Effects of extreme environments on cognitive processes using the method of event-related potentials

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"Én, Barkaszi Irén, teljes felelősségem tudatában kijelentem, hogy a benyújtott értekezés önálló munka, a szerzői jog nemzetközi normáinak tiszteletben tartásával készült, a benne található irodalmi hivatkozások egyértelműek és teljesek. Nem állok doktori fokozat visszavonására irányuló eljárás alatt, illetve 5 éven belül nem vontak vissza tőlem odaítélt doktori fokozatot. Jelen értekezést korábban más intézményben nem nyújtottam be és azt nem utasították el."

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Effects of extreme environments on cognitive processes using the method of event-related potentials

Ph.D. thesis

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Glossary of abbreviations

ACC Anterior Cingulate Cortex

ANT Attention Network Test

EEG Electroencephalography/Electroencephalogram

ERP Event-related brain potential

ESA European Astronaut Center

MMN Mismatch negativity

NASA National Aeronautics and Space Administration

IIH Idiopathic intracranial hypertension

ISI Interstimulus interval (offset-to-onset interval)

ISS International Space Station

LC Locus coeruleus

MMN Mismatch negativity

OR Orientation response

PVT Psychomotor vigilance test

REM Rapid eye movement

RON Reorientation negativity

SOA Stimulus onset asynchrony (onset-to-onset interval)

VIIP Visual impairment and intracranial pressure

1 General introduction

Nowadays many people live, for shorter or longer time, in environments considered extreme in many aspects, such as microgravity in space, or extreme cold in the Antarctica. Such environments involve many factors that may negatively affect cognitive functions, and, consequently, could jeopardize life. This highlights the importance of cognitive studies in this field.

Such studies conducted in extreme environments are important in many ways. On one hand, these investigations expand our knowledge about how the stress factors in space station and Antarctic environment influence cognitive functions. On the other hand, there is an increasing demand for space tourism and Antarctica is also visited by many for tourist purposes, so the results of these researches are relevant for more and more people. Thirdly, mainly concerning the astronauts, impairments in their cognitive functions may have disastrous outcome. If evidence support such impairments, the negative effects of the cognitive deterioration can be avoided with the development of appropriate countermeasures. The final goal is to create a method which enables rapid detection of alterations in cognitive status during space missions. Obviously, due to the time-consuming nature of the multichannel event-related potential (ERP) method, it is not appropriate for the continuous evaluation of cognitive status in space station, however, this measurement would be feasible with some easy-to-install electrodes before a critical event, like a spacewalk. Moreover, if this method is proved to be sensitive to changes in cognitive performance on the behavioral level, a shortened version may even be used routinely.

At the beginning of the dissertation, two extreme environments, outer space, and Antarctica are introduced: first, microgravity-induced physiological alterations in space describing cephalad-fluid shift, visual impairment and intracranial pressure (VIIP) syndrome, neurovestibular acclimatization, and sensory-motor system are overviewed. Furthermore, two important stress factors – elevated CO₂ concentration, and radiation – are detailed. This is followed by a brief description of environment-related syndromes in the Antarctica. At the end of this section, results of sleep studies in space and Antarctica are also summarized.

In the next section, studies of cognitive functions in space and Antarctica are reviewed as categorized into six main functions: Perception and visuomotor performance, Attention, Memory, Learning, Executive functions, and Reasoning and mathematical processing. This is followed by relevant studies in space and/or in Antarctic analog environments. Connected

research fields (elevated intracranial pressure, elevated CO₂ concentration, isolated and confined environment, sleep deprivation) are also discussed.

The third section of the "General introduction" focuses on the event-related potentials related to the theses. The P3a ERP component is described in details, as it has a substantial role in each thesis study. Furthermore, N1, MMN, N2, P3b, no-go P3 and RON components are briefly presented.

After the General introduction, the "Objectives and thesis points" section summarizes the goals and results of the studies. This is followed by the detailed presentation of the studies. In the first study, the role of the relative complexity of irrelevant unexpected stimuli compared to relevant ones are shown in a 3-stimulus oddball paradigm. In the second study, the effects of Antarctic winterovering, and in the third study, the effects of spaceflight on cognitive functions are presented.

The last section is the "General discussion" that summarizes findings of the three thesis points and places them within the literature.

1.1 Extreme environments

According to Kanas and Manzey (2008), "any environment to which humans are not naturally suited, and which demands complex processes of physiological and psychological adaptation" (p. 15) can be considered extreme, such as space, Antarctica, North Pole, high mountains, submarines among others. In the following, space and Antarctica will be shown in detail.

1.1.1 Space

Spaceflight is considered extreme because of several aspects, such as microgravity, radiation, confinement and isolation (Kanas & Manzey, 2008). Another main factor is the altered light-dark cycle, as the sun rises about every 90 minutes in the low earth orbit where the recent and most of the former manned spaceflights take place.

1.1.1.1 Physiological alterations and stress factors in space

This section briefly reviews factors in space that are relevant to cognitive performance.

1.1.1.1.1 Cephalad-fluid shift and VIIP syndrome

In space, the distribution of blood and other fluids shift from the lower limbs to the torso and head resulting in an about 10% decrease in the lower limbs (cephalad-fluid shift). This restructuring takes place mainly in the first 6 to 10 hours after entering microgravity and is followed by a short decline or plateau (Alexander et al., 2012). The puffy face of astronauts is a visible sign of this phenomenon. It may result in headache, nasal congestion, altered sense of taste and smell (Kanas & Manzey, 2008). According to Mader et al. (2011), visual impairment and intracranial pressure (VIIP) syndrome is a consequence of the cephalad-fluid shift. Visual performance decrements, choroidal folds, cotton-wool spot, optic-disc edema, optic nerve sheath distention, globe flattening and increased intracranial pressure are the main symptoms of this syndrome. Although studies and reports of the past 40 years described declined visual acuity of astronauts, these changes have been considered as a temporary phenomenon until recently. These symptoms could be observed in flight and after landing, even years later. The connection between the cephalad-fluid shift, the increased intracranial pressure, and the visual impairment or the role of other factors influencing VIIP syndrome are not clear (Alexander et al., 2012). Probably the fluid shift can cause increased intracranial pressure, and this also contributes to visual impairment. Other factors are also assumed to cause increased intracranial pressure such as high concentration of sodium in the food and elevated CO₂ concentration (Alexander et al., 2012). The alteration of CO₂ concentration in space habitats will be discussed later.

1.1.1.1.2 Neurovestibular acclimatization

Another main challenge for the physiological system at the beginning of space flight and for 1-2 days after landing is neurovestibular acclimatization. The otolith organs (sacculus and utriculus) in the vestibular system are sensitive to the linear accelerations of the head and the changes of the positions of the body compared to the direction of gravitational force, thus it serves information about vertical direction (Kanas & Manzey, 2008). Without gravity, these organs do not fulfill this function, thus the consistency with information from other sources (e.g. visual, proprioceptive) no longer exists. One of the main consequences of this modification is space motion sickness¹ in the first days of flight (some authors suggest that it may be related to fluid shift), which is more common in inexperienced astronauts (first flight

¹ It is very similar to the terrestrial motion sickness that occurs when there is a discrepancy between visual and vestibular signals. The main symptoms of this sickness are enhanced malaise, loss of appetite, lack of initiative, stomach awareness, brief and sudden vomiting, nausea, and drowsiness (Kanas & Manzey, 2008).

or less training before the flight) and shows inter-individual variations. Higher cognitive functions, such as spatial orientation, spatial attention, pattern and object recognition may also be modified by afferent signals directly from the otolith (Glasauer & Mittelstaedt, 1998; Kanas & Manzey, 2008).

1.1.1.1.3 Sensory-motor system

The absence of gravity also has a direct effect on the *sensory-motor* system, causing sensory-motor discordance, disrupting the usual relationships among afferent and efferent signals (Bock, 1998). The central motor programs (responsible for the efferent control signal to muscles) and the afferent feedback from the ongoing movement to the center are responsible for planning and coordination of voluntary coordinated movements. The afferent feedback signals usually consist of visual (the observation of movement) and proprioceptive (from proprioceptors in the skin, muscles, and joints) signals. On Earth, many central motor programs are evolved by adapting to gravity. In microgravity, the afferent feedback is degraded. As a consequence, the central motor program does not work properly at the beginning of spaceflight until it adapts to the new conditions.

1.1.1.1.4 CO₂ concentration

On the ISS (International Space Station), the ambient CO₂ level is elevated because of respiration (Strangman, Sipes, & Beven, 2014). Even though it is usually diminished by ventilation and chemicals, this concentration is much higher than on Earth (Strangman et al., 2014). On the ISS, the required level of 24-h average of CO₂ is less than 0.7%. According to studies on Earth, this level is lower than what may elicit narcotic effect or cause cognitive impairment. However, the sensors are in fixed positions and therefore, they do not measure local increments in CO₂ levels. For example, in the exercising areas, this concentration is likely higher. Additionally, the elimination is probably not perfect. In addition to the fixed sensors, astronauts are able to use lower-resolution portable sensors, but the data generated by this sensors must be transmitted to the Earth (Matty, 2010), which is time-consuming and often not feasible because of the high workload of astronauts.

1.1.1.1.5 Radiation

There are three main sources of radiation in the low Earth orbit (at which the ISS is): galactic cosmic rays, which arise from outside our solar system, the Earth's trapped radiation belts (Van Allen belts) and the rare solar particle events (Benton & Benton, 2001; Cucinotta,

Alp, Sulzman, & Wang, 2014). On the ISS, the galactic cosmic rays are the dominant radiation source, which consists of protons, helium nuclei and high charge and energy nuclei (Cucinotta et al., 2014).

1.1.1.1.6 Other physiological alterations

In microgravity, the body posture and body movements require less effort than on Earth. Mainly because of this factor and partly because of stress and malnutrition, mass and strength of muscles are diminished in space. Bone density may also decrease, mainly because of microgravity and partly because of low levels of light (resulting in decreased vitamin D3 level) and higher levels of ambient CO₂ (which can lead to respiratory acidosis). The effect of spaceflight on the immune system is less known, but some studies show that it may also be impaired (see review Williams, Kuipers, Mukai, & Thirsk, 2009).

The appetite of astronauts also decreases (it can conclude from anecdotal reports and food consumption) (Da Silva et al., 2002) which contributes to the decrement of body weight during spaceflight (-2,4% per 100 days in space, Matsumoto et al., 2011). The degree of weight loss depends on several factors, such as flight experience (first flight or more), the number of extravehicular activities during the mission, existence of space motion sickness, or preflight exercise habits (Matsumoto et al., 2011; Stein, 2013).

The slight increment of body temperature in space is known (Gundel, Nalishiti, Reucher, Vejvoda, & Zulley, 1993), but a recent, not yet published study (http://www.esa.int/Our_Activities/Human_Spaceflight/Research/Space_fever) shows that body temperature is elevated by 1 °C during the first 2 months of flight and remains on this level for the whole mission. According to Charles and Platts (2010), both arterial systolic and diastolic blood pressure of resting astronauts are lower in space than on Earth, while others report only in the daytime diastolic blood pressure to be changed (Karemaker & Berecki-Gisolf, 2009).

