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The nature of interrelations of brain event-related potentials to behavioral measures and temperament dimensions was studied in the situation of attention under the auditory oddball paradigm. Several components of event-related potentials were found to be related to Extraversion, Mobility, Ergonicity and Emotionality. The results are discussed within the framework of the resource model of attention. New putative internal dimensions of temperament are suggested. The data obtained lay the foundation for further psychophysiological studies of attention in the context of individual differences.

Keywords: cognitive processes, attention, temperament, personality, electroencephalogram, event-related potentials.

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Introduction

Attention serves to select appropriate sources of information for detailed mental processing, and thus it often appears to be an integral part of other basic mental processes such as perception, thinking, memory, consciousness, etc. [Vygotsky, 1991; Gippenreiter, 2005; Rubinshtein, 2005]. Although attention has already been studied by many generations of psychologist, in psychology there is still no generally accepted definition of attention [Falikman, 2006]. The internal functional structure of attention and corresponding brain processes are in the focus of increasing interest in the field of psychophysiology [Machinskaya, 2003].

According to D. Kahneman's resource theory, attention can be viewed as a limited resource shared between ongoing mental processes [Kahneman, 1973]. The amount of available resources depends upon the level of activation, which in turn is determined by a number of factors of both external and internal nature [Kahneman, 1973; Shneider, Shiffrin, 1977]. In addition to activation aspect of attention, which stresses the intensity (i.e. power) of processes and which is traditionally referred to in resource theories, there probably exists a temporal aspect of attention. The existence of a temporal aspect is logical to expect, since the process of evaluation of required resources and the following process of distribution of these resources, postulated in resource theory, must actually be represented by computational processes, which need time to be executed. Moreover, these processes should take up some share of computational brain resources from some big but not unlimited pool (one may expect that this pool does not overlap with the pool of attentional resources per se). The temporal aspect of the processes of attentional resource allocation must be most critical in tasks requiring immediate decision after presentation of a stimulus (such as oddball, Go/NoGo etc).

Although currently it is not possible to find an unequivocal correspondence between the elements of D.Kahneman's conceptual scheme and brain processes, the resource theory may become a promising theoretical paradigm for physiological and psychophysiological studies of attention. Studies in animals allowed to propose the physiological nature of the attentional resource allocation mechanism and to demonstrate that this process is controlled by certain neuromodulatory systems – especially by the cholinergic system [Chernyshev et al., 2005; Börgers et al., 2005; Sarter et al., 2006; Yu, Dayan, 2002; Everitt, Robbins, 1997; Woolf, Butcher, 2011].

As an indirect measure of a relatively stable internal level of activation and temporal characteristics of mental process it is possible to use temperament. Temperament is viewed by most authors as a totality of biologically determined and stable characteristics that shape intensity and temporal aspects of behaviour and mental processes [Eysenck, 1970; Rusalov,

2002; Strelau et al., 2005]. Thus in the description of temperament the same two aspects are used – intensity and temporal – that are important for the analysis of the processes of attention. Moreover, there are some hints that individual differences in temperament may be explained through variations in functioning of a number of neuromediator brain systems [Bond, 2001; Mulder, 1992], which seem to be also implicated in attentional brain systems. Thus the study of attention in the context of temperament may be a valid way towards psychophysiological analysis of temperament.

A promising way of studying brain functioning is recording gross electrical activity of the brain in relation to external events – the so-called event-related potentials (ERP). ERPs proved to be a very informative method for studying attention: it is well known that the pattern of ERPs in response to events that attract attention clearly differs from those to ignored events. A number of long-latency ERP component, which are generated in sensory and association cortices, are either modulated by attention (including N1 and P2) or appear exclusively when a stimulus attracts attention – both voluntary and involuntary (including N2 and P3) [Gnezditskiy, 1997; Donchin, Coles, 1988; Ivanitsky, 1976; Näätänen 1992; Patel, Azzam, 2005; Polich, 2007; Rutman, 1979].

In a very simple but widely used experimental task – the so-called oddball paradigm – the participant is presented with two stimuli differing in some sensory characteristic (pitch of a tone, outlines of a geometrical shape, etc.). One of the stimuli (rare, target, significant) is presented relatively less frequently than the other (frequent, non-target, insignificant). A participant should make some response – either covert (such as silent counting) or overt (such as pressing a button) – to a rare target stimulus. The other stimulus does not require a response. In such a task ERPs to target and non-target stimuli differ greatly [Gnezditskiy, 1997].

Auditory N1 and P2 represent mostly exogenous processes, i.e. they generally reflect physical stimulus attributes. In auditory modality both waves usually have a central amplitude maximum distribution, and both are at least partially a result of information processing with the auditory cortex [Coles, Rugg, 1995; Näätänen, Picton, 1987]. Although under the oddball paradigm N1 and P2 are generated equally to both target and non-target stimuli, N1 still can be modulated by attention [Hillyard et al., 1973].

Under the oddball paradigm, N2 and P3 waves are generated only in response to the target stimulus. N2 wave, known also as N200, peaks within 180-350 ms after stimulus onset. N2 is classified by some authors into a number of different subcomponents. Classical subcomponents N2b and N2c are generated under conditions of mismatch of the presented stimulus with the expected one and also under conditions of stimulus classification respectively [Folstein, Van Petten, 2008; Patel, Azzam, 2005]. For auditory modality both components have frontocentral distribution over the scalp surface and are very similar. Functional role of N2 is not

yet settled in literature, which may be a consequence of its heterogeneous composition and a diversity of attentional tasks used. On the whole, one can accept that N2 reflects different aspects of stimulus identification [Gnezditskiy, 1997; Czigler, Csibra, 1992] – mostly in the aspect of mismatch of the current stimulus with the one that was expected [Patel, Azzam, 2005], although currently N2 component has also been associated with cognitive control [Folstein, Van Petten, 2008].

P3, or P300, usually follows N2 and peaks between 250 and 500 ms and sometimes later. P3 is not homogeneous, and at least two its main subcomponents are known. P3a subcomponent, which is mostly pronounced in frontal locations, has been associated with passive (involuntary) attention and is often viewed as a correlate of orienting response to a new unexpected stimulus [Näätänen 1992; Polich, 2007; Squires et al., 1975; Yamaguchi, Knight, 1991].

P3b subcomponent, most prominent in frontoparietal sites, has generally more caudal distribution than P3a and arises under active (voluntary) attention to relevant stimuli that require covert or overt response under conscious control [Näätänen, 1992; Rockstroh et al., 1982; Polich, 2007]. Generally accepted is a hypothesis of E. Donchin that P3 reflects the process of context updating, i.e. reformulation of a prognosis, of an internal model of the external world [Donchin, Coles, 1988]. There are also other theories associating P3 with expectancy, memory and other mental phenomena. According to the point of view of A.M. Ivantisky [1976], P3 wave is associated with the detection of significance of stimulus on the basis of the previous experience.

Currently there are relatively few reports linking ERPs with individual differences in personality and temperament domains. In a Go/NoGo task it was shown that N2 amplitude was positively correlated with anxiety, while P3 amplitude was reduced in those participants who reported greater number of cognitive failures [Righi et al., 2009]. P3 amplitude was found to be generally smaller in introverts compared to extraverts [Cahill, Polish, 1992]. With the help of the oddball task it was demonstrated that P3 amplitude negatively correlates with neuroticism and positively – with extraversion [Gurrera et al., 2005]. It has also been shown that in psychopathic personalities N2 amplitude is increased and P3 amplitude is decreased [Kiehl et al., 2006], and P3 amplitude is higher in individuals less prone to domination [Pavlenko, Konareva, 2000]. Earlier we have shown that high plasticity and tempo scores are related with lower N2 amplitude and earlier N2 and P3 latencies, and that neuroticism and emotionality are positively related to the duration of N2-P3 complex [Chernyshev et al., 2010; Chernyshev et al., 2011].

