the bias towards fast errors, which is characteristic of tasks used in this research area.

Next, we divided the participants' responses into fast and slow relative to their individual median response time (RT) – expecting thus to selectively study responses committed in one of the two opposing conditions – low nonspecific motor threshold and compromised specific task-related attentional mechanisms.

Following a two-level hypothesis of decisions involving feature binding [Chernyshev et al., 2016], we expected that earlier responses would manifest stronger dependence upon sensory representation quality. Next, we expected that delayed responses would have greater involvement of cognitive control mechanisms.

We chose two distinctive components of the auditory ERPs as correlates of sensory representation formation and cognitive control involvement – P2 and N2 respectively. P2 component is believed to be a correlate of suppression of irrelevant information processing [Alho et al., 1987; Coenen, 2012; Melara et al., 2002], thus it may be used as an indirect measure of quality of sensory representation. N2 component is now generally viewed as a correlate of cognitive control processes – specifically of the response conflict detection [Folstein and Van Petten, 2008; Yeung, 2014].

Methods

Participants

Eighty volunteers participated in the experiment (age 20.0 ± 1.7 years, 21 males). This is an extended participant sample that included the smaller sample of 56 participants reported in our previous study [Chernyshev et al., 2015]. All participants had normal hearing, normal or corrected to normal vision and reported no neurological or mental disorders. The experiments were carried out in accordance with the Declaration of Helsinki and its amendments and were approved by the ethics committee of the National Research University 'Higher School of Economics'. Informed consent was signed by each participant before the experiment. Experiments were conducted in a sound-attenuated chamber.

Materials

Experimental settings. The experiment was performed in a sound-attenuated chamber. Participants were comfortably seated in an encephalographic chair.

Electrophysiological recording. Electroencephalogram (EEG) was recorded with an NVX-52 system (Medical Computer Systems, Russia) with Neocortex Pro software (Neurobotics, Russia) from 27 electrodes following the modified international 10-10% system referred to linked earlobes, with a forehead ground and impedance lower than 10 kΩ in all channels. EEG was recorded with frequency bandpass of 0.5–200 Hz, at sampling rate of 1000 Hz.

Auditory stimulation and experimental procedure. Auditory stimuli were presented to the participants by means of E-Prime software (Psychology Software Tools, Inc., U.S.A.) through a high-quality stereo headset with in-ear design, which additionally reduced ambient noises. Four pre-recorded auditory tones were presented. The stimuli were sinusoidal signals of either 500 Hz (“low”) or 2000 Hz (“high”) – either a pure tone (“pure”) or the same tone with broadband noise admixed to the signal (“noised”). The duration of all stimuli was 40 ms, with rise and fall time 10 ms each, sound pressure level was 95 dB.

Participants made their responses by pressing one of the two buttons of a handheld gamepad. The instruction did not stress the necessity of speeded responses or the necessity of forced random responses in the event of inability to make a reasonable choice. Participants were also informed that after each response they would receive the feedback signal: if they pressed the correct button, a “smiley” schematic sign would be briefly presented on the screen in front of them.

Table 1 specifies the stimulus-to-response mapping involved in the task. High performance within this task required mental conjunction of the two stimulus features. This is a basic characteristic of the condensational task specifically designed to create high attentional load [Gottwald and Garner, 1975; Posner, 1964].

Table 1. Response contingencies in the experimental task: this table was read as well as handed in printed form to the participants before the experiment

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

Before the start of the experiment, participants were made familiar with the stimuli: while the printed table was in front of the subject, all four stimuli were manually played to him/her several times, each one named by the experimenter ("low pure", "low noised" etc.). Then the stimuli were manually repeated without annotations as many times as needed until the participants confirmed that they could easily identify each of them and new what button corresponded to each sound stimulus. Thus all participants explicitly confirmed that they understood the instruction and could follow the stimulus-to-response mapping required.

Two control behavioral series were also run after the main experiment. These series involved discrimination of the same four stimuli by a single feature (pitch and noisiness separately) rather than by the combination of features. This was done in order to ensure that errors were made by participants due to incorrect implementation of "task rules" rather than due to psychophysical discriminability limitations. During control procedures, all participants performed at accuracy level of 98-100%, thus excluding any physical and psychophysical limitations in sound discrimination.

The experiment consisted of 6 experimental blocks. Each block consisted of 100 stimuli of 4 types (see above) interleaved in a random order. The four stimuli were presented with equal probability ratio (1:1:1:1) (figure 1). The stimuli were presented with random stimulus onset asynchrony (SOA) of 2500 ± 500 ms.