1.1.2 Antarctica

Due to the restricted ability to conduct studies in space (experimental circumstances, mission time of astronauts, the cost of the experiments, etc.) experiments in space analog environments are of great importance, especially for the future space travels. Confinement, isolation and extreme light condition made Antarctic environment a good analog of space. Beyond that, studies in the Antarctica are important per se, because these investigations

increase our knowledge about stressors, such as confinement and isolation that affect several people in residential homes (old people's homes, military bases, boarding schools, submarines, etc.).

Antarctica is the highest, coldest and driest continent on Earth (Olson, 2002). Moreover, the light conditions are also extreme which has a negative effect on circadian rhythm (Arendt, 2012) and consequently worsens sleep. Almost the whole continent is located south of the Antarctic Circle. As a consequence of this geographical position, the constant darkness and constant sunlight, the length of which is increasing from Antarctic Circle to South Pole (1-1 day in the Antarctic Circle and 6-6 months in the South Pole) are both observed in this continent.

There are several research stations on this continent located high above sea level. Consequently, dwelling there may result in hypoxia. Effects of hypoxia on cognitive functions will be described in the second study.

1.1.2.1 Symptoms in the Antarctica

People participating in polar expeditions reported several symptoms, like fatigue, headache, increased appetite, weight gain, decreased motivation, increased sensitivity to social and physical stimuli, sleep problems, interpersonal conflict, and negative affect (Palinkas & Suedfeld, 2008). The occurrence of these symptoms shows seasonal variations. According to the third-quarter phenomenon idea, these symptoms increase after the midpoint of the expedition and diminish toward the end. Thyroid function may also change with seasons (Palinkas & Suedfeld, 2008; Reed et al., 2001), which could lead to cognitive slowing and decline of mood (Palinkas & Suedfeld, 2008). Furthermore, the decreased light intensity and light-dependent melatonin level in winter can cause subsyndromal seasonal affective disorder characterized by negative affect and loss of energy among others.

1.1.3 Sleep in the extreme environments

According to the two-process model of sleep regulation (Achermann, 2004; Borbely, 1982), sleep is regulated by the interaction of two systems; homeostatic and circadian. The characteristic of the homeostatic system is that sleep propensity increases over time spent awake and declines during sleep. The circadian system has an endogenous circadian pacemaker, the nucleus suprachiasmaticus, located in the hypothalamus. Due to this regulation, there are two nadirs, one in the early morning and one in the afternoon, concerning

vigilance, arousal, and performance. Vigilance and performance are also regulated by exogenous factors or "zeitgebers" (e.g. light-dark cycle, time spent awake, social interaction, and mealtime). Among these factors, the light plays crucial role in adjusting to the 24-h circadian rhythm, which has an effect on the retinal ganglion cells that project to the nucleus suprachiasmaticus.

In space, circadian rhythm and sleep are affected by several factors. Astronauts are frequently required to modify their sleep-wake schedules (for example when a cargo spacecraft is arriving, the crew is required to modify their schedule in the preceding days; Mallis & DeRoshia, 2005) that, in turn, will disturb their circadian rhythm. Furthermore, the alteration of the light-dark cycle can also disrupt circadian rhythm in the above-described manner. Additionally, other stress factors, such as microgravity, temperature, noise, and isolation can also negatively affect sleep (e.g. Mallis & DeRoshia, 2005; Pavy Le-Traon & Roussel, 1993). Accordingly, several studies investigated sleep and circadian rhythm in space during both short-term and long-term missions (Dijk et al., 2001; Gundel et al., 1993; Gundel, Polyakov, & Zulley, 1997; Mallis & DeRoshia, 2005; Monk, Buysse, Billy, Kennedy, & Willrich, 1998; Monk, Kennedy, Rose, & Linenger, 2001). Many studies reported alteration in indicators of circadian rhythm (such as circadian phase delay of body temperature, reduced amplitude of the circadian body temperature, phase delay of alertness) (Dijk et al., 2001; Gundel et al., 1993; Gundel et al., 1997), but others report no changes (Monk et al., 1998), or changes limited only to the last part of a 122 days-long mission (Monk et al., 2001). Numerous factors may contribute to the contradictory results. Sample size, for example, may make comparisons between studies difficult as several studies had only one subject (Gundel et al., 1993; Monk et al., 2001), while the others studies had 4-5 subjects. Another factor is related to timing of data collection and methodology were chosen for comparing data time points. While in-flight measurements were compared to the pre-flight data in the studies of Dijk et al. (2001); Gundel et al. (1993); Gundel et al. (1997), in the study of Monk et al. (2001) there was no data collection before flight and the in-flight measurements were compared to each other. Additionally, in the research of Monk et al. (1998), in-flight data was compared to the post-flight measurements in three subjects out of four and compared to preflight measurement in one subject.

Changes in some stages of sleep are also observed in space: proportion and latency of REM sleep is decreased, slow-wave sleep is redistributed from the first to the second sleep cycle (Gundel et al., 1993; Monk et al., 1998). These latter could reflect changes of the homeostatic system (Kanas & Manzey, 2008).

Barger and her colleagues (Barger et al., 2014) were the first who investigated the effects of short-term (space shuttle missions) and long-term (ISS) missions on sleep in a large sample. They have monitored sleep and related habits including the usage of sleep medications of astronauts three months before launch, 11 days before launch, in-flight and for a week after landing. Despite NASA's recommendation of 8 hours sleep per day (Evans-Flynn et al., 2016), participating astronauts slept less than 8 hours during he whole mission. They only slept 6 hours per day on average during in-flight and 11 days before the flight. They have slept only 6.5 hours on average 3 months before launch which is also less than 8 hours, but it is significantly more than 11 days before launch and during flight. Results also revealed that sleep medications were also used frequently during flight, which was also common on previous flights (Mallis & DeRoshia, 2005). Additionally, several studies confirmed that sleep medication use is more prevalent in space than on Earth (Evans-Flynn et al., 2016).

Concerning Antarctica, several Antarctic studies have reported sleep problems and negative impact of Antarctic winter on circadian rhythm (Arendt, 2012; Palinkas & Suedfeld, 2008). Studies with polysomnogram from the 60s and 70s show that slow-wave sleep (stage 4) is decreased during Antarctic winter (Arendt, 2012). In a more recent study, Bhattacharyya, Pal, Sharma, and Majumdar (2008) investigated sleep of 6 subjects during a year in Antarctica and they show decreased slow-wave sleep (stages 3 and 4) in each month of the year compared to pre-antarctic measurements, however this decrement was most prominent during winter months. Additionally, they found decreased sleeping time in Antarctica and increased proportion of stages 1 and 2 sleep, especially during winter. They also reported increment of REM sleep proportion during winter months while other studies found oppositing results (Natani, Shurley, Pierce, & Brooks, 1970).

Even though sleep research in space and Antarctica is controversial (e.g. the number of subjects, measurement points), results show that astronauts sleep less in space than on Earth. The quality of sleep is also seem to be lower both in space and in Antarctica, although further research is needed on this specific field.

1.1.4 Short summary

The previous section shows that several stress factors are present both in the space station and in Antarctica such as isolation, confinement, extreme light condition. Furthermore, the disturbed circadian rhythm caused by extreme light condition together with other stress factors might lead to sleep problems. The thyroid functions may be altered in both environments, although concerning the spaceflight, this conclusion derives solely from post-flight thyroid measurements (Bricker, 1979). In addition to the common stress factors, there are specific effects in both environments that can further hinder cognitive functions. Such factor in space is microgravity that causes neurovestibular, sensory-motor and cardiovascular changes and may cause visual impairment and intracranial pressure syndrome (i.e. VIIP syndrome). In addition, CO₂ level is much higher in spacecraft than on Earth. The elevated CO₂ concentration and ionizing radiation may also adversely affect cognitive functions. There are no such stress factors in Antarctica, but due to the high altitude of research stations, this condition may cause moderate hypoxia, which may also impact cognitive performance.

In the next section, studies of cognitive functions in space and Antarctica are reviewed. This is followed by a description of the effect of VIIP syndrome, elevated CO2, cephalad-fluid shift, isolation, confinement, sleep deprivation and ionizing radiation on cognitive functions.

1.2 Cognitive performance

1.2.1 Cognitive performance in space

During ongoing and past space missions in recent years, astronauts have to spend half a year in space which is a remarkable amount of time. Half year in microgravity imposes many tasks for astronauts, some of which are not completely unknown to them due to the training sessions on Earth. Despite these training the new environmental factors such as alteration of light-dark cycle, microgravity could make the execution of tasks way harder. Cognitive performance in space has been investigated for years, but by relatively small number of studies compared to the number of investigations of physiological changes. Furthermore, these studies are very diverse concerning the mission length, sample size, measurement points, tasks and analysis of results. As the oldest studies are more than 30 years old when the duration of the majority of the missions was limited, the effects of short-term missions on cognitive functions are more investigated than the effects of long-term missions. Due to the nature of space missions, samples sizes are relatively low in microgravity-related cognitive studies, the largest number of subjects in a study is 8, which is very rare (Leone, Lipshits, Gurfinkel, & Berthoz, 1995a, 1995b), on average it is 2-6 (e.g. Kelly, Hienz, Zarcone, Wurster, & Brady, 2005; Pattyn et al., 2009). Studies with only one subject are also common (e.g. Manzey, Lorenz, & Poljakov, 1998; Manzey, Lorenz, Schiewe, Finell, & Thiele, 1993). In general, these studies compared several (or rarely one) in-flight measurements to pre-flight and post-flight measurements. Except for some investigations, these studies measured only behavioral data. Only Cheron et al. (2014) investigated the impact of space mission on cognitive functions with event-related potentials method, but they measured only the P1 and N1 visual evoked potentials.

In the following, the effect of space mission on cognitive functions will be summarized. The cognitive tasks used in space research will be classified into six main categories based on the most required cognitive function for the given task. The categories are as follows: Perception and visuomotor performance, Attention, Memory, Learning, Executive functions, Reasoning and mathematical processing.

1.2.1.1 Perception and visuomotor performance

Although anecdotal reports suggest that sense of time changes in space (Christensen & Talbot, 1986) studies of time estimation conducted in space do not support it (e.g. Benke,

Koserenko, & Gerstenbrand, 1993; Kelly et al., 2005; Ratino, Repperger, Goodyear, Potor, & Rodriguez, 1988). For example results of Ratino et al., (1988) show that astronauts gradually overestimate short intervals (2s) during their flight, but this was only significant on the day of landing compared to pre-flight.