There are relatively few studies linking N1 and P2 components with temperament and personality. N1 and N1-P2 were found to be related to such dimensions as sensation-seeking, extraversion and neuroticism [Doucet, Stelmack, 2000; Hegerl et al., 1995; Philipova, 2008].

Thus it is now clear that the brain processes associated with attention depend upon individual personality characteristics, but there is still no agreement on the pattern of this dependency and on its psychophysiological basis.

The aim of the current study was to find the pattern of statistical relations between ERPs on the one side, and temperament dimensions, together with behavioral measures of successfulness of attentional performance, on the other side, with emphasis on the dynamics of attentional processes (from preattention to attention) in two aspects – intensity and temporal.

Methods

The study was performed in 30 university students aged 18-27 years (20 females and 10 males, including 26 right-handed, 1 left-handed and 3 ambidexter persons). All participants had normal hearing and reported no history of auditory, neurological or mental illness.

On the day of the experiment all participants completed 3 questionnaires: Eysenck Personality Inventory (EPI) [Eysenck, 1982; Shmelyov, 2002], Pavlovian Temperament Survey (PTS) [Strelau et al., 1999], and Structure of Temperament Questionnaire (STQ) [Rusalov, 1990, 2002]. The following temperament dimensions were assayed: Extraversion (EPI1), Neuroticism (EPI2), Strength of excitation (PTS1), Strength of inhibition (PTS2), Mobility of nervous processes (PTS3), Object-related ergonicity (STQ1), Social-related ergonicity (STQ2), Object-related plasticity (STQ3), Social-related plasticity (STQ4), Object-related tempo (STQ5), Social-related tempo (STQ6), Object-related emotionality (STQ7), Social-related emotionality (STQ8). Besides, Strength of excitation to strength of inhibition ratio (EIR) was calculated as follows:

$$EIR = \frac{PTS1}{PTS2}$$

The experiments were performed in a quiet room; participants were comfortably seated in an encephalographic chair with a headrest and armrests. Tonal auditory stimuli were presented to the participants through loudspeakers located directly in front of them approximately at their chest level. The stimuli were presented in quasirandom order according to the oddball paradigm, with target to non-target probability ratio of 1:4 (with no target stimuli standing in direct succession). Participants were instructed to press a button of a miniature gamepad in response to the rare target stimulus, which was higher in pitch. Target stimulus was a 1050 Hz tone, non-target – 1000 Hz. Both stimuli were pure sinusoidal tones. The length of both stimuli was 40 ms, rise and fall time 10 ms each, loudness near participant head approximately 85 dB. The series

included 250 stimuli (50 target and 200 non-target) with a random intertrial interval 2500 ± 500 ms. Stimuli were presented via "Neostimul" software (Neurobotics, Russia).

Behavioral data outcome of each trial recorded automatically could be one of the following: correct response to the target stimulus, false alarm to the non-target stimulus (erroneous pressing the button when one shouldn't), response omissions (erroneous failure to press the button when one should), and correct rejections to non-target stimulus. Latencies of correct responses were automatically detected, and mean latencies as well dispersion (average standard deviation) of latencies within each participant were calculated with the internal function of Neocortex Pro software (see below).

Electroencephalogram (EEG) was recorded with NVX-52 system (Medical Computer Systems, Russia) with Neocortex Pro software (Neurobotics, Russia) from 32 symmetrical electrodes in accordance with the international 10-10% system and 1 electrooculogram electrode. Electrode impedance was kept below 10 k Ω for all channels. EEG data were digitally recorded at 2000 kHz sampling rate and stored on the hard disk for further analysis. Analysis reported here was performed on 15 pericentral electrodes (F3, Fz, F4, Fc3, Fcz, Fc4, C3, Cz, C4, Cp3, Cpz, Cp4, P3, Pz, P4). EEG artifacts were manually rejected, and electrooculographic artifacts were corrected with internal Neocortex Pro software function based on regression approach. The data were post hoc filtered with 1 Hz high-pass and 30 Hz low-pass using fast Fourier transformation, which does not affect signal phase. Evoked activity was calculated by way of coherent averaging of target trials. Zero line was adjusted separately for each record based on prestimulus interval of 250 ms before stimulus onset.

Event-related potential (ERP) peaks were manually marked in averaged ERP recordings in each electrode separately with internal function of Neocortex Pro software as most negative and most positive potential deflections (for positive and negative ERP components correspondingly) in the following time ranges: N1 — 50-120 ms, P2 — 120-260 ms, N2 — 190-310 ms, P3 — 250-530 ms. Peak amplitudes and latencies were measured from zero line, as well as peak-to-peak for N1-P2 and N2-P3 complexes.

Statistical relations between questionnaires data, as well as between questionnaires data and behavioral data, were tested with nonparametric Spearman correlation. No additional verification (see below) was implemented, since these analyses bear an auxiliary role needed for the interpretation of ERP results.

Statistical analyses of ERP data and their relations to questionnaire data were performed with the help of the general linear model (GLM). Two repeated measures factors were used: Rostrality (5 levels: F, Fc, C, Cp, P) and Laterality (3 levels: left side, central line and right side); questionnaire and behavioral data were separately taken into analysis as covariates.

Since the purpose of this paper is to explore the relations between temperament and ERP measures and a large number of data vectors were simultaneously analyzed, in order to preclude false positive null hypothesis rejection due to the nature of multiple hypotheses testing, we used the following statistical procedure. For those cases where general linear model indicated significant relation between questionnaire data and ERP data ($p < 0.05$), the whole analysis was repeated 30 more times according to the number of participants, each time in 29 remaining participants excluding one participant data one by one, with subsequent return (as a simplified version of jackknifing approach [Wu, 1986]). Unless otherwise specified, relations between questionnaire data and ERP data were considered valid only if all repetitions of the analysis produced significance of $p < 0.05$ (on an exceptional basis only one repetition with the significance of $p < 0.10$ was allowed). As a measure of additional verification, each analysis producing significant results was supplemented with a nonparametric Spearman correlation between ERP parameters on the one side, and behavioral data and questionnaire data on the other side. ERP data reported here passed both verification procedures, unless stated otherwise.

Data are presented as mean \pm standard error of mean unless otherwise specified. Significance levels reported are rounded to the first non-zero high-order digit.

Results

Since the main purpose of this report was to study ERPs as correlates of preattention and attention in the framework of individual temperament differences, the Results section is organized in two different parts. In the first subsections we describe statistical nature of the data, and analyze correlations within questionnaire data, between behavioral and questionnaire data, and within ERP data. Only significant correlations ($p < 0.05$) are reported; exact significance levels are given in tables. Due to the nature of multiple hypotheses testing, these sections may contain cases of false null-hypothesis rejection. These subsections are intended only to describe the nature of the data and to reveal correlations between them; these subsections play exclusively an auxiliary role needed for interpretation of the remaining part of results. Analysis presented in the final subsection of Results section involves a number of additional statistical verification procedures intended to avoid false null-hypothesis rejection.

Questionnaire data

Summary questionnaire data statistics are given in Tab. 1 in Appendix. Before examining the relationships between behaviour, ERP parameters and individual characteristics of temperament, it was necessary to determine the relations between different temperament dimensions. The results of correlation analysis are given in Tab. 2 in Appendix, where exact correlation coefficients and significance levels are shown.