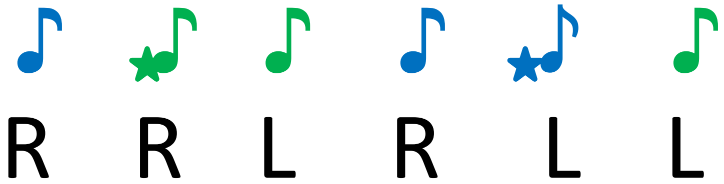

Figure 1. Example fragment of a stimulus sequence and responses required during the experiment: different target stimuli (color notes) of different pitch and with or without admixed noise (notes with stars and notes alone correspondingly), requiring left (L) or right (R) button presses.

Data extraction and analysis

Behavior. We considered two possible behavioral outcomes of each trial: correct responses (pressing the correct button) or erroneous responses (pressing the wrong button); response omissions were rare and such trials were excluded from the analysis.

For each participant, median RT was calculated for all responses pooled together; this measure was used in further analyses to account for the response speed: the responses were classified as 'fast' if RT was smaller than the individual RT median, or 'slow' if RT was greater.

Electroencephalography. The initial experiment block was the training block used for the participants to get acquainted with the task, and it was excluded from the analysis. Thus, for the purpose of EEG analysis, blocks 2 to 6 were taken into account (i.e. 5 blocks). EEG was analyzed by custom-made scripts using internal functions of the EEGLAB toolbox [Delorme and Makeig, 2004] for MATLAB (MathWorks, USA). Major EEG artifacts were manually rejected, and other artifacts including electrooculographic and electromyographic ones were removed with the help of an independent component decomposition (ICA) using custom-made scripts based on internal EEGLAB functions [Delorme and Makeig, 2004].

Event-related potentials (ERPs) were calculated by way of coherent averaging relative to stimulus onset separately for each condition. Zero baseline was adjusted separately for each condition based on prestimulus interval of 250 ms before stimulus onset.

In order to measure ERPs in sufficient and comparable numbers of averaged trials, the following procedure was applied to the data. ERPs were calculated only for those participants, whose recordings contained no less than 12 artifact-free trials of each response type. Thus, the ERP analysis reported here was carried out in a subsample of 40 participants.

ERP component amplitudes were averaged within the following time-spatial regions of interest (ROI): P2 – 125-230 ms; N2 – 230-300 ms, 9 pericentral electrodes (Fc3, Fcz, Fc4, C3, Cz, C4, Cp3, Cpz, Cp4). These time and spatial ROI limits were based on the vast body of literature for P2 [Alho et al., 1987; Coenen, 2012; Crowley and Colrain, 2004; Melara et al., 2002], and N2 [Chernyshev et al., 2013; Folstein and Van Petten, 2008; Nieuwenhuis et al., 2004; Senkowski and Herrmann, 2002; Yeung, 2014], and verified by visual inspection of the ERPs.

Statistical analysis. Two-factor analysis of variance (ANOVA) was used with the following repeated measure factors: “Accuracy” (two levels: correct vs. erroneous) and “Speed” (two levels: fast and slow). *Post hoc* comparisons were made with Fisher least significant difference test (LSD test).

Results

Behavior

In the sample of 80 participants, performance accuracy during five experimental blocks was 85.1 ± 9.7% (mean ± standard deviation). Errors were committed on 10.1 ± 7.6% of trials, and response omissions on 4.8 ± 4.0% of trials. RT of correct responses was 861 ± 282 ms, while RT of erroneous responses was 927 ± 325 ms. Erroneous responses were committed significantly slower than correct ones (paired t-test, $t_{79} = 9.57$, $p < 0.001$).

We included into the analysis reported here only 40 participants that performed at sufficiently high level of accuracy greater than 60%, while their EEG datasets over 5 experimental blocks contained no less than 12 fast erroneous trials and no less than 12 slow erroneous trials. In this subsample of 40 participants, performance accuracy during five experimental blocks was 80.5 ± 7.3%. Errors were committed on 14.0 ± 6.4% of trials, and response omissions were on 5.5 ± 3.7% trials. RT of correct responses was 872 ± 292 ms, and RT of erroneous responses was 932 ± 319 ms. Erroneous responses were committed significantly slower than correct ones (paired t-test, $t_{39} = 6.04$, $p < 0.001$).

Event-related potentials

ERP component morphology. Recordings comprised a typical set of auditory ERP components, including P1, N1, P2, N2, and P3 (figure 2). N1 and P2 were most prominent, with latencies of 100 and 180 ms respectively. N1 and P2 were followed by an N2 component with the latency of 250-280 ms. P3 component was small and lacked a distinct peak, thus not allowing measuring its latency.