A relatively large number of studies investigated the sensory-motor system in space. Two tasks, the tracking, and pointing arm movement² are frequently used to measure evehand coordination in space. Table 1 shows that performance decrement in space can be observed with both tasks. Several studies demonstrated that astronauts tend to make more errors in space in the tracking task during the whole 8-days mission (Manzey et al., 1993), in the first 2 weeks (Manzey et al., 1998) or during 5-6 months in a long-term flight (Bock, 1998). Additionally, Manzey, Lorenz, Heuers, and Sangals (2000) reported more tracking errors even in a 3-weeks long flight, however, only half of their measurements differed significantly from the baseline. Another performance indicator, the movement time also increased in flight in a modified tracking task (Newman & Lathan, 1999) and pointing arm movement task (Berger et al., 1997; Bock, Fowler, & Comfort, 2001). In contrast to these results, others did not report performance decrement in the tracking task (Bock et al., 2001; Eddy, Schiflett, Schlegel, & Shehab, 1998; Fowler, Bock, & Comfort, 2000). Moreover, Eddy et al. (1998) showed performance improvement in 2 out of 4 astronauts, but contrary to other tracking task studies they fitted learning curve to the pre-flight measurements and they measured a different performance index.

According to Kanas and Manzey (2008), the impairments in these tasks could be explained by the "re-interpretation hypothesis" (Bock, Arnold, & Cheung, 1996). In line with this hypothesis, astronauts use inadequate muscle strength in space for executing a movement, they underestimate the mass (Manzey et al., 2000), so the microgravity has a direct effect on motor control which is supported by many other studies (Heuer, Manzey, Lorenz, & Sangals, 2003; Manzey et al., 2000). The reason is that contrary to Earth, information about the weight is not available in space³. The loss of weight information can also contribute to a worsening mass discrimination in space (Ross et al., 1987).

² The control of hand movements is important for both tasks. The hand moves in a specified trajectory in the tracking task while a specific point should be approached in the pointing task.

³ In the static position or constant speed motion of the objects the pressure-sensing system plays a role in the perception of weight while when causing active accelerated movement the active muscular system plays a role in the perception of weight and mass (Kanas & Manzey, 2008; Ross, Schwartz, & Emmerson, 1987). In space, the static pressure-sensing system does not provide information only the active system, and it serves information only about the mass.

Besides the sensory-motor coordination, a greater emphasis was placed on spatial orientation, spatial perception, and representation in the cognitive space research. On Earth, gravity provides a reference framework, assigning what is upright and it helps to detect when the body position differs from that direction. Besides, the sight of the surrounding objects can also help us, such as the orientation of the tree (the leaves are up, and the root is down). In the absence of gravity in space, the vestibular, proprioceptive and tactile operations are changed, and visual system is the main source of information (Clément, Berthoz, & Lestienne, 1987). Consequently, spatial illusions are quite frequent. Most of the illusions appear at the beginning of space travel for minutes or hours, less often it takes for a few days or weeks, and sometimes they reappear. For example, Clément et al. (1987) found that while even a smaller rotation of the environment is enough for astronauts not to be able to reconstruct the original environment at the beginning of the mission, they could mentally reconstruct the surroundings even in the upside-down position after few days in space. Several studies have pointed out the importance of self-centered reference frames in the absence of gravity, such as the retinal frame or the own body-head orientation which is confirmed by the study of McIntyre, Lipshits, Zaoui, Berthoz, and Gurfinkel (2001). In this study, the task of the subjects was to adjust the position of the second line of the pairs to the first one (reference line). Their results show that the oblique effect, i.e., the horizontal and vertical preference against the oblique, remains unchanged in the space. According to the authors, spatial orientation works well after a short adaptation period in space despite the lack of the multi-modal reference frame that people use for visual orientation on Earth. However, the time frame of adaptation is not clear from this study since only two subjects performed measurements at the beginning of the 6month space mission, the oblique effect was present in the first measurement (5 days after launch) only in one subject, while it was present in the other subject only during the subsequent measurements. Another example of the importance of egocentric reference frame is the phenomenon that inverted faces are difficult to be detected, which remains the same in space (de Schonen, Leone, & Lipshits, 1998), therefore, the authors concluded that the retina serves as the reference frame for face recognition.

1.2.1.2 Attention

Spaceflight-related changes in psychomotor speed and attention, divided-attention and directed attention were investigated in several studies.

The reaction time tasks used to measure psychomotor speed and attention were shown no performance degradation in space (see Table 1) in most studies. Out of the two studies that

demonstrated changes in space, one found increased reaction times only in a subset of the subjects at the beginning of the mission (Ratino et al., 1988). The other study found increased error rates variability in space (Fowler et al., 2000), what the authors attributed to the decline of strategic control.

The divided-attention has been measured by dual-tasks in which subjects had to perform two task simultaneously. In several studies the Sternberg task and the tracking task were used same time (Eddy et al., 1998; Manzey et al., 1998; Manzey, Lorenz, Schiewe, Finell, & Thiele, 1995). In other studies the tracking task and a reaction time task was required to perform at the same time with the tracking task being the primary task (Bock et al., 2001; Bock, Weigelt, & Bloomberg, 2010; Fowler et al., 2000). Most of these studies (except for Eddy et al., 1998) compared the change of the difference between the performance of dual and single⁴ tasks in space to baseline conditions. Manzey et al. (1995) and Manzey et al. (1998), for example, found decreased performance during the first 1-2 weeks in space in some measurements. In the set of dual-tasks in Fowler et al. (2000) which applied four types of reaction time task, the performance was impaired in the tracking task only when the reaction time task required complex motor programming (rhythmic tapping).

Measuring the directed attention, Eddy et al. (1998) assessed mathematical and manikin (they had to judge the orientation of small figures) tasks in a random order. The switching time was increased in two of the four subjects during the mathematical task (when preceding by manikin) in-flight.

1.2.1.3 *Memory*

To examine short-term memory in space the Sternberg task was the most often used paradigm (Eddy et al., 1998; Kelly et al., 2005; Manzey et al., 1998; Manzey et al., 1993, 1995; Newman & Lathan, 1999), while the probed recall memory task and continuous recognition memory task was only used by one study (Dijk et al., 2001; Eddy et al., 1998). Performance decrement in space with the modified Sternberg task was only found by Kelly et al. (2005), but contrary to others, they analyzed Yes and No trials separately. Dijk et al. (2001) also found declined performance in the probed recall memory task in space, but they did not describe which inflight-ground pairs were significantly different. In addition, except

⁴ when subjects had to perform only one task that is part of the dual-task

⁵ They found that the reaction time differences between Yes and No trials are significantly increased as a function of number of digits in the memory set during in-flight.

for one astronaut (out of 4) in the research of Eddy et al. (1998), performance did not change in space in spatial memory tasks (Benke, Koserenko, & Gerstenbrand, 1993; Benke, Koserenko, Watson, & Gerstenbrand, 1993) and in the line orientation task that requires short-term memory and visuospatial perception (Benke, Koserenko, & Gerstenbrand, 1993; Benke, Koserenko, Watson, et al., 1993; McIntyre et al., 2001).

Long-term memory changes in space were investigated by only one study. Results of de Schonen et al. (1998) show that astronauts remember faces learned on Earth as well in space as in the ground.

1.2.1.4 *Learning*

There are some experimental data concerning learning in space. Most of these data are not directly derived from research on learning. For example, Leone et al. (1995b) and Leone et al. (1995a) found improvement in mental rotation and polygon symmetry detection tasks in space, which is clearly a practice effect as the control group showed the same results.

Additionally, some research directly investigated learning new things in space. de Schonen et al. (1998) found that learning and recognition of new faces are impaired in space, but Kelly et al. (2005) did not show any significant changes in learning new sequences.

1.2.1.5 Executive functions

Only two studies investigated the effect of spaceflight on executive functions (Benke, Koserenko, Watson, et al., 1993; Pattyn et al., 2009) using the Stroop paradigm. One of them used emotional version along with the classical paradigm (Pattyn, Migeotte, Kolinsky, Morais, & Zizi, 2005; Pattyn et al., 2009). Decreased in-flight performance was only found in the personally relevant emotional Stroop, while not in the classical Stroop task. However, the lack of change in the classical Stroop may be –at least partly attributed to the fact that Benke, Koserenko, Watson, et al. (1993) did not analyze the congruent and incongruent events separately.

1.2.1.6 Reasoning and mathematical processing

While none of the studies found performance changes in grammatical/logical reasoning task in space (Manzey et al., 1998; Manzey et al., 1993), Eddy et al. (1998) showed decreased performance in mathematical processing task in two subjects out of four.

1.2.1.7 Summary of the results of cognitive performance in space

In most of the studies, sensory-motor functions were investigated as these functions play a crucial role for example in the landing, vehicle management, joining space module to another space module in which tasks any fault can lead even to disaster. Early anecdotal reports drew attention to the importance of these functions, although this notion is less supported by the results of the research.

Taking the above-described results together it can be said that contrary to the expectations, most of the research has not found clear performance impairment in space. Decreased performance was most commonly observed with the tracking task. Among tasks that require attentional functions, performance deterioration was revealed in some cases with the dual task. As for memory, results show that this function is not impaired in space except for one or two cases. Regarding the executive functions in space, very few studies have been conducted so far and found no performance change, except for one study, which used an emotional version of the Stroop task.

Several factors complicate the interpretation of the results: 1. Various analysis methods were used even in research with the same or similar tasks; 2. The baseline measurement points are also diverse, especially regarding the timeframe before launch; 3. The in-flight measurements are often merged while all measuring points are treated separately in other studies; 4. Single subject data analysis was used in some studies while individual data was grouped in other studies; 5. In some cases, learning curve was fitted to the data or subjects practiced many times before the first measurement, and in many cases, the comparison with the control group serves to eliminate learning effect, while many studies did not account for practice effect; 6. The majority of the research which showed performance decrement in space are single-subject case studies.

Kanas and Manzey (2008) distinguished two main factors that could affect cognitive performance in space. One main factor consists of the direct effects of microgravity. Microgravity has a direct impact on vestibular and sensory-motor systems as described at the beginning of the introduction. The other main factor includes nonspecific stress factors, that are not limited to space, but may also occur in other environments, such as high workload, sleep loss, mental fatigue, and physical or emotional burden. They did not give a full list of these factors, so they did not describe where the elevated CO2 level and ionizing radiation belong in this nomenclature. The effects of workload and fatigue on performance were investigated in some studies described above (e.g. Eddy et al., 1998; Kelly et al., 2005;

Manzey et al., 1998; Manzey et al., 2000) and the results of Manzey et al. (1998), Manzey et al. (2000) and Eddy et al. (1998) show that the higher subjective workload and/or fatigue is associated with performance decrement in many cases.

According to Kanas and Manzey (2008), the performance decrement can solely be attributed to the nonspecific stress factors in dual-tasks (Manzey et al., 1998; Manzey et al., 1995) while both factors (microgravity and stress) may play a significant role in the tracking task (Manzey et al., 1998; Manzey et al., 1993, 1995; Manzey et al., 2000). In line with their idea, the tracking task requires attentional processes besides the sensory-motor functions and the nonspecific stress factors affect these attentional processes while microgravity has a direct impact on sensory-motor functions.

