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TOP-DOWN AND BOTTOM-UP PROCESSES IN NORMAL AND EXTREME ENVIRONMENTS: ELECTROPHYSIOLOGICAL AND BEHAVIORAL RESULTS

– PhD thesis booklet –

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INTRODUCTION

Many aspects of human behavior are governed by top-down and bottom-up processes (Schneider & Shiffrin, 1977). Top-down processes are manifestations of our inner behavioral plans, while bottom-up processes originate from the outside world and constitute mainly automatic processes. One of the most well-known example of top-down processes are the executive functions, which are high-level cognitive processes controlling lower level processes (Friedman & Miyake, 2017). A typical example of bottom-up processes is the orienting reaction elicited by perceptually salient stimuli. Top-down and bottom-up processes can be separated conceptually, however in many cases they work together in synergy, as in the case of perception of noisy stimuli or in the case of orienting reaction leading to exploration of the recently appeared stimuli.

The orienting reaction can be measured by electrophysiological methods, as salient stimuli usually evoke a large amplitude event related potential, the P3a (Escera & Corral, 2007; D. Friedman, Cycowicz, & Gaeta, 2001; Schomaker & Meeter, 2015). The P3a is maximal over the midline central, fronto-central electrodes, and peaks between 250-400 ms after the onset of the eliciting stimulus. Although stimuli from different modalities elicit P3a components with somewhat different waveforms and scalp topography, the P3a can be considered mostly modality-independent. The three most important features that govern its amplitude are the novelty, rarity and complexity of the stimulus. The most often applied paradigm for the elicitation of P3a is the three-stimulus oddball task (Courchesne, Hillyard, & Galambos, 1975) in which frequent standard stimuli are interspersed with infrequent target stimuli and infrequent task-irrelevant, but perceptually salient novel stimuli - the latter eliciting the P3a.
Numerous findings suggest that the amplitude of P3a depends heavily on the “amount” or intensity of attentional processes. Under dual-task conditions, increased task difficulty in the primary task often results in decreased P3a in the to-be ignored or secondary task (Legrain, Bruyer, Guérin, & Plaghki, 2005; SanMiguel, Corral, & Escera, 2008; Ullsperger, Freude, & Erdmann, 2001; Zhang, Chen, Yuan, Zhang, & He, 2006). Similar phenomenon might be responsible for the so-called P3a difficulty effect: the harder is to discriminate the standard and target stimuli, the higher the amplitude of P3a elicited by the irrelevant stimuli (Comerchero & Polich, 1999; Hagen, Gatherwright, Lopez, & Polich, 2006; Kimura, Katayama, & Murohashi, 2008; Polich & Comerchero, 2003; Sawaki & Katayama, 2006, 2007; Sugimoto & Katayama, 2017). In study 1 of the dissertation we investigated this phenomenon on different time scales than previously done in the literature.

In addition to task difficulty, the intensity of attentional processes also depends on the effort devoted to task performance. To counteract the potentially deleterious effects of stressors, most of us consciously or unconsciously invoke additional, compensatory effort (Hockey, 2011; Hockey, 1997). One such stressor is the long and cognitively demanding mental work that frequently gives rise to feelings of mental fatigue. Can this compensatory effort be tracked by electrophysiological methods? If P3a is sensitive to the increase of attentional intensity dictated by increases in task difficulty, can it also be sensitive to compensatory effort? In study 2 we explored this question. We applied a fatigue inducement technique to facilitate compensatory effort and used the P3a event related component to track that.

According to the influential work of Miyake et al. (2000) executive functions can be divided to inhibition, shifting and updating, three correlated but separable functions. Inhibitory control is responsible for the slowing down of prepotent,
almost automatic behavioral responses, and can be measured by tasks such as the Stroop, the go/nogo or the stop-signal task. A central element of the orienting reaction is the stoppage of ongoing activity (inhibition) and the immediate pursuit of another one (shifting), thus orienting reaction has parallels with the basic building blocks of executive functions. This idea motivated us to test P3a and executive functions together in study 3. In that study subjects were tested among extreme environmental conditions to see whether P3a and executive functions show comparable changes. The extreme environmental condition was lack of oxygen (hypoxia).