No significant correlation between the two scores of Eysenck Personality Inventory (EPI) – extraversion and neuroticism – was present.

Extraversion manifested highly significant positive correlation with Mobility of nervous processes. No correlation between Extraversion and Strength of excitation was detected.

Numerous positive correlations between Extraversion and Structure of Temperament Questionnaire (STQ) dimensions were found, including 3 social ones: Social-related ergonicity, Social-related plasticity, and Social-related tempo, as well as one object-related dimension – Object-related tempo. Extraversion was also positively correlated with Strength of excitation to strength of inhibition ratio. Thus Extraversion was found to be positively correlated both with intensity and temporal aspects of temperament.

Neuroticism was positively correlated with both Object-related and Social-related emotionality.

Predictably, within the block of Pavlovian Temperament Survey (PTS), a significant positive correlation between Strength of excitation and Mobility of nervous processes was found.

Strength of excitation was positively correlated with Object-related ergonicity, and, due to the method of its calculation, it was also positively correlated with Strength of excitation to strength of inhibition ratio. Strength of excitation did not significantly correlate with Object-related plasticity and Object-related tempo.

Strength of inhibition manifested negative correlations with Social-related plasticity and Social-related tempo, and also, due to the method of its calculation, negative correlation with Strength of excitation to strength of inhibition ratio. We did not find two other correlations, reported by V.M. Rusalov [1997], who, in addition to the correlations reported here, found Strength of inhibition to be positively correlated with Object-related ergonicity and negatively correlated with Object-related emotionality.

Mobility of nervous processes had positive correlations with Object-related plasticity, Object-related tempo and Social-related tempo, as well as a positive correlation with Strength of excitation to strength of inhibition ratio.

Within the STQ block a large number of significant correlations were found (all positive). Object-related ergonicity positively correlated with social-related ergonicity. Social-related ergonicity manifested positive correlations with Social-related plasticity and Object-related tempo. The STQ temporal dimensions of temperament – Plasticity and Tempo – both in object-related and social-related aspects were correlated with each other (with the exception of the pair of Object-related and Social-related tempo) and formed a distinct separate block of dimensions. All four dimensions were also positively correlated with Strength of excitation to strength of inhibition ratio.

Two dimensions of emotionality – Object-related and Social-related emotionality – were strongly positively tied together.

Behavioral data and their relations to questionnaire data

All participants were successful at fulfilling the demands of the oddball task. As can be seen from Tab. 3 in Appendix, the number of false alarms (incorrect responses to non-target stimuli) did not exceed 1.5% of the total number of responses to non-target stimuli, while the average was only 0.27%. The majority of participants (22 out of 30, 73.3%) committed no false alarms at all. The average number of response omissions to target stimuli was 4.7%. A large number of participants (13 out of 33, 43.3%) did not commit a single omission, including the 9 participants who committed no errors of any kind (9 out of 30, 30%).

Mean latency of correct responses to target stimuli was 725.8 ± 65.1 ms. The latency of correct responses was quite stable within participants: dispersion (average standard deviation) of the latency, calculated separately for each participant, was only 22.9 ± 1.4 ms.

Among behavioral data only latency and within-participant latency dispersion were correlated with questionnaire data (see Tab. 4 in Appendix for exact correlation coefficients and significance levels).

Social-related ergonicity manifested positive correlation with latency of correct responses. On the other part, this same temperament dimension was negatively correlated with latency dispersion. Thus the higher was Social-related ergonicity, the later but the more stable in time were correct responses.

Two temporal dimensions of temperament – Mobility of neural processes and Social-related plasticity – manifested negative correlations with latency dispersion. Thus the higher were these temporal characteristics of temperament, the more stable were latencies of correct responses within participants.

ERP parameters and interrelations between them

ERP grand-average in response to target stimuli and ERP scalp maps are shown in Fig. 1. Tab. 5 in Appendix contains summary ERP data. As can be seen from Fig. 1, all peaks and peak complexes studied had almost symmetrical frontocentral distribution with amplitude maximums at Fz (N2), Fcz (N1, N1-P2, P3, N2-P3), and Cz (P2). Thus all of the waves and wave complexes studied had at Fcz a maximum or near-maximum amplitude. For illustrational purposes, ERP data are presented in figures at Fcz and Fz.

Multiple correlations were found within ERP data (see Tab. 6 in Appendix for exact correlation coefficients and significance levels).

Most of the obvious and expected correlations between peak complexes and their constituent peaks were present in the correlation matrix with one important exception: N1-P2 complex duration did not correlate with N1 latency. This may mean that the processes which lead to generation of N1-P2 complex do not depend upon the history of events preceding N1. Still, N1 and P2 latencies were weakly positively correlated ($p=0.05$, not shown in Tab. 6 in Appendix). Latencies of P2 and N2 were also found to be positively correlated.

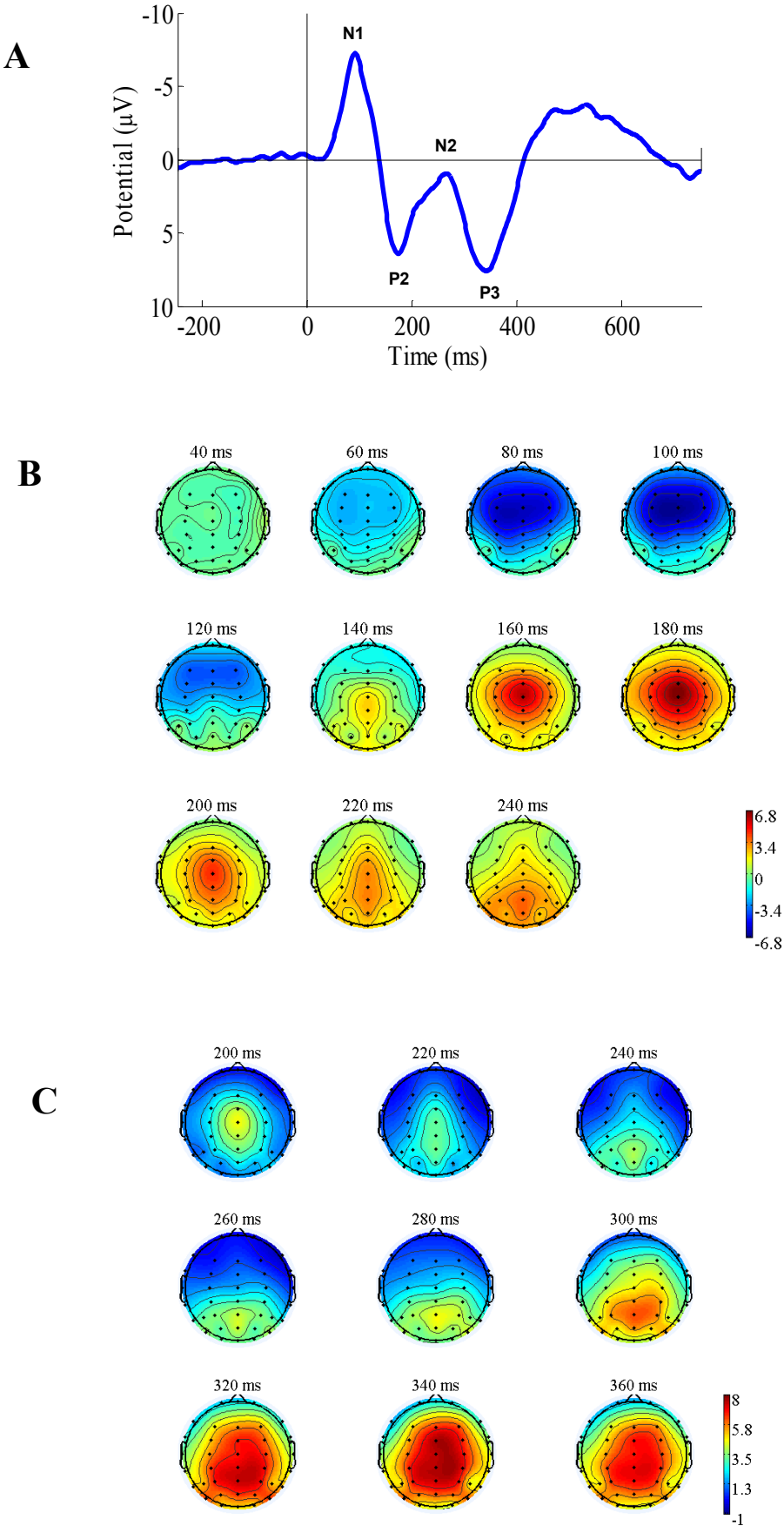
Duration of N2-P3 complex was negatively correlated with both P2 amplitude and P2 latency (the earlier and smaller was P2, the longer was N2-P3 complex duration). Also N2-P3 complex duration was found to be negatively correlated with N2 amplitude (the more negative, i.e. more pronounced was N2 peak, the longer was N2-P3 complex duration).