In the following, the factors that could affect cognitive functions are categorized into three groups, namely: (1) the direct effect of microgravity, (2) nonspecific stress factors, and (3) other environmental factors. Although Kanas and Manzey (2008) categorize changes related to the vestibular and the sensory-motor system as a direct effect of microgravity, I also include the cardiovascular changes and the VIIP syndrome into this category. Concerning the nonspecific stress factors, this category includes mental fatigue, workload, sleep loss or sleep problems, physical and emotional burden, isolation and confinement. Other environmental stress factors include elevated CO2 and ionizing radiation.

Table 1. Cognitive tests in which performance has been measured in space.

Cognitive test	Changes found in space	Authors
Perception, visuomotor performance		
tracking task	\	Manzey et al. (1993) Manzey et al. (1995)
	\	Manzey et al. (1998)
	\	Manzey et al. (2000)
	$\leftrightarrow \uparrow$	Eddy et al. (1998)
	1	Bock et al. (2010)
	1	Newman and Lathan (1999)

Cognitive test	Changes found in space	Authors
tracking task	\leftrightarrow	Fowler et al. (2000)
	\leftrightarrow	Bock et al. (2001)
pointing arm movement	↓	Bock et al. (2001)
	↓	Berger et al. (1997)
digit-symbol substitution	\leftrightarrow	Kelly et al. (2005)
line orientation test	\leftrightarrow	Benke, Koserenko, Watson, et al. (1993) Benke, Koserenko, and Gerstenbrand (1993)
spatial processing (manikin task)	\leftrightarrow	Eddy et al. (1998)
step-tracking kinematics	1	Sangals, Heuer, Manzey, and Lorenz (1999)
time-estimation	\leftrightarrow	Benke, Koserenko, and Gerstenbrand (1993)
	\leftrightarrow	Kelly et al. (2005)
	\leftrightarrow	Ratino et al. (1988)
motor timing	↓	Semjen, Leone, and Lipshits (1998)
mass discrimination	↓	Ross et al. (1987)
mental rotation	1	Leone et al. (1995b)
	1	Leone et al. (1995a)
	1	Clément et al. (1987)
	1	Matsakis, Lipshits, Gurfinkel, and Berthoz (1993)
polygon symmetry detection	1	Leone et al. (1995a)
observed movement and orientation	↓	Tafforin and Lambin (1993)
Attention		
simple RT task	$\downarrow \leftrightarrow$	Fowler et al. (2000)
	$\downarrow \leftrightarrow$	Ratino et al. (1988)
simple RT task	\leftrightarrow	Benke, Koserenko, Watson, et al. (1993) Benke, Koserenko, and Gerstenbrand (1993)

Cognitive test	Changes found in space	Authors
simple RT task	\leftrightarrow	Bock et al. (2010)
PVT	\leftrightarrow	Dijk et al. (2001)
choice/complex RT	$\downarrow \leftrightarrow$	Ratino et al. (1988)
	\leftrightarrow	Benke, Koserenko, Watson, et al. (1993) Benke, Koserenko, and Gerstenbrand (1993)
	\leftrightarrow	Bock et al. (2010)
dual-task	$\downarrow \leftrightarrow$	Manzey et al. (1995)
	$\downarrow \leftrightarrow$	Manzey et al. (1998)
	\leftrightarrow	Eddy et al. (1998)
	\leftrightarrow	Fowler et al. (2000) Bock et al. (2001)
	$\downarrow \longleftrightarrow$	Bock et al. (2010)
directed attention: random switching between Manikin and Mathematical processing	$\downarrow \leftrightarrow$	Eddy et al. (1998)
Memory		
Sternberg paradigm	\leftrightarrow	Manzey et al. (1993)
	\leftrightarrow	Manzey et al. (1995)
	\leftrightarrow	Manzey et al. (1998)
	\leftrightarrow	Eddy et al. (1998)
	\leftrightarrow	Newman and Lathan (1999)
	↓	Kelly et al. (2005)
probed recall memory (PRM)	↓	Dijk et al. (2001)
continuous recognition memory (WM)	\leftrightarrow	Eddy et al. (1998)
spatial WM	\leftrightarrow	Benke, Koserenko, Watson, et al. (1993), Benke, Koserenko, and Gerstenbrand (1993)
spatial matrix test	$\downarrow \leftrightarrow$	Eddy et al. (1998)
line orientation memorized	\leftrightarrow	McIntyre et al. (2001)

Cognitive test	Changes found in space	Authors
line orientation memorized	\leftrightarrow	Benke, Koserenko, Watson, et al. (1993),
		Benke, Koserenko, and Gerstenbrand (1993)
long-term memory of faces	\leftrightarrow	de Schonen et al. (1998)
Learning		
	↓	de Schonen et al. (1998)
	\leftrightarrow	Kelly et al. (2005)
Executive functions		
Stroop paradigm	\leftrightarrow	Benke, Koserenko, Watson, et al. (1993)
	\leftrightarrow	Pattyn et al. (2009), Pattyn et al. (2005)
emotional Stroop	↓	Pattyn et al. (2009), Pattyn et al. (2005)
Reasoning and mathematical processing		
grammatical reasoning	\leftrightarrow	Manzey et al. (1993)
	\leftrightarrow	Manzey et al. (1998)
mathematical processing	$\downarrow \leftrightarrow$	Eddy et al. (1998)

Note. Upwards arrow - performance improvement; downwards arrow - performance deterioration; left right arrow - unchanged performance.

1.2.2 Cognitive performance in Antarctica

Although there are several research stations in Antarctica, only a few studies investigated the effects of Antarctic environment on cognitive functions. In this environment fluctuations of sunshine duration, hypoxia, isolation, confinement and consequently impaired sleep are the main factors that could affect cognitive performance adversely.

In the following, the impact of Antarctic conditions on cognitive functions will be summarized. Similarly to the description of cognitive research in space, Antarctic studies will be categorized as follows: Perception and visuomotor performance, Attention, Memory, Learning, Executive functions, and Reasoning and mathematical processing.

1.2.2.1 Perception and visuomotor performance

Perception and visuomotor performance were investigated in some studies in Antarctica. These studies found that performance in the time estimation, perceptual constancy (Necker-cube) and digit-symbol substitution tasks did not change (Defayolle, Boutelier, Bachelard, Rivolier, & Taylor, 1985; Palinkas, Reedy, Shepanek, et al., 2007; Taylor, 1991) or even improved (Defayolle et al., 1985; Palinkas, Reedy, Smith, et al., 2007; F. U. J. Paul, Mandal, Ramachandran, & Panwar, 2010). Although these studies did not report performance decrement in this environment, it is not possible to clearly interpret the results in many studies due to the methods they used. Such complicating factor is the use of combined performance index in the study of Palinkas, Reedy, Shepanek, et al. (2007) for example, and in the study of Palinkas, Reedy, Smith, et al. (2007) which analyzed the data of the digit-symbol substitution task together with other tasks (Sternberg task, delayed digit-symbol substitution, continuous performance, delayed match-to-sample). While several studies investigated performance with the tracking task during spaceflight, only one research applied it as a single task and as a part of dual-task in Antarctic environment (Le Scanff, Larue, & Rosnet, 1997). The results are not clear since the authors did not report the results of the single version. As a part of the dual task, tracking performance decreased in midwinter (root mean square deviation increased), but this study did not specify which measurement pairs were significant.

1.2.2.2 Attention

Although deterioration of attention was described by anecdotal reports (Palinkas, 1992) and self-report studies (Mullin, 1960), it is not supported by any research. As Table 2 shows, performance did not deteriorate (Abeln et al., 2015; Defayolle et al., 1985; Le Scanff et al., 1997; Palinkas, Reedy, Shepanek, et al., 2007; Palinkas, Reedy, Smith, et al., 2007; Taylor, 1991) in simple and complex reaction time tasks, speed match task, visual discrimination task and continuous performance task, while some studies even found improved performance in visual discrimination task, continuous performance task and serial search task (Monk et al., 2001; Palinkas, Reedy, Smith, et al., 2007; Taylor & Duncum, 1987). Although one study applied dual-task in Antarctica (Le Scanff et al., 1997), the authors did not analyze the dual-simple differences, so no data is available concerning the divided attention.

1.2.2.3 *Memory*

Several studies investigated memory in Antarctica with Sternberg, recognition memory, delayed recognition memory, digit span, delayed match-to-sample, delayed digit-symbol substitution and memory matrix tasks (see Table 2). Except for the study of Reed et al. (2001), which reported impaired performance in a match-to-sample task in the first four months of the Antarctic residence, the rest of the studies found no decrement in this environment.

1.2.2.4 Learning

Although the impact of Antarctic environment on learning has not yet been examined directly, similarly to space-related research, improvement in some studies can be attributed to practice effect (e.g. Defayolle et al., 1985).

1.2.2.5 Executive functions

Two studies applied the Stroop task in Antarctica (see Table 2). One of them reported improved performance (Defayolle et al., 1985) and the other found unchanged performance (Taylor, 1991). However, none of them serve clear evidence concerning executive functions in this environment, as Defayolle et al. (1985) did not show separate performance calculation for different stimuli types and Taylor (1991) did not describe any analysis of the data.

1.2.2.6 Reasoning and mathematical processing

As Table 2 shows that results of these tasks demonstrated all kind of outcomes from deterioration to improvement. Concretely, Palinkas, Reedy, Shepanek, et al. (2007), McCormick, Taylor, Rivolier, and Cazes (1985) and Taylor (1991) did not found any change in the various reasoning tasks, while Palinkas, Reedy, Smith, et al. (2007), and Monk et al. (2001) demonstrated improvement in a logical reasoning task. Only White, Taylor, and McCormick (1983) found performance deterioration in a paper folding task. Concerning studies investigating mathematical processing, results are also controversial (Abeln et al., 2015; Terelak, Turlejski, Szczechura, Rozynski, & Cieciura, 1985, cited by Strangman et al., 2014). Abeln et al. (2015) found unchanged performance in the Chalkboard Challenge task, in which participants had to indicate which sum is greater of two arithmetical sums. The other study (Terelak et al., 1985, cited by Strangman et al., 2014) found mixed results (work capacity decreased, but efficiency improved) in a continuous math addition task.

1.2.2.7 Summary of the results of cognitive performance in Antarctica

Most of the results indicate that cognitive functions are maintained in Antarctica. However, several factors complicate the interpretation of these results. There are studies that only reported the analysis of the combined performance indexes of many tasks (Palinkas, Reedy, Shepanek, et al., 2007; Palinkas, Reedy, Smith, et al., 2007) making the evaluation of single task performance impossible. In other studies, authors described only part of their results (Le Scanff et al., 1997), or just reported the findings without any detailed description of their analysis (Taylor, 1991). In several cases, the lack of appropriate baseline and/or control group also makes the interpretation difficult. For example, Sauer, Hockey, and Wastell (1999b) suggested that the unchanged performance in the simulated life support system task could be attributed to the lack of expected learning effect, which is only a speculation without any control group. Additionally, the number of measurement points is also diverse in the available research. Furthermore, when interpreting results, the location of research stations compared to see level is important since it determines the level of hypoxia and the dark-light condition which influence the level of sleep impairment. As various studies investigated performance on various research stations, this factor should also be taken into account. The study of Collet et al. (2015) for example demonstrated that subjects from a sea level station slept more, their sleep efficiency (the ratio of sleeping time and time in bed) was higher and their wake time after the first stage of sleep was shorter compared to subjects from a high altitude station (3233 m that correspond to 3880 m along the Equator). The adverse effects of impaired sleep on cognitive functions are described below.