Acute hypoxia is still a major hazard in aviation and mountaineering due to its adverse effects on cognition. Depending on the severity of hypoxia, subjects usually show a generalized deterioration of cognitive performance across all investigated domains. In study 4 we investigated whether different inhibitory control functions react similarly to hypoxia, or there are functions that are more resistant to this stressor.
THESES

1. The P3a difficulty effect can be evoked by short-term modulation of task difficulty

Aims
Katayama & Polich (1998) were the first to report the powerful effect of perceptual task difficulty on neural responses elicited by irrelevant stimuli. In task blocks in which perceptual differences between standards and targets were large and thus task difficulty was low, irrelevant sounds evoked a small, parietally maximal positivity with a scalp distribution similar to the P3b ERP component (for P3b, see Donchin & Coles, 1988; Polich, 2007; Verleger, Jaśkowski, & Wascher, 2005). However, when perceptual differences between standards and targets were small, and hence the task difficulty was high, irrelevant stimuli evoked much larger and more anterior P3 components that were identifiable as P3a.

The main aim of the present experiment was to investigate whether the P3a difficulty effect can be evoked by short-term (i.e. few second-long) modulation of task difficulty.

Methods
Young adult subjects (n=21, mean age: 21 years) performed two versions of a cued two-choice discrimination task. The schematic depiction of the task can be seen on Figure 1. Subjects had to decide if the circle presented second in order (probe stimuli) was larger or smaller than the circle presented first (standard stimuli). The difference between the onsets of the two stimuli was 1.4 seconds. In the „block” version of the task, the physical difference between the standard and the probe

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stimuli was constant over the approx. 6 minute-long blocks. In some task blocks the difference the first and the second stimuli was large (and the task easy), while in some task blocks the difference was small (and the task hard), this way imitating the structure of the classic P3a difficulty effect studies. However, in the “trial” version of the task, task difficulty was varied randomly between trials, and a cue stimulus, presented together with the standard circle, indicated the difficulty of the given trial.

In both task versions, in 12% of the trials, probe stimuli were replaced with irrelevant stimuli requiring no response, aimed at eliciting P3a. We hypothesized that increased task difficulty will have an amplificatory effect on P3a.
Figure 1. Schematic depiction of the task in the trialwise version. Subjects had to decide if the probe circle was larger or smaller than the standard circle. Irrelevant stimuli (pictures of butterflies) had to be ignored. In the blockwise version the cue was constant during the task block, and only two types of second circles were presented.

Results

Confirming our hypothesis, irrelevant stimuli elicited larger P3a components when the task was hard, compared to when it was low, and there was no difference in this respect between the two task versions (Figure 2).
Figure 2. Event related potentials elicited by irrelevant stimuli. Dashed line frame indicates amplitude measurement windows for P3a. P3a amplitudes were significantly larger in hard compared to easy conditions both in the „block” and „trial” task versions.
2. The compensatory effort induced by mental fatigue can be tracked by P3a

Aims
Compensatory effort is a natural consequence of cognitively demanding task performance. The aim of the present study was to test if P3a can be used for tracking compensatory effort. The emergence of compensatory effort was facilitated by having subjects perform a long (2 hours) and demanding task.

Methods
The experiment was built on the fatigue-inducing task – testing task scheme (Figure 3). Subjects (young adults, n=36, mean age: 23 years) were divided into two groups. In the second phase of the experiment, members of the fatigue group performed a demanding, multimodal task (the MATB), while members of the control group watched documentary films. In the first and third phase of the experiment, both groups performed the same set of tasks. Two tasks (the Oddball and the Distraction task) were used to elicit P3a.

![Diagram](image)

Figure 3. Experimental design. PVT: Psychomotor Vigilance Task

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Results
Subjective fatigue increased more in the fatigue than in the control group. Despite that, the amplitude of P3a has not changed differentially between the two groups (see Figure 4). Since cognitive task performance also remained essentially the same between the two groups, it is difficult to infer whether the fatigue group invoked compensatory effort, but P3a was not sensitive to that, or they did not invoke compensatory effort at all.

Figure 4. Event related potentials elicited by irrelevant stimuli in the Oddball task. The P3a peaking around 300 ms remained unaffected by the fatigue manipulation.
3. **Acute hypoxia leads to diminished P3a amplitude, while response inhibition and interference control remain intact**³

**Aims**

There are parallels between the neural correlate of orienting reaction, the P3a and the inhibitory executive functions. One aim of the present study was to better understand this relationship, following the logic that if these functions respond comparably to hypoxia, that it can be considered a sign of a closer relationship. The second aim of the study was to investigate the effect of hypoxia on the investigated cognitive abilities. The cognitive effects of experimental hypoxia are still not fully understood, especially the sensitivity of executive functions remains largely debated.

**Methods**

Subjects were recreational mountaineers (n=11, mean age: 33 years). The experiment was run in the National Korányi Institute of Pulmonology, under close medical supervision. Hypoxia was induced with low O₂ content breathing mixture. The level of hypoxia corresponded to 5500 meter altitude. Subjects performed two tasks. We assessed interference control with a number-size Stroop task. A modified CPT O-X task served as an assessment of response inhibition using the measures of false alarms to nogo stimuli and the nogo P3 event related potential. P3a (or in other words, Novelty P3) was elicited by irrelevant stimuli interspersed between

the regular stimuli of the CPT O-X task. Subjects performed the same set of tasks before, during and after the hypoxic exposure.