P3 latency was found to be negatively correlated with both N2 amplitude and P3 amplitude (the more negative, i.e. more pronounced was N2 peak and the less pronounced, i.e. less positive was P3 peak, the later was P3).

Relations of ERP parameters with behavioral and questionnaire data

General linear model (GLM) was used in order to reveal statistical relations between ERPs on one side and behavioral and questionnaire data on the other side. In each of the analyses behavioral and questionnaire data were introduced as a covariate, one at a time, with two repeated measures factors: Rostrality (5 levels) and Laterality (3 levels); see Methods section for greater details.

Fig. 1. ERP grand mean (30 participants). A – ERP grand mean recorded at Fz. B – ERP scalp maps at 40 – 240 ms, showing N1 and P2. C – ERP scalp maps at 200 – 360 ms, showing N2 and P3. Scale: μV



For the purpose of verification of the results of GLM analyses, two additional statistical procedures were used – multiple repetition of each analysis with exclusion of all participants one by one and nonparametric Spearman correlation. Data reported below are those that were confirmed by both procedures (unless specified otherwise).

First significant behavioral data will be presented, and then significant temperament questionnaire data.

The number of response omissions to the target stimulus was negatively related to P3 amplitude ($F(1,28)=7.99$, $p=0.009$; $R(28)=-0.51$, $p=0.004$) (Fig. 2A); i.e. the more often participants erroneously missed the response to the target stimulus, the less pronounced was P3 wave, while good attentive performance was associated with higher P3 amplitude (Fig. 3A).

Dispersion of latencies was related to three ERP parameters (Fig. 2B). Firstly, dispersion of latencies was negatively linked to N2 amplitude ($F(1,28)=7.70$, $p=0.01$; $R(28)=-0.43$, $p=0.02$): the more negative (more pronounced in absolute amplitude) was N2 peak, the greater was dispersion of latencies (Fig. 3B). In other words, stable responses were more likely to be observed in individuals with poorly manifested N2 peak. Secondly, dispersion of latencies was positively linked to N2 latency ($F(1,28)=6.30$, $p=0.02$, $R=0.48$, $p=0.007$) (Fig. 3C). Thirdly, dispersion of latencies was positively linked to P3 latency ($F(1,28)=5.86$, $p=0.02$; $R=0.44$, $p=0.01$) (Fig. 3D). Thus the later were N2 and P3 peaks, the greater was dispersion of response latencies. In other words, stable responses were most often observed in individuals who's N2 was early and small, and P3 was early.

No behavioral data manifested any statistically significant relation to N1 and P2 peaks.

Two temperament questionnaire dimensions – Extraversion and Mobility of nervous processes – manifested significant negative relation to the amplitude of N1-P2 complex ($F(1,28)=8.80$, $p=0.006$, $R=-0.53$, $p=0.003$ and $F(1,28)=8.50$, $p=0.007$, $R=-0.44$, $p=0.02$ accordingly) (Fig. 2C and D). In other words, the higher were individual's Extraversion and Mobility of nervous processes, the smaller was N1-P2 complex (Fig. 3E and F).

Of N1-P2 complex constituents, only N1 amplitude manifested the same significant relation to Mobility of nervous processes ($F(1,28)=6.50$, $p=0.02$, $R=0.37$, $p=0.04$) (Fig. 3H), that was confirmed with the help of the two statistical methods as described above. N1 amplitude also had a similar weaker relation to Extraversion ($F(1,28)=4.96$, $p=0.03$, $R=0.46$, $p=0.01$), but it was not confirmed by a series repetitions of the analysis with exclusion of participants (only 27 out of 30 repetitions were significant) (Fig. 3G). Thus according to the criteria set above this result may be regarded as a tendency rather than a statistically significant observation.

P2 amplitude did not show any significant relations to the abovementioned temperament dimensions at all. Altogether, it is likely that relation of Extraversion and Mobility of nervous

Fig. 2. ERP grand means recorded at Fcz in 30 participants divided in two groups according to the medians the following behavioral and questionnaire scores: **A** – percentage of response omissions, **B** – dispersion of response latencies, **C** – Extraversion (EPI1), **D** – Mobility of nervous processes (PTS3), **E** – Object-related emotionality (STQ7), **F** – Social-related ergonicity (STQ2).