Table 2. Cognitive tests in which performance has been measured in Antarctica.

Cognitive test	Changes found in Antarctica	Authors
Perception, visuomotor performance		
tracking task	$\leftrightarrow \downarrow$	Le Scanff et al. (1997)
digit-symbol substitution	1	F. U. J. Paul et al. (2010)
	1	Palinkas, Reedy, Smith, et al. (2007)
	\leftrightarrow	Palinkas, Reedy, Shepanek, et al. (2007)
time estimation	\leftrightarrow	Defayolle et al. (1985)

Cognitive test	Changes found in Antarctica	Authors
time estimation	\leftrightarrow	Taylor (1991)
Necker cube (perceptual constancy)	1	Defayolle et al. (1985)
	\leftrightarrow	Taylor (1991)
Attention		
simple RT	\leftrightarrow	Defayolle et al. (1985)
	\leftrightarrow	Palinkas, Reedy, Smith, et al. (2007)
	\leftrightarrow	Palinkas, Reedy, Shepanek, et al. (2007)
	\leftrightarrow	Taylor (1991)
complex RT	\leftrightarrow	Le Scanff et al. (1997)
dual-task	?	Le Scanff et al. (1997)
speed match task	\leftrightarrow	Abeln et al. (2015)
visual discrimination task	\leftrightarrow	Defayolle et al. (1985)
	1	Taylor and Duncum (1987)
	\leftrightarrow	Taylor (1991)
serial search task	1	Monk et al. (2001)
continuous performance task (sustained attention)	1	Palinkas, Reedy, Smith, et al. (2007)
	\leftrightarrow	Palinkas, Reedy, Shepanek, et al. (2007)
Memory		
Sternberg paradigm	1	Palinkas, Reedy, Smith, et al. (2007)
	\leftrightarrow	Palinkas, Reedy, Shepanek, et al. (2007)
	?	Le Scanff et al. (1997)
digit span	\leftrightarrow	F. U. J. Paul et al. (2010)
	1	Defayolle et al. (1985)
	\leftrightarrow	Taylor and Duncum (1987)
	\leftrightarrow	Taylor (1991)
recognition memory	1	F. U. J. Paul et al. (2010)

Cognitive test	Changes found in Antarctica	Authors
delayed match-to-sample	1	Palinkas, Reedy, Smith, et al. (2007)
	\leftrightarrow	Palinkas, Reedy, Shepanek, et al. (2007)
	\	Reed et al. (2001)
memory matrix (spatial memory)	\leftrightarrow	Abeln et al. (2015)
Executive function		
Stroop	1	Defayolle et al. (1985)
	\leftrightarrow	Taylor (1991)
Reasoning and mathematical processing		
logical reasoning	↑	Palinkas, Reedy, Smith, et al. (2007)
	\leftrightarrow	Palinkas, Reedy, Shepanek, et al. (2007)
	↑	Monk et al. (2001)
paper folding test (nonverbal reasoning)	\leftrightarrow	McCormick et al. (1985)
	\leftrightarrow	Taylor (1991)
	↓	White et al. (1983)
series completion (verbal reasoning)	\leftrightarrow	McCormick et al. (1985)
Kraepelin test (continuous math addition)	↑↓	Terelak et al. (1985) (cited by Strangman et al., 2014)
Chalkboard Challange (arithmetical task)	\leftrightarrow	Abeln et al. (2015)
Others		
Cabin Air Management System	\leftrightarrow	Sauer, Hockey, et al. (1999b)

Note. Upwards arrow - performance improvement; downwards arrow - performance deterioration; left right arrow - unchanged performance; question mark - no data available.

1.2.3 Effects of VIIP syndrome and CO_2 concentration on cognitive functions

As described in the "Extreme environments" section, the VIIP syndrome can be observed during flight and after landing. The effect of VIIP syndrome on cognitive functions has not been investigated yet, although a very similar syndrome, the idiopathic intracranial hypertension (IIH) is known to impair vision and cognitive functions (Strangman et al., 2014) (executive functions, visuospatial memory, verbal and nonverbal learning and memory; these functions were assessed by neuropsychological tests, such as the Wechsler memory scale, Rey-Osterreich's complex figure test, and Trail making test etc.). According to more recent studies (Yri, Fagerlund, Forchhammer, & Jensen, 2014; Zur, Naftaliev, & Kesler, 2015) IIH syndrome may also damage attentional functions. Although IIH and VIIP are similar syndromes, the conclusions derived from IIH syndrome studies could only be applied with care to the VIIP syndrome as astronauts with VIIP syndrome do not display all of the IIH symptoms (for example, chronic headache and pulsatile tinnitus; Alexander et al., 2012).

One study (Chen, Wang, Mao, Dong, & Yang, 2012) found negative correlation between intracranial pressure (ICP) and EEG spectrum in patients who suffered from elevated ICP. Since they calculated a global index from the spectral components (1/(median frequency x delta ratio)), it does not give information about which components are affected. Animal studies predominantly report increased ICP to have no effect on EEG (e.g. Notermans & Boonstra, 1969).

The elevated CO₂ concentration in space vehicles is another factor that could impair cognitive functions. Manzey and Lorenz (1998) (cited by Strangman et al., 2014) investigated the effects of 0.7 and 1.2 % CO₂ levels in several cognitive tasks. They did not find any changes in the Sternberg, grammatical reasoning and dual tasks during both levels of CO₂ exposures but performance deteriorated in the tracking task during the 1.2 % CO₂ exposure. Additionally, two studies (James & Zalesak, 2013; Satish et al., 2012) found that decision making impaired when subjects are exposed to about 0.2% CO₂ for 2.5 hours. Other studies measured the effect of higher CO₂ concentrations (see review Strangman et al., 2014). Although the required level of 24-h average of CO₂ is less than 0.7% (5.3 mmHg) on the ISS (0.23 mmHg on Earth), the results of these studies should also be taken into account, as airflow is greatly reduced in microgravity and local pockets of CO₂ are formed around the mouth and nose. The extent of this letter effect is unknown as the sensors do not measure it. Furthermore, there are peaks when the value of CO₂ is significantly higher than 0.7%. As a

consequence, it can occur that astronauts are exposed to a much higher concentration of CO₂ than permitted. This is supported by the fact that astronauts frequently report the so-called CO₂ headache. Higher CO₂ concentration could significantly impair cognitive functions, such as perception, reasoning, mathematical processing (see review Strangman et al., 2014) and visuomotor performance as confirmed by the above-described results of Manzey and Lorenz (1998).

Increased CO₂ concentration (hypercapnia) causes dilation of cerebral arteries and arterioles and increased blood flow (Cipolla, 2009). In line with this, Ogoh et al. (2014) found that 2% CO₂ inhalation resulted in increased cerebral blood flow, however, this had no effect on the performance of the Stroop task (that consisted of incongruent stimuli) during rest or prolonged exercise (50 minutes).

1.2.4 Cognitive functions in bed rest studies

The effect of cephalad fluid shift on cognitive functions had been investigated during head-down bed rest (HDBR) studies in which subjects remain in head-down tilt position (from -6° to -10°) for prolonged time. This position not only simulates the fluid shift but other physiological effects of microgravity (e.g. decline of bone density etc) and physical inactivity (Pavy-Le Traon, Heer, Narici, Rittweger, & Vernikos, 2007).

The review of Lipnicki and Gunga (2009) includes several studies in which attentional functions were investigated in HDBR by various tasks (simple reaction time, squares, number finding, cancellation, and directed attention tasks). Only one study reported impaired performance during the first and third day of HDBR in the number finding and cancellation test (and in other non-attentional tests, such as spatial conceptions and logical memory tasks), while the other studies reported unchanged or even improved performance. Two additional studies (Seaton, Slack, Sipes, & Bowie, 2007; Seaton, Slack, Sipes, & Bowie, 2009) investigated attention with a combination of vigilance and one-back task. These studies also investigated memory with code memory delayed (delayed digit-symbol substitution), and delayed matching to sample tasks and mathematical processing with simple addition and subtraction. Results of these studies did not find any significant performance changes in HDBR. Lipnicki and Gunga (2009) also mentioned three other studies in which short-term memory did not impair or even improved in HDBR. They also found unchanged or improved reasoning performance during verbal cognitive reasoning or grammatical reasoning tasks.

Three studies investigated the executive function during 60-90 days long HDBR. In the study of Lipnicki, Gunga, Belavy, and Felsenberg (2009a), performance of subjects impaired during bedrest compared to baseline in the Iowa Gambling task, but not in the 2-back and in the flanker tasks. In another study, in order to avoid learning effect, Lipnicki, Gunga, Belavy, and Felsenberg (2009b) compared two groups, one performed the Iowa Gambling task before HDBR, the other performed this task on the 51st day of HDBR. The authors reported equal performance in the two groups, but lack of the development of adaptive strategy during the task in the HDBR testing group compared to the other group. Furthermore, Liu, Zhou, Chen, and Tan (2012) found significantly worse performance in HDBR in an emotional flanker task.

1.2.5 Cognitive functions in isolation and confinement

Many studies investigated cognitive functions in artificial confined and isolated environment. The longest study lasted for 520 days which simulated a Mars mission with six crewmembers (Basner et al., 2013; Basner et al., 2014). Additionally, a 135-days long simulation was conducted by Sauer, Hockey, and Wastell (1999a) and a 365-days long mission was mentioned by Gushin, Kholin, and Ivanovsky (1993) in their summary of soviet isolation studies. Other studies simulated a shorter period of isolation (7-60 days). Most of the results show that isolation and confinement have no adverse effect on short-term and working memory (Hockey & Wiethoff, 1993; Lorenz, Lorenz, & Manzey, 1996; Vaernes, Bergan, Lindrup, Hammerborg, & Warncke, 1993) and on attentional functions (Basner et al., 2013; Basner et al., 2014; Basner et al., 2015; Lorenz et al., 1996; Rizzolatti & Peru, 1993; Vaernes et al., 1993). Concretely, Lorenz et al. (1996), Vaernes et al. (1993) and Hockey and Wiethoff (1993) found no significant adverse effect of 60-days or four-weeks long simulated mission in a Sternberg task or in another short-term memory tasks or in a decision-making task that requires working memory. Concerning studies assessing attentional functions, Basner et al. (2013) and Basner et al. (2014) investigated the effect of 520-days long isolation and confinement using a short version of the PVT task. They only found significant performance decrement in 1 subject out of 6. Attentional functions were also investigated in 60 days-long (Lorenz et al., 1996) and four-weeks long (Rizzolatti & Peru, 1993; Vaernes et al., 1993) simulated missions. These studies reported no significant impairments of the performance in the dual task (Lorenz et al., 1996), reaction time task (Vaernes et al., 1993) and in the distribution of attention, in the visual search and in the orientation of attention tasks (Rizzolatti & Peru, 1993).