**Results**
The amplitude of P3a (Novelty P3) significantly decreased in hypoxia (Figure 5). Subjects had very few false alarms throughout the experiment. The nogo P3 reflecting response inhibition remained unaffected. Performance in the Stroop task, reflecting interference-control, also remained unchanged in hypoxia.

![Scalp topographies demonstrating the effects of hypoxic exposure on the P3 components](image)

**Figure 5. Scalp topographies demonstrating the effects of hypoxic exposure on the P3 components.** Scalp maps illustrate the mean amplitude difference (in μV) between Normoxia (Pre and Post conditions averaged together) and Hypoxia conditions at peak latency (338 ms post stimulus presentation for NoGo and 356 ms for Novelty P3).
4. Acute hypoxia has differential effect on the inhibitory executive function of response inhibition and interference control

Aims
We observed very low false alarm rate in the previous study, limiting our ability to fully examine response inhibition. It is well-known that stimulus presentation rate correlates positively with response inhibition (Benikos, Johnstone, & Roodenrys, 2013; Jodo & Kayama, 1992): the faster is the presentation rate, the harder is to inhibit the motor response, and as a consequence inhibitory processes are activated more. In this study we therefore applied considerably faster presentation rates (a stimulus was presented in each 0.6 seconds) than in the previous study, to increase the need for response inhibition. To prevent serious task performance drop, we applied an easier response inhibition task: a go / nogo task (GNG). Additionally, two versions of a Stroop task measuring interference control were also included (Voice-Stroop, Name-Stroop).

Methods
The experiment was conducted in hypobaric hypoxia; EEG was not recorded. In accordance with the previous study, measurements were taken before, during and after hypoxia. The level of hypoxia corresponded to 5500 meter altitude. Subjects were military fighter jet and helicopter pilots of the Hungarian Defense Forces (n=25, mean age: 35 years). The experiment was performed at the Aeromedical, Military Screening and Health Care Institute of the Hungarian Defense Forces, Kecskemét, Hungary.

Results

The Stroop-effect, reflecting interference control, increased in hypoxia (Figure 6). In contrast, false alarm rate to nogo stimuli changed similarly in hypoxia, as error rate to go stimuli, reflecting unaffected response inhibition.

Figure 6. Results in the Voice-Stroop task. Stroop-effect (difference between congruent and incongruent stimuli) increased in hypoxia. Error bars represent standard error of mean.
DISCUSSION

Orienting reaction and P3a can be considered typical manifestations of bottom-up processes, however, the amplitude of P3a is dependent on the direction and, according to our hypothesis, intensity of the underlying attentional processes. The first two studies of dissertation tested this hypothesis. In study 1 of the dissertation we explored the P3a difficulty effect. This effect is usually investigated in experiments in which task difficulty is varied between the approx. 4-6 minute-long task blocks. However, in the present study we tested whether the P3a difficulty effect emerges when difficulty is varied on a much shorter time scale. Our results provide positive answers, which we interpreted as a confirmation of our hypothesis that increases in task difficulty lead to increases in the intensity of attentional processes, and the amplification of P3a is a side-effect of this process.

In study 2 we intended to manipulate the intensity of attentional processes by inducing compensatory effort. As a result of long and demanding task performance the fatigue group reported higher levels of mental fatigue, however, this did not translate to changes in P3a amplitudes. Thus the study remained inconclusive regarding the attention intensity hypothesis. In our view, the study is more informative in terms of factors influencing behavioral fatigue in a fatigue-inducing task – testing task design.

Study 3 set out to test the relationship between P3a and executive functions in an extreme environment setting. Replicating previous results we observed a marked decrease of P3a amplitudes in acute hypoxia, while response inhibition and interference control remained preserved. This result suggests that the P3a – executive function link is not too strong. The additional finding that nogo P3a was
also unchanged in hypoxia argues against the theory (Polich, 2007), which suggests that these are only instances of the same ERP component.

In study 4 of the dissertation we probed inhibitory executive functions (response inhibition and interference control) in acute hypoxia. Results exhibited pronounced dissociation: while interference control was weakened, response inhibition remained intact. This result supports the notion that executive functions are fragmented and largely inhomogeneous. From a practical point of view, results highlight that the impact of hypoxia on executive functions is not uniform, and intact performance in one domain does not mean that hypoxia might not have detrimental effects in another.
REFERENCES