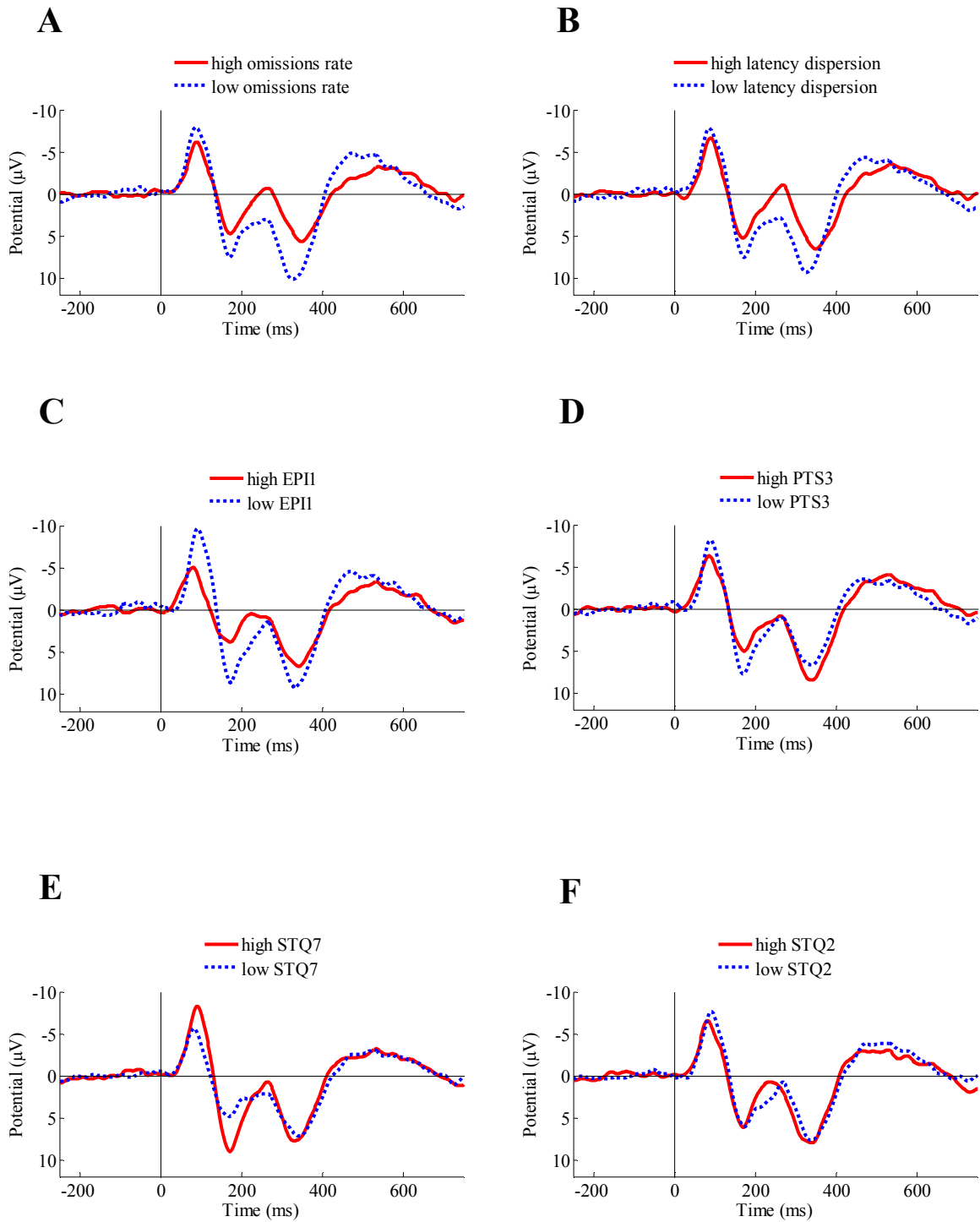
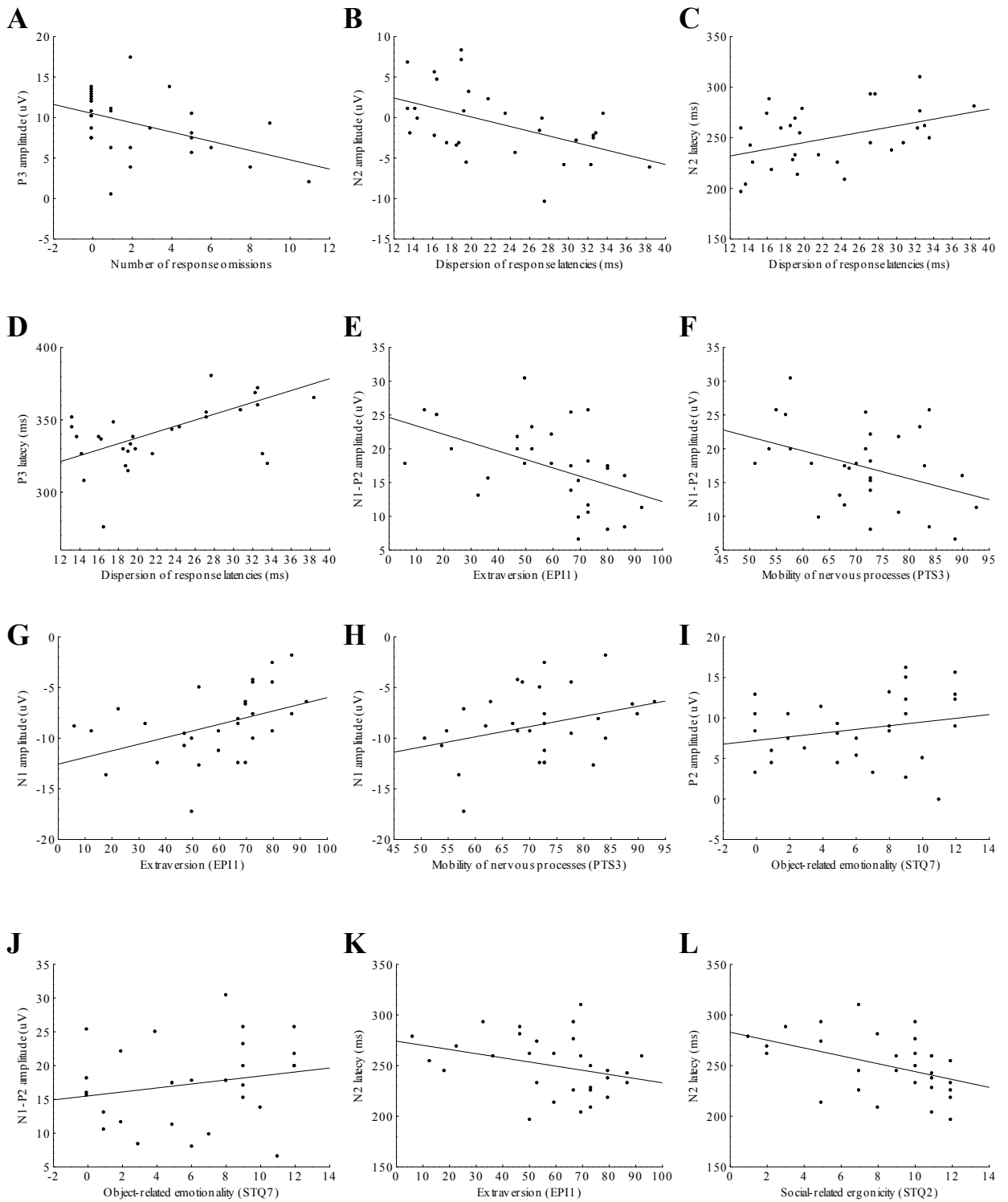


Fig. 3. Scatterplots and regression lines of behavioral and ERP data vs. ERP parameters (30 participants)



processes to N1-P2 amplitude may arise mainly due to N1 rather P2 amplitude variation, but the amplitude of the complex seems to be more valid predictor of the abovementioned temperament dimensions than N1 alone. As one can see from ERPs in Fig. 2C, P3 wave was apparently greater in amplitude in participants with low compared to high Extraversion, but statistical analysis did not confirm this observation.

Object-related emotionality manifested positive relation to two ERP parameters: P2 amplitude ($F(1,28)=7.72$, $p=0.01$, $R=0.46$, $p=0.01$) and amplitude of N1-P2 complex ($F(1,28)=7.68$, $p=0.01$, $R=0.48$, $p=0.007$) (Fig. 2E). Thus the higher was Object-related emotionality, the more robustly pronounced were P2 and N1-P2 complex (Fig. 3I and J). N1 peak seemingly was not related to emotionality.

Other temperament dimensions, correlated with Object-related emotionality – namely Neuroticism and Social-related emotionality – did not produce verified significance in this analysis. Neuroticism was very far from significance and thus seems to be completely unrelated to P2 and N1-P2 complex amplitudes. Social-related emotionality was significant in GLM analysis with amplitude of N1-P2 complex, but its significance was not confirmed by a series repetitions of the analysis with exclusion of participants (only 28 out of 30 repetitions were significant) ($F(1,28)=5.19$, $p=0.03$, $R=0.47$, $p=0.008$).

Two temperament questionnaire dimensions – Extraversion and Social-related ergonicity – revealed significant negative relation to N2 latency ($F(1,28)=6.93$, $p=0.01$, $R=-0.46$, $p=0.1$ and $F(1,28)=12.40$, $p=0.001$, $R=-0.55$, $p=0.001$ correspondingly) (Fig. 2C and F). Thus the higher were Extraversion and Social-related ergonicity, the shorter was N2 latency (Fig. 3K and L).