Furthermore, in the 60-days and 4-weeks long studies of Sauer, Hockey, et al. (1999a) and Sauer, Wastell, and Hockey (1999) performance did not change in the simulation of life support system task. One study (Vaernes et al., 1993) investigated the effect of 4-weeks long isolation on event-related brain potentials in a 2-stimulus auditory oddball task. They did not measure the amplitude of N1 and P3b components (these components are described in the "Task-irrelevant stimuli processing" section below), only the latency of these components which did not show significant changes in isolation. Less research reported negative effects of isolation on some cognitive functions, such as sensory-motor (tracking task; Lorenz et al., 1996) and decision-making performance (Hockey & Sauer, 1996). Although in the latter study performance improved during the whole isolation but after the elimination of the impact of learning effect, authors concluded that decision making slows down in the second part of the isolation. Additionally, Gushin et al. (1993) also reported slower decision making in their summary of soviet isolation research.

1.2.6 Effects of sleep loss on cognitive functions

Sleep problems that could impair cognitive functions are common in space and Antarctica (Alhola & Polo-Kantola, 2007). The majority of studies which investigated the impacts of sleep loss focused on the effects of total sleep loss, although chronic partial sleep loss, is more common in everyday life and in extreme environments including space and Antarctica. However, according to Van Dongen, Maislin, Mullington, and Dinges (2003) insufficient sleep sums up: 6 hours sleep per day for two weeks, for example, show similar results as two full nights of sleep deprivation. Results show that attentional functions are impaired due to both total and partial sleep loss. Total sleep loss may also damage working memory, long-term memory, executive functions, visuomotor performance and reasoning (see Table 3; Alhola & Polo-Kantola, 2007), but the effects of sleep loss show individual differences (Van Dongen, Vitellaro, & Dinges, 2005).

Two main theories exist concerning the impact of sleep loss. One theory says that sleep deprivation can generally affect attention (see reviews Alhola & Polo-Kantola, 2007; Colrain & Campbell, 2007), while the other suggests that sleep loss selectively influences certain brain areas, functions (see review Alhola & Polo-Kantola, 2007). According to the first theory (Colrain & Campbell, 2007), sleep deprivation reduces the level of arousal and external stimuli are necessary to regain the appropriate level, so performance is deteriorated in long and boring tasks. One version of the other theory highlights the role of prefrontal functions. According to this theory, sleep loss impairs performance in those tasks that require

prefrontal functions (Horne, 1993). The prefrontal theory is supported by the results of A. Gosselin, De Koninck, and Campbell (2005), as total sleep deprived subjects showed decreased P3a (P3a and other relevant components are described in the "Task-irrelevant stimuli processing" section below) in response to novelty events in the frontal channel. Some other studies have demonstrated that, besides P3a, various ERP components are sensitive to sleep deprivation. For example, the amplitude of parietal N1 and P3b diminished in a modified ANT task (Trujillo, Kornguth, & Schnyer, 2009) and the amplitude of MMN was also impaired (Raz, Deouell, & Bentin, 2001) as a result of sleep deprivation. Furthermore, the amplitude of no-go P3 also decreased due to disturbed sleep (Schapkin, Falkenstein, Marks, & Griefahn, 2006).

Table 3. Summary of cognitive studies during acute sleep deprivation reporting impaired performance in at least one test (a slightly modified version of the table presented by Alhola & Polo-Kantola, 2007).

Cognitive test	Effect	Authors
Simple reaction time	\downarrow	Choo et al 2005, Karakorpi et al 2006
Choice reaction time tasks	\downarrow	Wilkinson et al 1990, Smulders et al 1997, Wright and Badia 1999, Frey et al 2004, Karakorpi et al 2006, Kendall et al 2006
Serial reaction time test	\leftrightarrow	Nilsson et al 2005
Vienna Test System (computerized): Vigilance, simple reaction time; Cognitrone (visual analytical ability, attention and working memory Vigilance)	\leftrightarrow	Lee et al 2003
	\downarrow	Wu et al 1991, Corsi-Cabrera et al 2003, Karakorpi et al 2006, Sagaspe et al 2006, Taillard et al 2006
Flanker task (computerized: attention, vigilance?)	\downarrow	Tsai et al 2005
Dichotic listening (vigilance)	\downarrow	Johnsen et al 2002
Psychomotor vigilance task (PVT)	\	Dinges et al 1994, Wright and Badia 1999, Doran et al 2001, Van Dongen et al 2003, Frey et al 2004, Graw et al 2004, Van Dongen et al 2004, Adam et al 2006, Blatter et al 2006
Serial addition and/or subtraction task	\downarrow	Drummond et al 1999, Thomas et al 2000, Van Dongen et al 2003 and 2004, Kendall et al 2006
Two column addition	\downarrow	Wright and Badia 1999, Frey et al 2004
Visuo-spatial attention (saccadic eye movements)	\downarrow	Bocca and Denise 2006

Cognitive test	Effect	Authors		
Finding Embedded Figures Test	\downarrow	Blagrove et al 1995		
Auditory attention task	\downarrow	Blagrove et al 1995, Linde et al 1999		
Dual task	\downarrow	Wright and Badia 1999, Frey et al 2004		
Dual task	\leftrightarrow	Drummond et al 2001, Alhola et al 2005		
Paced Auditory Serial Addition Test (PASAT)	\leftrightarrow	Binks et al 1999		
N-back	\downarrow	Smith et al 2002, Choo et al 2005		
LTR, PLUS	\downarrow	Chee and Choo 2004, Chee et al 2006		
PLUS-L (verbal working memory)	\downarrow	Chee et al 2006		
Delayed-match-to-sample task	\downarrow	Habeck et al 2004		
Choice-reaction time task (with working memory component)	\downarrow	Jennings et al 2003		
Brown-Peterson	\downarrow	Forest and Godbout 2000		
Sternberg verbal working memory task	\downarrow	Mu et al 2005		
Working memory task	\downarrow	Wimmer et al 1992		
Digit recall	\downarrow	Frey et al 2004		
Digit span	\leftrightarrow	Linde and Bergström 1992 (2 studies), Quigley et al 2000		
Word recall (working memory)	\leftrightarrow	Quigley et al 2000		
Verbal working memory, visuo-spatial working memory test	\leftrightarrow	Nilsson et al 2005		
Spatial working memory task	\leftrightarrow	Heuer et al 2005		
Attentional power (effortful information processing)	\leftrightarrow	Linde and Bergström 1992 (2 studies)		
Word memory test	\downarrow	Drummond et al 2000		
Temporal memory for faces (recency)	\downarrow	Harrison and Horne 2000		
Probed forced memory recall and digit recall	\downarrow	Wright and Badia 1999		
Memory search	\downarrow	McCarthy and Waters 1997		
Paired word learning (implicit memory)	\downarrow	Forest and Godbout 2000		
Episodic memory (Claeson-Dahl test)	\leftrightarrow	Nilsson et al 2005		
Implicit memory test, prose recall, Mill Hill vocabulary test (chrystallized semantic memory), procedural memory, face memory	\leftrightarrow	Quigley et al 2000		

Cognitive test	Effect	Authors		
Benton visual retention test	\leftrightarrow	Alhola et al 2005		
Critical tracking	\downarrow	Van Dongen et al 2004		
Letter cancellation task (visual search)	\downarrow	Casagrande et al 1997, De Gennaro et al 2001		
Trail-making task	\downarrow	Wimmer et al 1992		
Maze tracing task	\downarrow	Blatter et al 2005		
Digit symbol	\downarrow	Van Dongen et al 2003, 2004		
Digit symbol, Bourdon-Wiersma, other psychomotor tests	\leftrightarrow	Quigley et al 2000, Alhola et al 2005		
Procedural motor task	$\downarrow \longleftrightarrow$	Forest and Godbout 2000		
Critical reasoning, Masterplanner	\downarrow	Harrison and Horne 1999		
Decision-making task	\downarrow	Linde et al 1999, Kilgore et al 2006		
Logical reasoning	\downarrow	McCarthy and Waters 1997		
Logical reasoning test (Baddeley)	\downarrow	Blagrove et al 1995, Monk and Carrier 1997		
Logical reasoning test (Baddeley)	\leftrightarrow	Linde and Bergström 1992 (2 studies), Quigley et al 2000, Drummond et al 2004		
Word detection task, repeated acquisition of responce sequence task	\downarrow	Van Dongen et al 2004		
Vowel/consonant discrimination task, letter recognition task	\downarrow	Wimmer et al 1992		
Sentence processing, categories test, spot the word, word recognition	\leftrightarrow	Quigley et al 2000		
Word fluency, Booklet form of the Category test	\leftrightarrow	Binks et al 1999		
Response inhibition (the Haylings sentence completion task), verb generation to nouns	\downarrow	Harrison and Horne 1998		
Go-NoGo (response inhibition)	\downarrow	Drummond et al 2006		
Stroop (color-word, emotional, specific)	\downarrow	Sagaspe et al 2006		
Spatial Stroop (suppression of prepotent responses)	\downarrow	Heuer et al 2005		
Stroop	\leftrightarrow	Binks et al 1999		
Dichotic temporal order judgment	\downarrow	Babkoff et al 2005		
Negative priming (effect vanished during SD)	\downarrow	Harrison and Espelid 2004		
Task-shifting	\downarrow	Heuer et al 2004 (2 studies)		
Simon task	\downarrow	Heuer et al 2005		

Cognitive test	Effect	Authors
Raven's progressive matrices	\downarrow	Linde and Bergström 1992
Figural form of the Torrance Tests of Creative Thinking	\downarrow	Wimmer et al 1992
Modified Six Elements test (story-telling, simple arithmetic calculations and object naming)	\downarrow	Nilsson et al 2005
Switching Task	\downarrow	Frey et al 2004
Implicit sequence learning in the serial reaction task	\downarrow	Heuer et al 1998, Heuer and Klein 2003
Explicit sequence learning task (serial reaction tasks)	\leftrightarrow	Heuer et al 1998
Luria-Nebraska Neuropsychological Battery, Calculation and digit span from WAIS	$\downarrow \leftrightarrow$	Kim et al 2001
Number-series inductions	\leftrightarrow	Linde and Bergström 1992
Novel oddball task (auditory)	$\downarrow \leftrightarrow$	Gosselin et al 2005
Random generation tasks	$\downarrow \longleftrightarrow$	Heuer et al 2005 (3 studies)
Complex navigation task	\leftrightarrow	Strangman et al 2005
Wisconsin Card Sorting Test (computerized), WAIS-R short form	\leftrightarrow	Binks et al 1999

Abbreviations: SD, sleep deprivation; WAIS, Wechsler Adult Intelligence Scale; WAIS-R, Wechsler Adult Intelligence Scale-Revised.

Note. Downwards arrow - performance deterioration; left right arrow - unchanged performance.