P2 component was clearly visible, its spatial distribution had a distinct maximum at Cz - Cpz electrodes (figures 2, 3A). Visual inspection of waveforms (figure 2) indicates that P2 amplitude was greater for both types of errors compared with correct responses. Two-factor repeated measures ANOVA (factors: “Accuracy”, “Speed”) revealed a significant effect of “Accuracy” ($F_{1, 39} = 6.70$, $p = 0.01$) (figures 2, 4A). Factors “Speed” and “Accuracy” x “Speed” interaction were not significant ($p > 0.05$). *Post hoc* tests revealed that the effect of “Accuracy” could be explained mostly by the difference within fast responses ($p = 0.008$) rather than by the difference within slow responses ($p >> 0.05$) (table 2). This can be clearly seen in figure 4A.

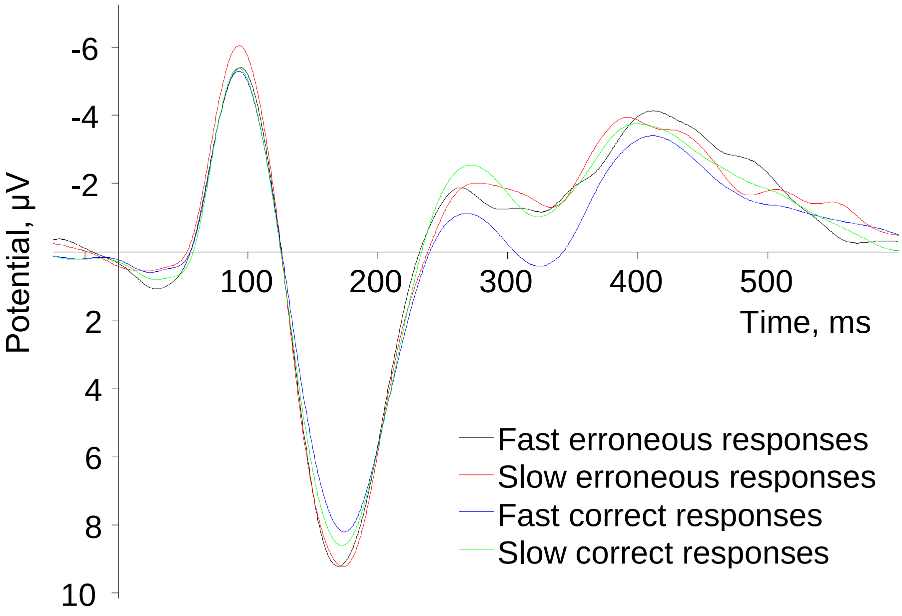

Figure 2. ERP grand mean for the four response types.

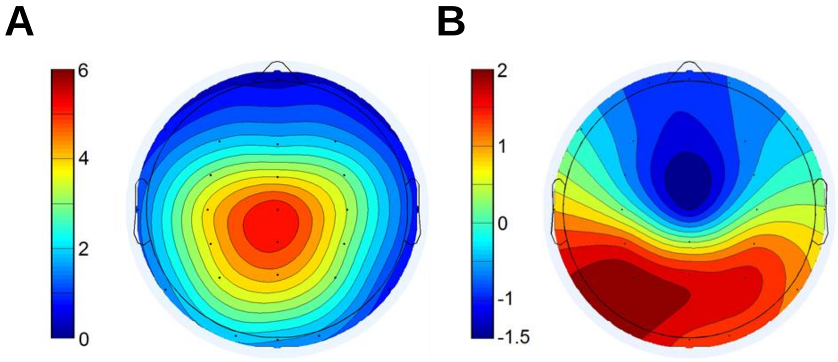

Figure 3. ERP scalp maps for P2 averaged over 125-230 ms (A) and for N2 averaged over 230-300 ms (B). Scale: µV.