Discussion

Questionnaire data, behavioral data and ERP data

Questionnaire data and correlations between them generally agree with reports by questionnaires' authors [Eysenck, 1970; Rusalov, 1997, 2002; Strelau, 1982; Strelau et al., 2005], but some of the expected correlations were absent. This may happen due to the fact that the validation studies mentioned above were performed in larger samples.

According to our data, Extraversion positively correlated not only with social-related dimensions of V.M. Rusalov's questionnaire – Ergonicity, Plasticity and Tempo [1997], but also

with a number of other dimensions, namely with Mobility of nervous processes, Strength of excitation to strength of inhibition ratio and Object-related tempo.

On the other part, according to our data, there was no significant relation between Extraversion and Strength of excitation, which was reported by J. Strelau [2005]. Thus, although Extraversion is related to the quantity and quality of social communication, it also reflects some temporal rather than intensity aspects of the nervous system functioning.

Neuroticism scale was expectedly found to work in a similar way to Emotionality dimensions – Object-related and Social-related emotionality scales.

Strength of inhibition manifested fewer correlations with STQ dimensions than it was reported by V.M. Rusalov [1997]. According to V.M. Rusalov's report [1997], Strength of excitation was expected to correlate with Object-related plasticity and Object-related tempo – the observation that did not show up in our study.

Strength of excitation to strength of inhibition ratio proved to be more informative dimension for the search of correlations with other questionnaire dimensions than Strength of excitation and Strength of inhibition per se. According to our data, Strength of excitation to strength of inhibition ratio actually reflects temporal characteristics of the nervous system rather than its intensity characteristics: this dimension positively correlates with Mobility of nervous processes, as well as with all temporal STQ dimensions – both Object-related and Social-related plasticity and Tempo. Generally, within our set of data a block of temporal characteristics of temperament was quite distinguishable and more prominent than intensity (i.e. strength) characteristics, while the latter traditionally attracted more attention among psychophysicologists [Golubeva, 2005].

Behavioral data indicate that the oddball task was quite easy for all participants: nearly 1/3 of participants did not commit a single error (9 out of 30, 30%); others made almost a negligible number of errors of both kinds (response omissions and false alarms). Judging by very small latency dispersions, all participants had quite stable latencies of correct responses. Exactly these parameters – response latencies and latency dispersions – proved very informative as they were found to have multiple statistical relations with questionnaire data and ERP parameters.

According to the data obtained, the higher was Social-related ergonicity, the later but the more stable in time were behavioral responses. Also, the higher were the temporal dimensions of temperament – Mobility of nervous processes and Social-related ergonicity, the more stable in time were behavioral responses.

ERPs recorded to target stimuli were quite typical for the oddball paradigm and other similar tasks [Gnezditskiy, 1997; Donchin, Coles, 1988; Ivanitsky, 1976; Näätänen, 1992; Patel, Azzam, 2005; Polich, 2007; Rutman, 1979]. N1-P2 complex was very clearly pronounced with

maximums at Fcz for N1 and at Cz for P2. N2 was small in relation to zero line, but at least at pericentral electrodes it was easily distinguishable as a negativeward (upward in reversed potential axis) deflection separating two positive deflections – P2 and P3. Although in some participants N2 did not cross zero line and had actually positive amplitude values, clear morphological characteristics and typical latency gave us reason to measure it in all cases (measured was the most negative peak in 190-310 ms interval – see Methods section).

N2 amplitude reached maximum at the most rostral electrodes taken into analysis (F3, Fz, F4, Fc3, Fcz, Fc4), which is typical to N2b and N2c components in tasks involving auditory stimuli [Folstein, Van Petten, 2008; Patel, Azzam, 2005]. P3 wave was clearly apparent over frontoparietal electrodes and looks identical to classical P3b components [Näätänen, 1992; Polich, 2007; Rockstroh et al., 1982].

Assumptions taken at the interpretation of ERP data

ERP latency supposedly reflects the time of occurrence of corresponding information processing in the brain: shorter latency presumably indicates that a given process in the brain takes place earlier after stimulus onset, while increased latency may hint at a delay in the given process under consideration. This effect is well studied under conditions of varying task difficulty: for example, the more difficult is a stimulus classification task, the greater is latency of the late "cognitive" evoked potential P3 [Coles et al., 1995; Kutas et al., 1977], which is generally viewed as a correlate of some of the final stages of attention and perception, evoked by a sudden stimulus. There are also some reports stating the dependence of N1 latency upon complexity of a visual stimulus [Ivoshina, 2009]. Much less studied is the question whether latency of evoked potential depends upon individual properties of personality. Anyway, whenever there is no ambiguity concerning subcomponent composition of a component, the latency of ERP peaks seems to be a straightforward indicator of speed of corresponding brain processes. Obviously, if an ERP component consists of two similar overlaid subcomponents with a slightly different latency, which cannot be readily distinguished under conditions of a particular experiment, then a peak latency of the whole wave may depend upon relative amplitude of both components rather than upon actual latency of each subcomponent.

ERP amplitude, which is more readily analyzed in literature than latency, is actually much more difficult to interpret. Generally there is a prevailing view that ERP amplitude reflects the intensity of information processing in the brain, i.e. the extent of brain resource allocation to a particular task [Kok, 2001].

Still other possibilities cannot be excluded from the interpretation of ERP amplitude, and they appear to be a direct result of a method of coherent averaging traditionally used for ERP extraction from ongoing EEG activity. For example, ERP amplitude may become lower if a given process occurs at variable unstable latency after stimulus onset; this may happen if the time, needed for processing of particular information, varies from one trial to another (as a result of varying stimulus complexity, functional state of the participant such as habituation or fatigue, etc.). As a result of coherent averaging, a strong process that would otherwise generate large potential due to its jitter will appear as a "smeared" low amplitude ERP wave. On the other part, a much less strong process occurring exactly at one and the same time during each trial will after averaging produce a strong ERP peak. Apparently, this consideration is applicable only to short processes with time jitter range comparable with its length in time.

The second problem in interpretation of ERP amplitude is that electrical potentials recorded from the brain or scalp surface may be (and usually are) a result of spatial summation, being generated by a number of different processes happening in the brain at overlapping periods of time after stimulus onset. Summation of potentials of the same sign will increase, while overlapping occurrence of a positive and negative potentials – decrease the amplitude of the resulting deflection.

Possibly, one or both effects contribute to the paradoxical result observed in a number of experiments and discussed in several reviews: under increased subjective difficulty of stimulus identification P3 amplitude decreases [Johnson, 1986; Kok, 2001; Parasuraman, Beatty, 1980].

Thus latency may be considered as a satisfactory index of speed at which a particular brain processes occurs. As far as amplitude concerns, while it cannot be thought of as an unambiguous index of resource allocation to a particular process, it is still a reflection of a real physiological processes occurring in the brain, and with due care it can be used as an indirect measure of organization of brain activity.

Relations of ERP parameters with behavioral and questionnaire data

The main purpose of this study was to find out how ERPs as correlates of the processes of preattention and attention are related to behavioral indexes of task execution and to temperament dimensions.

The behavioral data were found to be related to a number of ERP parameters. First of all, P3 amplitude was negatively related to the number of response omissions, i.e. the greater was P3 amplitude, the fewer omissions committed the participants. In other words, higher P3 amplitude

corresponds to better attention performance – better reliability of stimulus detection and recognition. At the same time, P3 latency was not related to response latency.