1.2.7 Effects of radiation on cognitive functions

The effect of radiation during spaceflight on the central nervous system is unknown, however, the studies of patients who underwent radiation treatments can provide some information. These studies report a decline of visual spatial ability, memory, and executive function (Cucinotta et al., 2014), although the dose of radiation in these treatments is much higher than in space. Cucinotta et al. (2014) also report impairment in attentional functions, reading, spelling and mathematical performance in children underwent radiation therapy for brain tumors. Another review (Keime-Guibert, Napolitano, & Delattre, 1998) separates early (between 2 weeks and 3-4 months after therapy) and delayed (from 4 months after therapy) cognitive impairments after radiotherapy. According to this review, attention deterioration and the modification of recent memory are frequent during early impairments. Attentional and

memory impairments are also common later (generally between 4 months and 4 years after therapy) with deteriorated immediate problem solving ability.

The impact of radiation on cognitive functions are better known from animal studies, but contrary to space, these studies did not apply mixed radiation field or chronic exposure of radiation (Cucinotta et al., 2014). In these studies, protons or high charge and energy (HZE) particles (for example 56Fe) were used. These studies reported significant deficit at 0.5 Gy or at higher doses of HZE (Cucinotta et al., 2014). Animal studies report sensory-motor deficit, deficit of the conditioned taste aversion, impairment of spatial memory (in maze tasks), hippocampal learning and memory, executive function (in the attentional set shifting task) and performance decrement in a reaction time task (PVT) (see reviews Cucinotta et al., 2014; Davis, DeCicco-Skinner, Roma, & Hienz, 2014). Furthermore, several studies demonstrated that age, gender, earlier radiation experience (see review Cucinotta et al., 2014) and individual differences (Davis et al., 2014) can influence the effect of radiation.

1.3 Task-irrelevant stimuli processing

In the thesis studies, the attentional functions and the effects of extreme environments on these functions were investigated in tasks which contain task-irrelevant or deviant stimuli by using the methods of event-related potentials. Additionally, behavioral data were also analyzed in two studies. The ERP reflects the summation of postsynaptic potentials of many neurons (neuron population) after the onset of certain events. The ERP waveform consists of several, consecutive components (for detailed description of ERP method see Luck, 2005). In the following, the ERP components relevant to our studies will be introduced. The main focus is on the P3a component, as it has a substantial role in each study. Besides the P3a, the N1, MMN, N2, P3b, no-go P3 and RON components will be briefly discussed.

The main advantage of the ERP method, contrary to the behavioral measurement, is the good time resolution, that allows separating the distinct processes after the occurrence of an event by ERP components. Using this method, it could be decided which cognitive functions are impaired in extreme environments, because several subprocesses could be summed up in behavioral data that could be separated by ERP components. Another advantage of this method is that it serves information in cases when no behavioral data is available. A typical example of this situation is the unexpected, task-irrelevant event which does not require response.

1.3.1 Oddball and distraction paradigms

In everyday life, we often encounter unexpected events while doing a task. These unexpected events could draw our attention away from the ongoing task resulting in an orientation response (Sokolov, 1963). If this process does not work properly, it can lead to serial consequences. It is particularly dangerous to ignore an unexpected event in the space station and particularly during extravehicular activity, but it may also cause a disruption in the life of crew in Antarctica. The brain electrical correlate of orientation is the novelty P3/P3a ERP component. Under laboratory conditions, this situation is typically investigated by the 3-stimulus oddball, the novelty, and the distraction paradigms. The 3-stimulus oddball and novelty paradigms, in which rare, unexpected, task-irrelevant stimuli appear within a series of rare target and frequent standard stimuli could be applied in multiple modalities. In these two paradigms, the standard and target stimuli belong to a single category, while the irrelevant stimuli belong to a different category. In the 3-stimulus oddball paradigm these task-irrelevant events are relatively simple and identical within a sequence of task-relevant stimuli

(Comerchero & Polich, 1999; Hagen, Gatherwright, Lopez, & Polich, 2006), but in the novelty paradigm these events are complex and different in each trial (Courchesne, 1978; Courchesne, Hillyard, & Galambos, 1975; Grillon, Courchesne, Ameli, Elmasian, & Braff, 1990). The late positive component elicited by rare task-irrelevant stimuli is called P3a in the 3-stimulus oddball paradigm and novelty P3 in the novelty paradigm, but numerous studies show that these two components are almost the same (Combs & Polich, 2006; Goldstein, Spencer, & Donchin, 2002; Polich & Comerchero, 2003; Simons, Graham, Miles, & Chen, 2001). The term P3a will hereafter be used.

The distraction paradigm is slightly different from the novelty and oddball paradigms. The typical auditory distraction paradigm is a length discrimination task in which occasionally task-irrelevant changes appear, i.e. these sounds differ in task-irrelevant features (e.g. frequency) from frequent stimuli. Subjects usually make more errors and respond slower to these, so-called distraction stimuli than to the frequent ones. In the ERP, these deviant sounds elicit the P3a component. Although this paradigm is mostly used in auditory modality (e.g. Horváth, Winkler, & Bendixen, 2008), visual (e.g. Berti & Schroger, 2001) and crossmodal versions also occur (e.g. Bendixen et al., 2010).

Hereinafter I will use the following nomenclature; *irrelevant* or *task-irrelevant* stimuli for simple, repeated stimuli that do not require response in the 3-stimulus oddball or modified oddball tasks; *novelty or novel stimuli*, if these irrelevant stimuli are variable and the variability of these stimuli is emphasized, otherwise the irrelevant or task-irrelevant name will be used for these variable stimuli; *distractor* or *deviant* for the stimuli with a rare task-irrelevant feature in the typical distraction paradigm.

1.3.2 P3a event-related component

The P3a ERP component typically occurs about 280-500 ms after the onset of the irrelevant or distraction stimuli. It has a scalp distribution with fronto-central amplitude maximum. There are two main theories concerning the meaning of this component. According to the most widespread theory, P3a reflects attention switch (Näätänen, 1990). In agreement with Escera, Alho, Winkler, and Näätänen (1998) this is an involuntary process, while others claimed that this attentional reallocation is voluntary (Chong et al., 2008). Furthermore, results of several studies show that humans not only detect the task-irrelevant event but also evaluate and categorize it (Friedman, Cycowicz, & Dziobek, 2003; Friedman, Cycowicz, & Gaeta, 2001). Another, less widespread theory assumes that P3a reflects

response inhibition (Goldstein et al., 2002). Task-irrelevant and target stimuli are similar in some respects; both of them are rare events and differs from standards. However, contrary to the task-irrelevant events, target stimuli require a response which has to be inhibited in case of a task-irrelevant stimulus (Goldstein et al., 2002).

The elicitation of P3a and the magnitude of its amplitude are affected by many factors. The relative complexity of irrelevant and other stimuli, the perceptual discrimination between standards and targets, and the working memory load all have an effect on this component.

The role of the *relative complexity of irrelevant and relevant (standard and target) stimuli* will be described in more details in the first study.

According to Polich and Comerchero (2003) and many other studies (e.g. Comerchero & Polich, 1999; Hagen et al., 2006), the *perceptual discrimination between standard and target* plays a crucial role in the generation of P3a by task-irrelevant deviant stimuli. In tasks where standards and targets are very similar and thus the perceptual discrimination is more difficult, the amplitude of P3a is larger and has a more central scalp distribution compared to those task in which this discrimination is easy. The authors argue that contrary to the easy standard-target discrimination task, the difficult discrimination requires significant attentional focus. The rare task-irrelevant stimuli interrupt this attentional process and the attentional redirection to this event results in the appearance of P3a.

Many studies investigated the change of P3a under various working memory load. In modified distraction (e.g. Berti & Schroger, 2003; Lv et al., 2010) and oddball tasks amplitude of P3a diminished as the memory load increased. Lv et al. (2010) proposed that the high memory load task requires more attentional resources, thus less attention remains to the deviant stimuli which results in decreased P3a. Contrary to these results (Berti & Schroger, 2003; Lv et al., 2010), in a study by Muller-Gass and Schroger (2007) P3a increased as memory load increased in a distractor paradigm. According to their interpretation, a task with increased memory load requires more attention, which enhances the processing of irrelevant change of deviant stimuli.

1.3.3 The effect of task-irrelevant events on performance

The most accepted idea says that the task-irrelevant stimulus disrupts the ongoing task and distracts subjects from task-set established by the repetitive events (e.g. Escera et al., 1998). A typical example of this process is the above-described distraction paradigm in which the irrelevant feature of the deviant stimulus impairs performance (less accurate response and

longer reaction time). In contrast, others claim that task-irrelevant deviant events may facilitate performance (see review Schomaker & Meeter, 2015). According to Schomaker and Meeter (2015), many factors could influence whether the task-irrelevant events inhibit or facilitate performance: the information that the task-irrelevant stimulus provides about the appearance of the target, the amount of attention required by the task and the context in which the stimulus appears. The task-irrelevant stimulus impairs performance when it provides information about the appearance of target events, but not in other cases (Parmentier & Andres, 2010; Wetzel, Widmann, & Schroger, 2012). Another influencing factor is the amount of attention required by the task. When it is high, the task-irrelevant event affects distraction, and when it is low, the task-irrelevant event results in facilitation. In the latter case, the task-irrelevant event acts as an alerting signal which increases arousal and refocusing attentional resources (SanMiguel, Linden, & Escera, 2010). An additional important factor is the context of the task-irrelevant event. For example in the study of Schomaker and Meeter (2014), performance for acoustic targets (beep) improved when these stimuli appeared shortly (SOA was 0 or 200 ms) after the rare task-irrelevant events that were more complex than the frequent stimuli.

1.3.4 Sources and neurotransmitters connected to P3a

Lesion studies suggest that the prefrontal regions are involved in the elicitation of P3a (Knight, 1997), the role of cingulum is of particular importance. Besides these, the hippocampus also plays a role in the generation of P3a (Knight, 1996). In addition, novel stimuli may also activate the amygdala (see review Schomaker & Meeter, 2015) from which the authors conclude that novelty could "enhance perception via the same mechanisms as by which emotional stimuli are thought to enhance perception" (p. 5).

According to Polich (2007), P3a is connected to the activation of the dopaminergic system while P3b (this component is described below) associated to the activation of LC (locus coeruleus) norepinephrine system. Others (e.g. Schomaker & Meeter, 2015) claim that the locus-coeruleus (LC) norepinephrine system also plays a role in the elicitation of P3a.

1.3.5 P3b

Besides the P3a, there are other ERP components in the similar time interval which together form the so-called P3 complex. Target events typically elicit the P3b component about 300-700 ms after the onset of stimulus with centro-parietal scalp distribution. In line

with the "context updating" model (Donchin, 1981), the standard stimuli establish a memory trace, and if the incoming stimuli differ from this trace, the mental representation has to be updated, and the P3b is a consequence of this process. Contrary to this model, others say that P3b is an index of decision making about the stimuli and not the index of memory (e.g. Verleger, 2008). The main generators of P3b are located in the temporo-parietal and medial temporal lobes (Molnár, 1994). Furthermore, some thalamic nuclei could also play a role in the elicitation of P3b (Molnár, 1994). Several factors could influence the P3b amplitude, such as the probability of the target event, the effort required to complete the task and decision uncertainty (Luck, 2005). Increased target probability, decreased effort and increased decision uncertainty all reduce P3b amplitude (Duncan-Johnson & Donchin, 1977; Isreal, Chesney, Wickens, & Donchin, 1980; R. J. Johnson, 1986; Luck, 2005). Concerning the latency of P3b, it can be the index of stimulus categorization time (Luck, 2005; Polich, 2003).