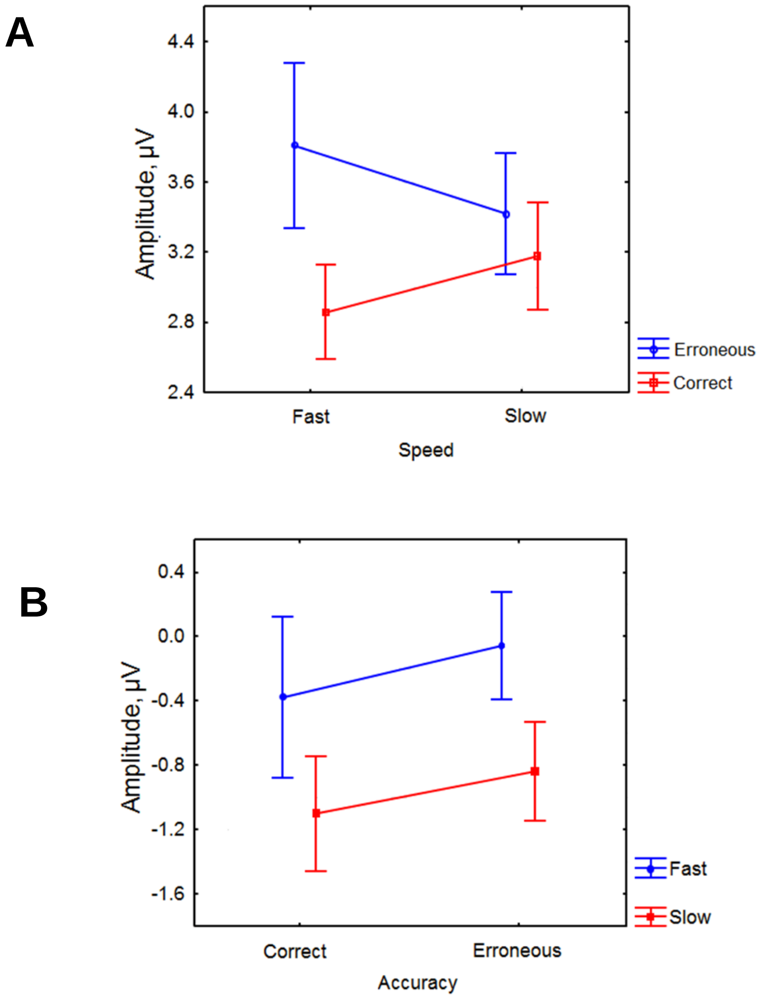

Figure 4. Amplitude of P2 (A) and N2 (B) components at Cz electrode for the four response types (N=40). Data are represented as mean ± standard error of mean.

Table 2. ***Post hoc*** **comparisons of P2 amplitude between conditions**

		1	2	3
1	Fast erroneous responses			
2	Slow erroneous responses	0.26		
3	Fast correct responses	0.008	0.10	
4	Slow correct responses	0.07	0.48	0.35

N2 peak was clearly visible, its spatial distribution had a distinct maximum at Fcz - Cz electrodes (figures 2, 3B). Visual inspection of waveforms (figure 2) indicates that N2 amplitude was greater for slow responses compared with fast responses. Two-factor repeated measures ANOVA (factors: "Accuracy", "Speed") revealed a significant effect of "Speed" factor ($F_{1, 39} = 6.24$, $p = 0.02$) (figures 2, 4B). Neither "Accuracy" factor nor "Accuracy" x "Speed" interaction were significant ($p > 0.05$). *Post hoc* tests revealed that the effect of "Speed" was significant for both correct responses ($p = 0.02$) and erroneous responses ($p = 0.03$) (table 3). Indeed, in figure 4B one can see that the effect is of comparable size for correct and erroneous responses.

Table 3. ***Post hoc*** **comparisons of N2 amplitude between conditions**

		1	2	3
1	Fast erroneous responses			
2	Slow erroneous responses	0.03		
3	Fast correct responses	0.32	0.002	
4	Slow correct responses	0.15	0.41	0.02

Discussion

Behavior

As in other studies using the same or other versions of the condensation task, in the current study participants committed a substantial number of errors while performing the task [Chernyshev et al., 2015; Novikov et al., 2015]. Error rate observed in the current study was even slightly higher than the one observed in the experiments of Dyson and Quinlan [2003], who used a different version of the condensation task: above 10% in the current study compared with 6-8% in the study of Dyson and Quinlan [2003].

Rather high error rate indicates that the task was substantially demanding. This was also evidenced by subjective reports of most of the participants collected after the experiment that the task was difficult and required a lot of effort and concentration to perform it sufficiently well – notwithstanding the fact that intertrial intervals were relatively long (SOA was from 2 to 3 s), thus being among the longest among the auditory ERP experiments. This emphasizes that the real difficulty of the task lay in the process of decision making, which had to be routinely done in a continuous manner.

As in our previous studies using the condensation task, RT was rather long. This confirms our previous data and shows that the condensation task clearly differs from behavioral tasks typically used for studies dealing with the cognitive control – such as Simon task, flanker task and SART task [Dudschig and Jentzsch, 2009; Ridderinkhof, 2002; Ridderinkhof et al., 2004; van Driel et al., 2012].