It is well known that P3 wave is generated in response to significant stimuli (rare target stimuli under the oddball paradigm), while it is weak or absent in response to nonsignificant stimuli. Earlier in experiments in animals one of the authors of the current report has shown that during response omissions P3 amplitude to the target stimulus was significantly decreased in comparison to the situation of proper performance in the oddball task [Chernyshev et al., 2005]. To our knowledge, this fact has not been shown in literature before. The absence of direct relations between P3 latency and overt behavioral response latency has been documented in literature (although P3 latency may depend upon stimulus evaluation time) [Magliaro et al., 1984].

Dispersion of behavioral response latency – an inverted measure of response stability – was found to be related to three ERP parameters. First, response latency was less stable in participants whose N2 was greater. According to our unpublished data and to some hints in the literature, increased N2 amplitude can be observed under increased difficulty of stimulus differentiation [Chernyshev et al., 2010; Senkowski, Herrmann, 2002]. Thus one can suppose that participants who had increased N2 amplitude faced with greater subjective task difficulty and consequently performed with less stable response latency.

In addition, behavioral response latency dispersion was positively related to latencies of N2 and P3. This means that the later were generated both cognitive components of ERP, the less stable was response latency. Presumably, late generation of N2 and P3 hints at slower processing of information about the stimulus and later occurrence of preattentive and attentional processes (as if during a more difficult task). It is known that P3 latency correlates with task difficulty [Näätänen, 1992; Donchin, Coles, 1988; Rockstroh et al., 1982]. It is likely that, again, individuals with unstable response latency found the task more difficult, and due to its difficulty latencies of N2 and P3 were increased, as well as N2 amplitude was increased.

Concerning relations between ERP parameters and temperament dimensions, three main results were obtained.

First, it was found that the higher was Extraversion and Mobility of nervous processes, the smaller was N1-P2 complex (thus it was higher in introverts than in extraverts). N1 manifested similar relation to Mobility of nervous processes, but it was not as significant in relation to Extraversion as N1-P2 complex. Apparently, although P2 itself was not involved in this effect, it was the entire N1-P2 complex that played the most important role. N1 amplitude was also found to be higher in introverts in the report of C. Doucet and R.M. Stelmack [2000].

As stated in the Results section, Extraversion and Mobility of nervous processes were themselves correlated and may partially represent one and the same unknown temperament dimension. Still note that no such effect was observed for several other temperament dimensions which were also correlated with Extraversion and Mobility of nervous processes.

One can suppose that some brain process at early preattentive stage of perception, which is manifested as N1-P2 complex, requires less brain resources in people with high Extraversion and high Mobility of nervous processes. If that is true, then it is likely that resource-effective early preattentive information processing may constitute the basis for effective and fast attention allocation mechanism. Possibly, such individuals may process more stimuli at the preattentive stage each time, and thus evaluate more potential future targets of attention before actually choosing the next relevant target and allocating attention to it. As a result, their attention can be switched faster to any new relevant target in conditions of a real world. Therefore, this characteristic of attention may be partially detected by the questionnaires used as Mobility of nervous processes and Extraversion.

The data described above stay in line with the report of H.J. Eysenck and M.D. Eysenck [2001] that introverts experience stronger excitation in response to the external stimuli.

We did not confirm the results of J.M. Cahill and J. Polich, who demonstrated that P3 was generally smaller for introverts than for extraverts [Cahill, Polich, 1992], and data of Gurrera et al. [2005], who demonstrated positive correlation of P3 amplitude with extraversion. In the report of J.M. Cahill and J. Polich only extreme introverts and extroverts were recorded, while participants in the current study often had intermediate Extraversion scores. P3 amplitude is also known to habituate more rapidly for extraverts than for introverts [Ditraglia, Polich, 1991], while no direct effect of extraversion on P3 was found in that report. The insignificant tendency of P3 being greater for individuals with low extraversion (introverts) in our data can be explained by faster adaptation in extraverts.

Second, the higher was Object-related emotionality, the greater were P2 and N1-P2 complex. Social-related emotionality demonstrated the same tendency. This result seemingly and unexpectedly puts emotionality in opposition to Extraversion and Mobility of nervous processes. However, the difference is that for Extraversion and Mobility of nervous processes the N1-P2 complex effect was mostly due to variation of N1 amplitude, while for Emotionality it was mostly due to variation of P2 amplitude. One can suppose that a more massive resource allocation to preattentive processes (which manifest themselves as enhanced P2 and N1-P2 amplitude) may lead to stronger emotional response to the stimuli in everyday life. Note that no such effect was found for Neuroticism which was strongly correlated with both aspects of Emotionality. Possibly due to some important difference in the author's models of Neuroticism

and Emotionality laid at the basis of the two questionnaires, and notwithstanding the strong correlation between the two, these dimensions are quite different, V.M.Rusalov's Emotionality being closer to the physiological basis of this phenomenon.

Third, the higher were Extraversion and Social-related ergonicity, the shorter was N2 latency. It should be mentioned that the two temperament dimensions correlate positively, and in their positive relation to N2 latency they partially reflect one and the same unknown dimension of temperament. Thus this temperament characteristic which predisposes the individual to greater quantity and intensity of social communication manifests itself as shortened N2 latency. The latter may supposedly hint at faster occurrence of some process at the moment of transition from preattentive to attentive processing.

It should be stressed that, as described above, Extraversion was related to different ERP parameters, each time in complex with another dimension: together with Mobility of nervous processes it was related to amplitude of N1-P2 complex, and together with Social-related ergonicity it was related to N2 latency. Thus in the first instance Extraversion behaves as a temporal dimension of temperament, and in the second one – as an intensity dimension. A number of psychological studies has already shown that Extraversion may be considered as a combination of both intensity and temporal dimensions of temperament [Golubeva, 2010; Ilyin, 2004; Gray, 1991; Strelau et al., 2005], and our results confirm this through relations of Extraversion to ERP data.

Conclusions

The present study combined two traditional research paradigms – ERP measurement during an oddball task, and temperament questionnaires. This allowed us to find out a number of important interrelations between hypothetical processes of preattention and attention in the brain, which are reflected in ERPs, and several temperament dimensions. Most important are several findings. First, we demonstrated that P3, which has long been viewed as a correlate of late stages of attentional processes, is in fact related to a behavioral measure of effectiveness of stimulus detection. Next, we obtained a psychophysiological confirmation of a classical notion that extraverts demonstrate lower excitation in response to external stimuli. Moreover, we demonstrated that the critical difference between extraverts' and introverts' response to stimuli lies at early preattentive stage of perception. And last, we obtained a psychophysiological demonstration of the idea that extraversion may not be a single dimension of temperament but rather it is likely be a combination of at least two dimensions, one of which belongs to intensity, and the other – to temporal aspects of temperament.

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Appendix

Tab. 1. Summary questionnaire data statistics.

	Mean	Median	Min.	Max.	St. dev.	St. err.
EPI1	58.7	67	6	93	22.7	4.1
EPI2	46.8	45	12	80	19.6	3.6
PTS1	68.8	68	45	89	9.8	1.8
PTS2	72.4	70.5	52	98	10.7	2.0
PTS3	71.4	72.5	51	93	11.1	2.0
STQ1	6.8	7.5	2	12	3.4	0.6
STQ2	8.5	10	1	12	3.4	0.6
STQ3	8.2	8.5	2	12	3.2	0.6
STQ4	6.4	6.5	1	12	3.0	0.6
STQ5	8.4	9	0	12	3.1	0.6
STQ6	9.2	10	1	12	3.0	0.5
STQ7	6.2	6.5	0	12	4.1	0.7
STQ8	7.0	7	1	12	2.9	0.5
EIR	0.97	0.95	0.54	1.35	0.19	0.03

Note: EPI1 – Extraversion, EPI2 – Neuroticism, PTS1 – Strength of excitation, PTS2 – Strength of inhibition, PTS3 – Mobility of nervous processes, STQ1 – Object-related ergonicity, STQ2 – Social-related ergonicity, STQ3 – Object-related plasticity, STQ4 – Social-related plasticity, STQ5 – Object-related tempo, STQ6 – Social-related tempo, STQ7 – Object-related emotionality, STQ8 – Social-related emotionality, EIR – Strength of excitation to strength of inhibition ratio.