Erroneous RTs were significantly longer than correct RTs. This is believed to be typical of complex attentional tasks [Cohen and van Gaal, 2013; Dyson and Quinlan, 2003; Luce, 1986; O'Connell et al., 2009; Ratcliff and McKoon, 2008; Wilding, 1971]. Moreover, increased erroneous RT compared to the correct RT is a hallmark of attentional lapses [van Driel et al., 2012; Weissman et al., 2006] and of uncertainty [Navarro-Cebrian et al., 2013; Pailing and Segalowitz, 2004; Wessel et al., 2011]. On the contrary, faster RTs on erroneous trials are typical of tasks that critically depend upon motor threshold [Dudschig and Jentzsch, 2009; Ratcliff and McKoon, 2008; Ridderinkhof, 2002]: in such tasks errors mostly result from premature action impulses, that were implemented into actions as a result of a low motor threshold [van Driel et al., 2012].

Thus, judging from high error rate, from long RTs and specifically from slower RT for erroneous responses compared to correct ones, we confirm that the task used in the present study was attentionally demanding. This stays in line with classical reports describing the condensation task being among the most difficult attentional tasks within a range of behavioral methods available for psychophysiological studies [Gottwald and Garner, 1975; Posner, 1964]. Thus, unlike the tasks with strong dependence on motor threshold, the current task allowed us to study a wider range of error types, including those related to attention – while tasks such as Simon task, flanker task and SART task have a strong bias towards fast errors related to low motor threshold rather than to attention [van Driel et al., 2012].

We included into the ERP analysis all experimental blocks excluding the initial one. Our previous behavioral investigation in the dynamics of behavioral performance under the auditory condensation task indicated that performance accuracy reached plateau after the first block and remained stationary during the following 5 blocks [Lazarev et al., 2014].

Event-related potentials

P2 component was significantly higher before errors compared to correct responses. This confirms our previous result obtained in a smaller sample of participants [Chernyshev et al., 2015]. P2 amplitude is usually inversely related to the intensity of ongoing stimulus processing. P2 is supposed to be related with suppression of irrelevant information processing [Alho et al., 1987; Melara et al., 2002]. Summarizing previous studies, Coenen [2012] proposed that P2 component reflects the inhibitory processes that follow the excitation. Applying this interpretation to the results obtained we assume that increased P2 amplitude for errors is related to impaired stimulus representation.

In the present study, we divided participants' responses into fast and slow ones relative to individual median RTs. This finer analysis revealed that the effect of response accuracy was statistically evident only for fast responses, with no evidence for slow responses. Assuming that increased P2 is related to increased inhibition in the auditory cortex that reduces the quality of stimulus representation, we can infer that the quality of stimulus representation is influencing response accuracy mostly for fast responses, while for slow responses such an influence is reduced. Thus, slow responses may instead involve some other factor influencing accuracy, which has no straight relation with the quality of stimulus representation.

N2 component amplitude was significantly higher for slow responses compared with fast responses. No significant relation between N2 amplitude and accuracy was found. N2 component is currently believed to be related to cognitive control and its subordinate phenomena, such as response inhibition, response conflict and error monitoring; the most strong emphasis was laid on the response conflict [Folstein and Van Petten, 2008; Yeung, 2014].

Thus, data obtained in the present study – increased N2 for slow responses – may find explanation in the literature data on N2. Supposedly, in the current study slower RTs resulted from response conflict – leading to uncertainty in response choice. Uncertainty is indeed known to delay RTs [Navarro-Cebrian et al., 2013; Pailing and Segalowitz, 2004; Wessel et al., 2011]. We have recently obtained a complementary result indicating that frontal midline theta oscillations were increased before slow responses compared with fast responses – using the same distinction between fast and slow responses as in the current report but in a different sample and under a substantially different version of the condensation task [Novikov, Nurislamova, Zhozhikashvili, Kalenkovich, Lapina, Chernyshev, submitted]. Very much as N2, frontal midline theta is known to reflect cognitive control processes related to response conflict and recruitment of the resources needed to overcome motor conflict.

Following Ridderinkhof et al. [2004], we define response conflict as a situation when under conditions requiring choosing from a set of responses a correct response is underdetermined. Importantly, Ridderinkhof et al. [2004] imply close relationship between response conflict defined as stated above, and decision uncertainty.

Thus, our results may be interpreted in the following way that decision uncertainty is related to delayed responses. Generally, such a finding stays well in line with the body of literature [Navarro-Cebrian et al., 2013; Pailing and Segalowitz, 2004; Wessel et al., 2011]. This might be a trivial result if decision uncertainty is understood as a consequence of poor quality of internal stimulus representation; such an attitude towards uncertainty is, for example assumed in the report of Pailing and Segalowitz [2004]. Yet such a simple interpretation apparently contradicts our findings concerning P2 amplitude: we found no relation between P2 amplitude and RT, hinting that the quality of sensory representation affects response accuracy but not response speed. The condensation task used in the current study involves high attentional load [Gottwald and Garner, 1975; Posner, 1964]. Importantly, attention is mostly required to properly apply “task rules” to stimulus representation. This may make a significant difference in the organization of brain processes under the current task compared with less attentionally demanding tasks used in other studies, including the study of Pailing and Segalowitz [2004].

Current findings may be fully accounted for if we assume a two-level model. The earlier level is related to sensory processes that result in integration of stimulus features and formation of an object representation. For auditory stimuli, this happens during the so-called “temporal window of integration” [Horváth et al., 2007; Naatanen et al., 2011] spanning through the first 200 ms after the stimulus onset; P2 component reflects the concluding stage within this time window. The second level is the process of applying “tasks rules” (stimulus-to-response mappings) to the stimuli representation; this can be described in terms of executive functions; notably, the phenomenon of response conflict belongs to this level. A similar two-level organization was recently proposed for decision making involving stimulus conjunctions [Chernyshev et al., 2016]. Importantly, the sensory representation produced as the output of the sensory level is used as an input into the decision making level. Since both levels apparently stay under top-down control, it is also important to find the nature of such top-down control. It may be reasonable to apply the dichotomy between orienting (sensory) and executive attentional systems: both of them have top-down components, but they control two different domains – sensory and executive respectively [Corbetta and Shulman, 2002; Petersen and Posner, 2012].

Applying this assumption to the current data, we can presume the following sequence of brain events:

(1) Sensory representations produced by the sensory level may be incorrect on some trials. Increased P2 is a signature of inhibition in the sensory processing, increasing the likelihood of producing an incorrect sensory representation. Such erroneous representations are believed to result from attentional lapses [van Driel et al., 2012; Weissman et al., 2006]. Specifically, the increase in P2 amplitude was interpreted as a direct sign of attentional lapses [Chernyshev et al., 2015]. Taking into account the considerations above, such attentional lapses should be regarded as failures of sensory attention.

(2) Sensory representations (both correct and incorrect) arrive at the executive level. Apparently, this level may operate in different modes [Cohen, 2014; Danielmeier and Ullsperger, 2011; Dudschig and Jentzsch, 2009; King et al., 2010; Ridderinkhof, 2002; van Driel et al., 2012]. In the state of low motor threshold and high level of executive attention, the sensory representation is immediately converted into action – whether it was correct or not – resulting in fast correct responses and fast erroneous responses. Thus, fast responses strongly depend upon the quality of the sensory representation, which explains our finding that accuracy of fast responses is related with P2 amplitude.

In the opposite state, which is characterized by high motor threshold and low level of executive attention, immediate action impulses cannot be implemented into action. Instead, recurrent reevaluation of sensory representations [Bullier, 2001] may be initiated, leading to the state of uncertainty and response conflict. This well explains why N2 is increased in amplitude for slow responses. Moreover, reevaluation of stimulus representations drastically decreases dependence of response accuracy upon the quality of sensory representations. This well explains why there is little statistical relation between P2 amplitude and accuracy of slow responses. Finally, we should explain the origin of slow erroneous responses: if we assume that sensory representations are reevaluated before slow responses why that does not increase the accuracy of slow responses? To the contrary, errors generally tend to be slow under the current type of task than correct responses – meaning, that slow responses generally include more errors than fast responses. The explanation lies in the nature of attentional lapses themselves (executive attentional lapses in this case). Decreased attention means decreased task-specific processing. Thus it is not surprising that attentional failures lead to increased likelihood of error commission.

Generally, there seems to be a continuous interplay of two complementary mechanisms of cognitive controls – maintaining motor threshold and maintaining attention. The explanation provided here is in line with the current understanding of cognitive control mechanisms [Cohen, 2014; Danielmeier and Ullsperger, 2011; Dudschig and Jentzsch, 2009; King et al., 2010; Ridderinkhof, 2002; van Driel et al., 2012].

Conclusions

In agreement with a two-level hypothesis of decisions involving feature binding [Chernyshev et al., 2016], we evidence here that fast responses had strong dependence on sensory stimulus representation, while cognitive control was less involved at the time of decision making. On the contrary, slow responses involved stronger involvement of cognitive control mechanisms – specifically response conflict detection and processing – that could override the initial sensory discrimination between the stimuli, but involved another kind of errors related to low level of executive attention and compromised implementation of stimulus-to-response mapping rules.

Acknowledgements

The authors are very grateful to Nikita A. Novikov and Evgenii E. Kalenkovich for designing the framework used for the current data analysis. The authors would like to acknowledge the invaluable contribution of Alyona A. Vyazovtseva, Anastasya A. Antonenko, Elena A. Arkhipova and Mark I. Iznyuk in conducting the experiments and data preprocessing.