Tab. 2. Correlation matrix within questionnaire data (Spearman R).

	1	2	3	4	5	6	7	8	9	10	11	12	13
1 EPI1													
2 EPI2	0.10												
3 PTS1	0.23	-0.31											
4 PTS2	-0.33	0.07	-0.03										
5 PTS3	0.62 ***	0.10	0.47 **	-0.22									
6 STQ1	-0.08	-0.19	0.46 *	0.08	0.17								
7 STQ2	0.51 **	-0.12	0.03	-0.13	0.26	0.23							
8 STQ3	0.25	-0.03	0.35	-0.32	0.49 **	0.36 *	0.32						
9 STQ4	0.62 ***	-0.06	0.26	-0.56 ***	0.33	-0.13	0.48 **	0.41 *					
10 STQ5	0.50 **	-0.09	0.27	-0.28	0.50 **	0.26	0.43 *	0.44 *	0.31				
11 STQ6	0.49 **	-0.01	0.25	-0.39 *	0.48 **	0.10	0.31	0.52 **	0.65 ***	0.56 **			
12 STQ7	-0.26	0.63 ***	-0.26	0.14	-0.13	0.17	-0.05	0.04	-0.14	-0.21	-0.12		
13 STQ8	-0.26	0.71 ***	-0.25	0.12	-0.13	0.22	-0.12	-0.07	-0.24	-0.04	-0.10	0.78 ***	
14 EIR	0.41 *	-0.12	0.71 ***	-0.65 ***	0.51 **	0.29	0.15	0.51 **	0.61 ***	0.39 *	0.48 **	-0.13	-0.09

Note: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; EPI1 – Extraversion, EPI2 – Neuroticism, PTS1 – Strength of excitation, PTS2 – Strength of inhibition, PTS3 – Mobility of nervous processes, STQ1 – Object-related ergonicity, STQ2 – Social-related ergonicity, STQ3 – Object-related plasticity, STQ4 – Social-related plasticity, STQ5 – Object-related tempo, STQ6 – Social-related tempo, STQ7 – Object-related emotionality, STQ8 – Social-related emotionality, EIR – Strength of excitation to strength of inhibition ratio.

Tab. 3. Behavioral data: percentage of false alarms, response omissions, response latency and deviation of response latencies in the experiment.

	Mean	Median	Min.	Max.	St. dev.	St. err.
False alarms, % of non-target stimuli	0.27	0.00	0.00	1.50	0.50	0.09
Response omissions, % of target stimuli	4.73	2.00	0.00	22.00	6.16	1.12
Response latency, ms	725.8	613.0	283.0	1663.0	356.5	65.1
Deviation of response latencies, ms	22.9	19.7	13.4	38.6	7.4	1.4

Note: For false alarms and response omissions percentage was calculated in relation to the number of corresponding stimuli in the experiment (200 non-targets and 50 targets).

Tab. 4. Correlation matrix between questionnaire data and behavioral data (Spearman R).

	False alarms	Response omissions	Response latency	Dispersion of response latencies
EPI1	0.05	0.10	0.17	-0.17
EPI2	-0.05	-0.30	0.07	-0.02
PTS3	0.09	0.04	-0.24	-0.15
PTS3	0.27	-0.25	-0.25	-0.01
PTS3	-0.04	-0.25	0.12	-0.47**
STQ1	0.17	-0.10	-0.04	-0.35
STQ2	-0.02	0.07	0.41*	-0.39*
STQ3	-0.33	-0.21	0.33	-0.43*
STQ4	-0.12	0.20	0.11	-0.10
STQ5	0.03	-0.08	0.13	-0.20
STQ6	-0.12	0.05	0.04	-0.11
STQ7	0.00	-0.15	0.20	-0.14
STQ8	0.11	-0.23	-0.01	-0.07
EIR	-0.10	0.10	0.09	-0.21

Note: * $p < 0.05$. ** $p < 0.01$. *** $p < 0.001$; EPI1 – Extraversion. EPI2 – Neuroticism. PTS1 – Strength of excitation. PTS2 – Strength of inhibition. PTS3 – Mobility of nervous processes. STQ1 – Object-related ergonicity. STQ2 – Social-related ergonicity. STQ3 – Object-related plasticity. STQ4 – Social-related plasticity. STQ5 – Object-related tempo. STQ6 – Social-related tempo. STQ7 – Object-related emotionality. STQ8 – Social-related emotionality. EIR – Strength of excitation to strength of inhibition ratio.

Tab. 5. Summary ERP data statistics to the target stimulus (data were averaged through 15 pericentral electrodes within each of 30 participants).

	Mean	Median	Min.	Max.	St. dev.	St. err.
N1 amplitude	-6.0	-5.8	-12.0	0.0	2.4	0.4
N1 latency	91.8	93.5	64.0	106.0	10.7	1.9
P2 amplitude	6.7	6.6	1.2	12.8	3.2	0.6
P2 latency	176.4	178.5	150.0	234.0	17.1	3.1
N1-P2 amplitude	12.6	12.4	5.7	23.1	4.2	0.8
N1-P2 duration	84.7	84.5	58.0	134.0	16.7	3.1
N2 amplitude	0.0	-0.4	-4.3	6.4	2.9	0.5
N2 latency	241.8	238.5	193.0	299.0	26.1	4.8
P3 amplitude	8.2	9.0	2.2	13.6	2.9	0.5
P3 latency	346.8	338.5	309.0	525.0	38.3	7.0
N2-P3 amplitude	8.2	7.9	1.6	15.4	3.4	0.6
N2-P3 duration	105.1	103.0	30.0	275.0	41.4	7.6

Tab. 6. Correlation matrix within ERP data (Spearman R).

	1	2	3	4	5	6	7	8	9	10	11
1 N1 amplitude											
2 N1 latency	-0.16										
3 P2 amplitude	-0.13	-0.12									
4 P2 latency	-0.28	0.36	-0.03								
5 N1-P2 amplitude	-0.60 ***	-0.02	0.83 ***	0.12							
6 N1-P2 duration	-0.20	-0.20	0.06	0.79 ***	0.15						
7 N2 amplitude	0.28	-0.16	0.24	-0.01	0.05	0.10					
8 N2 latency	-0.10	0.28	0.34	0.47 *	0.33	0.32	-0.10				
9 P3 amplitude	-0.08	0.13	0.29	0.25	0.24	0.19	0.32	-0.01			
10 P3 latency	-0.29	0.10	-0.15	0.10	0.05	0.11	-0.63 ***	0.33	-0.38 *		
11 N2-P3 amplitude	-0.26	0.16	-0.11	0.05	-0.01	-0.08	-0.54 **	-0.05	0.50 **	0.11	
12 N2-P3 duration	-0.09	-0.22	-0.39 *	-0.43 *	-0.24	-0.28	-0.45 *	-0.62 ***	-0.27	0.48 *	0.18

Note: *p<0.05, **p<0.01, ***p<0.001

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