References

Alho K., Tottola K., Reinikainen K., Sams M., Naatanen R. Brain mechanism of selective listening reflected by event-related potentials // Electroencephalography and clinical neurophysiology. 1987. V. 68. № 6. P. 458-70.

Botvinick M. M., Braver T. S., Barch D. M., Carter C. S., Cohen J. D. Conflict monitoring and cognitive control // Psychological review. 2001. V. 108. № 3. P. 624-52.

Bullier J. Integrated model of visual processing // Brain Research Reviews. 2001. V. 36. № 2-3. P. 96-107.

Chernyshev B. V., Bryzgalov D. V., Lazarev I. E., Chernysheva E. G. Distributed feature binding in the auditory modality: experimental evidence toward reconciliation of opposing views on the basis of mismatch negativity and behavioral measures // Neuroreport. 2016. V. 27. № 11. P. 837-842.

Chernyshev B. V., Lazarev I. E., Bryzgalov D. V., Novikov N. A. Spontaneous attentional performance lapses during the auditory condensation task: An ERP study // Psychology & Neuroscience. 2015. V. 8. № 1. P. 4.

Chernyshev B. V., Lazarev I. E., Chernysheva E. G. Temperament: An event-related potential study using the oddball paradigm // Psychology and Neuroscience. 2013. V. 6. № 3. P. 235-245.

Coenen A. Modelling of auditory evoked potentials of human sleep-wake states // International Journal of Psychophysiology. 2012. V. 85. № 1. P. 37-40.

Cohen M. X. A neural microcircuit for cognitive conflict detection and signaling // Trends in neurosciences. 2014. V. 37. № 9. P. 480-90.

Cohen M. X., van Gaal S. Dynamic interactions between large-scale brain networks predict behavioral adaptation after perceptual errors // Cerebral Cortex. 2013. V. 23. № 5. P. 1061-72.

Cohen M. X., van Gaal S. Subthreshold muscle twitches dissociate oscillatory neural signatures of conflicts from errors // NeuroImage. 2014. V. 86. P. 503-13.

Corbetta M., Shulman G. L. Control of goal-directed and stimulus-driven attention in the brain // Nat Rev Neurosci. 2002. V. 3. № 3. P. 201-15.

Crowley K. E., Colrain I. M. A review of the evidence for P2 being an independent component process: age, sleep and modality // Clin.Neurophysiol. 2004. V. 115. № 4. P. 732-744.

Danielmeier C., Ullsperger M. Post-error adjustments // Frontiers in psychology. 2011. V. 2. P. 233.

Delorme A., Makeig S. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis // J Neurosci Methods. 2004. V. 134. № 1. P. 9-21.

Dudschig C., Jentzsch I. Speeding before and slowing after errors: is it all just strategy? // Brain Research. 2009. V. 1296. P. 56-62.

Dyson B. J., Quinlan P. T. Feature and conjunction processing in the auditory modality // Perception & psychophysics. 2003. V. 65. № 2. P. 254-72.

Folstein J. R., Van Petten C. Influence of cognitive control and mismatch on the N2 component of the ERP: A review // Psychophysiology. 2008. V. 45. № 1. P. 152-170.

Gottwald R. L., Garner W. R. Filtering and Condensation Tasks with Integral and Separable Dimensions // Perception & psychophysics. 1975. V. 18. № 1. P. 26-28.

Horváth J., Czigler I., Winkler I., Teder-Sälejärvi W. A. The temporal window of integration in elderly and young adults // Neurobiol Aging. 2007. V. 28. № 6. P. 964-75.

King J. A., Korb F. M., von Cramon D. Y., Ullsperger M. Post-error behavioral adjustments are facilitated by activation and suppression of task-relevant and task-irrelevant information processing // The Journal of neuroscience : the official journal of the Society for Neuroscience. 2010. V. 30. № 38. P. 12759-69.

Lazarev I. E., Chernyshev B. V., Bryzgalov D. V., Vyazovtseva A. A., Osokina E. S. Investigation of the automation of decision making under conditions of mid-high cognitive load // Vestnik YarGU. Seriya Gumanitarnyye Nauki. 2014. V. 2. № 28. P. 87-91 [In Russian: Лазарев И. Е., Чернышев Б. В., Брызгалов Д. В., Вязовцева А. А., Осокина Е. С. Исследование автоматизации принятия решения в условиях умеренно высокой когнитивной нагрузки // Вестник ЯрГУ. Серия Гуманитарные науки. 2014. Т. 2. № 28. С. 87-91.].

Luce R. D. Response times: their role in inferring elementary mental organization. New York - Oxford: Oxford University Press; Clarendon Press, 1986. 562 с.

Melara R. D., Rao A., Tong Y. The duality of selection: excitatory and inhibitory processes in auditory selective attention // Journal of experimental psychology. Human perception and performance. 2002. V. 28. № 2. P. 279-306.

Naatanen R., Kujala T., Winkler I. Auditory processing that leads to conscious perception: A unique window to central auditory processing opened by the mismatch negativity and related responses // Psychophysiology. 2011. V. 48. № 1. P. 4-22.

Navarro-Cebrian A., Knight R. T., Kayser A. S. Error-monitoring and post-error compensations: dissociation between perceptual failures and motor errors with and without awareness // The Journal of neuroscience : the official journal of the Society for Neuroscience. 2013. V. 33. № 30. P. 12375-83.

Nieuwenhuis S., Yeung N., Cohen J. D. Stimulus modality, perceptual overlap, and the go/no-go N2 // Psychophysiology. 2004. V. 41. № 1. P. 157-160.

Novikov N. A., Bryzgalov D. V., Chernyshev B. V. Theta and Alpha Band Modulations Reflect Error-Related Adjustments in the Auditory Condensation Task // Front Hum Neurosci. 2015. V. 9. P. 673.

O'Connell R. G., Dockree P. M., Robertson I. H., Bellgrove M. A., Foxe J. J., Kelly S. P. Uncovering the neural signature of lapsing attention: electrophysiological signals predict errors up to 20 s before they occur // The Journal of neuroscience : the official journal of the Society for Neuroscience. 2009. V. 29. № 26. P. 8604-11.

Pailing P. E., Segalowitz S. J. The effects of uncertainty in error monitoring on associated ERPs // Brain and cognition. 2004. V. 56. № 2. P. 215-33.

Petersen S. E., Posner M. I. The attention system of the human brain: 20 years after // Annual review of neuroscience. 2012. V. 35. P. 73-89.

Posner M. I. Information Reduction in the Analysis of Sequential Tasks // Psychological review. 1964. V. 71. № 6. P. 491-504.

Ratcliff R., McKoon G. The diffusion decision model: theory and data for two-choice decision tasks // Neural Comput. 2008. V. 20. № 4. P. 873-922.

Ridderinkhof K. R. Micro- and macro-adjustments of task set: activation and suppression in conflict tasks // Psychological research. 2002. V. 66. № 4. P. 312-23.

Ridderinkhof K. R., Ullsperger M., Crone E. A., Nieuwenhuis S. The role of the medial frontal cortex in cognitive control // Science. 2004. V. 306. № 5695. P. 443-7.

Ridderinkhof K. R., van den Wildenberg W. P., Segalowitz S. J., Carter C. S. Neurocognitive mechanisms of cognitive control: the role of prefrontal cortex in action selection, response inhibition, performance monitoring, and reward-based learning // Brain and cognition. 2004. V. 56. № 2. P. 129-40.

Senkowski D., Herrmann C. S. Effects of task difficulty on evoked gamma activity and ERPs in a visual discrimination task // Clin.Neurophysiol. 2002. V. 113. № 11. P. 1742-1753.

Shadlen M. N., Newsome W. T. Neural basis of a perceptual decision in the parietal cortex (area LIP) of the rhesus monkey // Journal of Neurophysiology. 2001. V. 86. № 4. P. 1916-36.

van Driel J., Ridderinkhof K. R., Cohen M. X. Not all errors are alike: theta and alpha EEG dynamics relate to differences in error-processing dynamics // The Journal of neuroscience : the official journal of the Society for Neuroscience. 2012. V. 32. № 47. P. 16795-806.

Weissman D. H., Roberts K. C., Visscher K. M., Woldorff M. G. The neural bases of momentary lapses in attention // Nature neuroscience. 2006. V. 9. № 7. P. 971-8.

Wessel J. R., Danielmeier C., Ullsperger M. Error awareness revisited: accumulation of multimodal evidence from central and autonomic nervous systems // Journal of cognitive neuroscience. 2011. V. 23. № 10. P. 3021-36.

Wilding J. M. The relation between latency and accuracy in the identification of visual stimuli. I. The effects of task difficulty // Acta Psychol (Amst). 1971. V. 35. № 5. P. 378-98.

Yeung N. Conflict Monitoring and Cognitive Control // The Oxford Handbook of Cognitive Neuroscience: The Cutting Edges / Ochsner K. N., Kosslyn S. Oxford: Oxford University Press, 2014. C. 275–299.

Contact details and disclaimer:

Boris V. Chernyshev

National Research University Higher School of Economics, Laboratory of Cognitive Psychophysiology: Laboratory Head; National Research University Higher School of Economics, Department of Psychophysiology, Department Head and Assistant Professor.

E-mail: bchernyshev@hse.ru