1.3.6 no-go P3

Another component, the no-go P3 also belongs to the P3 complex. This component is typically elicited by the no-go stimuli in the go/no-go paradigm. In this paradigm, subjects have to respond to one part of the stimuli (so-called go stimuli; it is typically 50% of the stimuli), while participants have to withhold response from the other part (so-called no-go stimuli). It can also be observed in tasks (e.g. Eriksen flanker task) in which participants make a response on every trial, but there is a conflict between competing responses (Smith, Smith, Provost, & Heathcote, 2010). The no-go P3 component has a scalp distribution with frontocentral amplitude maximum and usually appears about 300-600 ms after the onset of stimuli. According to the widely accepted theory, this component reflects response inhibition (Pfefferbaum, Ford, Weller, & Kopell, 1985). The frontal lobe and the anterior cingulate cortex could play a role in eliciting no-go P3 (Bokura, Yamaguchi, & Kobayashi, 2001; Fallgatter, Bartsch, & Herrmann, 2002; Strik, Fallgatter, Brandeis, & Pascual-Marqui, 1998).

1.3.7 N2

N2 component could be divided into more subcomponents (for a review, see Folstein & Van Petten, 2008). In this paragraph, only the fronto-centrally distributed N2b and the so-called "control N2" (the terminology by Folstein and van Petten, 2007) component will be discussed.

N2b is a fronto-centrally distributed N2 component that appears in active discrimination tasks. In the above-described active oddball paradigms, infrequent (task-irrelevant deviant and target) stimuli often elicit N2b component approximately 200 ms after stimulus onset. This component represents a "stage of mismatch detection" (Folstein & Van Petten, 2008, p. 153) and often followed by P3a. The task-irrelevant deviant events elicit larger N2b than the target events (Folstein & Van Petten, 2008). The occurrence of N2b requires attention of the eliciting stimuli (Folstein & Van Petten, 2008; Näätänen & Picton, 1986) and might reflect orientation to the stimulus (Näätänen & Picton, 1986; Picton & Hillyard, 1988). The N2b component may indicate "how the attentional functions can serve the processing of particular stimulus" (Czigler, 2000). Based on the scalp map, the frontal and superior temporal cortex could play a role in the generation of N2b (Potts, Dien, Hartry-Speiser, McDougal, & Tucker, 1998), but the role of the anterior cingulate cortex is also feasible (Lange, Wijers, Mulder, & Mulder, 1998).

Another fronto-centrally distributed N2 component is the "control N2" (terminology of Folstein and Van Petten, 2008) in the similar time interval as the N2b. Several studies investigated this component in tasks which require cognitive control (Folstein & Van Petten, 2008), such as in the Eriksen flanker or modified flanker tasks. In these choice-reaction time tasks, in which subjects typically have to make a decision about the center letter in the string of letters, incongruent trials elicit larger N2 amplitude than congruent ones (see review Folstein & Van Petten, 2008). In contrast to N2b, this component is not sensitive to probability and mismatch detection (Folstein & Van Petten, 2008) and it might be related to the response monitoring and control of preparation for incorrect response (Folstein & Van Petten, 2008). According to Folstein and Van Petten (2008), both the control N2 component and the no-go N2 elicited by no-go stimuli in the above-described no-go paradigm, related to cognitive control. Several studies demonstrated that ACC plays a crucial role in the elicitation of control N2 (Folstein & Van Petten, 2008; Van Veen & Carter, 2002). Furthermore, other studies (e.g., Liddle, Kiehl, & Smith, 2001) demonstrated the role of prefrontal cortex in the response inhibition in go/no-go paradigms.

1.3.8 MMN, N1, RON

In the distraction paradigm, P3a is often preceded by mismatch negativity (MMN) and/or N1 and followed by reorientation negativity (RON) components in the distractor-standard difference wave (Escera & Corral, 2007; Horváth et al., 2008).

N1 is a modality-specific exogenous component which depends on the physical parameters of the stimulus. It appears about 50-150 ms after the onset of stimuli in auditory modality (Näätänen & Picton, 1987) and slightly later, about 100-200 ms after the onset of stimuli in visual modality (Luck, 2005). Both auditory and visual N1 has several subcomponents. In the visual modality, the earlier N1 subcomponent has an anterior scalp distribution. Additionally, there are at least two later posterior subcomponents, the generator of one of them is in the parietal cortex and the other posterior subcomponent originates from the lateral occipital cortex (Luck, 2005). In the auditory modality N1 has an earlier frontocentral subcomponent that is generated in the auditory cortex, a later subcomponent with vertex maximum with unknown generator, and an even later subcomponent with more lateral distribution of superior temporal gyrus origin (Luck, 2005). The selective attentional processes influence the amplitude of visual N1 component (Hillyard, Hink, Schwent, & Picton, 1973). The attended events elicit higher N1 amplitude than unattended stimuli, which has been shown, for example, by the results of Neuhaus et al. (2010). In this study, the more information (time, place) was provided by the preceding cue about the target the higher N1 amplitude was elicited (target-locked N1). Concerning the auditory N1, the attention has influence on this component as well (Luck, 2005).

The MMN appears approximately between 100 and 200 ms after the onset of the stimulus with fronto-central amplitude maximum in auditory modality. It typically appears in tasks in which infrequent mismatching stimuli are presented in the series of identical frequent ones (Luck, 2005). The infrequent stimuli elicit this negative deflection irrespective of the subject's direction of attention (Näätänen, Paavilainen, Rinne, & Alho, 2007). MMN can be considered as an index of change detection which does not require attention (Näätänen et al., 2007). Furthermore, according to the so-called trace-mismatch theory, it is assumed that the frequent stimuli build a sensory memory trace and MMN reflects the discordance between this representation and the incoming irrelevant stimuli. According to another, so-called regularity-violation theory, we build a prediction from the "regular intersound relationship" (Winkler, 2007, p. 147) of the auditory stimuli and these regularity representations are encoded in the memory. The MMN is a sign that the incoming event does not meet this prediction (for review, see Winkler, 2007; Winkler & Cowan, 2005). The main generator of this component is in the auditory cortex. Furthermore, the right frontal lobe and prefrontal cortex might also play a role in the generation of auditory MMN (Alho, Escera, & Schroger, 2003; Kujala & Naatanen, 2003). In the auditory modality, it is a much-researched component

which is extended by more and more visual research by now (for review, see Czigler, 2007; Stefanics, Kremláček, & Czigler, 2014).

After orientation to the irrelevant feature of stimuli we have to return to the relevant aspects of stimuli, we have to reorientate (Schroger & Wolff, 1998). RON is the brain electrical correlate of this reorientation of attention, which is elicited about 500-600 ms after the onset of events with fronto-central scalp distribution (Schröger & Wolff, 1998). This component is modality-independent, it can be also observed in visual and auditory-visual distraction tasks (Berti & Schroger, 2001; Escera, Yago, & Alho, 2001). The generators of this component probably located in the frontal and centro-parietal regions (Alho et al., 2003). According to Horvath, Maess, Berti, and Schroger (2008) the primary motor area contributes to the generation of RON, from which authors concluded that the activity related to action-selection is also part of the reorientation process.

2 Objectives and thesis points

This thesis aimed to investigate the effects of extreme environments, such as space and Antarctica on cognitive functions by using the method of event-related potentials. We particularly focused on the impact of these environments (second and third studies) on the mobilization of attentional processes reflected by P3a ERP component. As the P3a component was of particular importance in these studies we explored the prerequisites of stimuli evoking this component in a laboratory experiment (first study).

In our first study, we hypothesized that the complexity of the task-irrelevant stimuli is an important aspect of attention switch and the emergence of the P3a ERP component. More specifically, we assumed that simple unexpected events in a complex environment, contrary to complex events in a simple environment, do not capture attention. Accordingly, we hypothesized that unlike complex events within a sequence of simple stimuli, simple events within a sequence of complex stimuli do not generate P3a and N2b ERP components. Furthermore, we also hypothesized that various complex task-irrelevant events capture more attention, thus elicit larger P3a, than identical complex task-irrelevant events. As predicted by our initial hypothesis, simple task-irrelevant stimuli within a sequence of complex taskrelevant events did not elicit P3a or N2b. Our results show that there is a significant role of complexity, therefore infrequency, and task irrelevance are not sufficient to elicit orienting response. We can conclude that P3 is reflecting the elaborate processing of irrelevant stimuli. As we hypothesized, variable complex task- irrelevant stimuli elicited larger P3a than identical ones in auditory modality, but contrary to our hypothesis, identical task-irrelevant stimuli elicited larger P3a than variable ones in visual modality. We speculated that this difference between the two modalities reflects differences in category level identification processes. Unlike auditory variable complex task-irrelevant stimuli, visual variable stimuli belong to the same category, thus these stimuli did not require category level identification and consequently needed less elaborative processes.

In our second study, we hypothesized that cognitive processes, especially attention, became deteriorated during long-term Antarctic residence, particularly in the winter months due to isolation, confinement, hypoxia, altered dark-light cycle and sleep problems mainly caused by this extreme light condition. Contrary to our expectations behavioral responses and N1/MMN (mismatch negativity), N1, N2, P3, RON (reorientation negativity) event-related potential components did not show any sign of deterioration. Early stages of information processing were marginally sensitive to the passage of the time in the ANT task (N1

component), but not in the distraction task (N1/MMN). Moreover, reaction time decreased in both tasks during the course of the mission. The alerting effect increased, the inhibition effect decreased and the orienting effect did not change in the ANT task. The reaction time decrements and the N1 amplitude reduction in ANT task could be attributed to the practice effect. These results indicate that the Antarctic conditions had no negative impacts on cognitive activity despite the presence of numerous stressors; the overwintering crewmembers adapted to this environment.

In the third study, we hypothesized that the attentional functions become impaired during a space missions due to several stressors, like sleep loss, high workload, cephalad-fluid shift and VIIP syndrome, sensory-motor changes, modification of the vestibular system, higher ambient CO₂ level, radiation, isolation, and confinement. We also assumed that attentional functions remain impaired 2-3 days after landing, the readaptation is not immediate. In line with our initial hypothesis, attentional functions connected to irrelevant stimuli (amplitude of P3a) diminished in space due to the combined effect of stressors and remained impaired after several weeks in space. Furthermore, these attentional functions were also sensitive to readaptation.

3 Studies

3.1 Study 1. Stimulus complexity effects on the event-related potentials to task-irrelevant stimuli⁶

3.1.1 Introduction

3.1.1.1 Orienting response and P3a

In everyday life, humans often encounter sudden, unexpected events while otherwise engaging in a specific task. If this unexpected event significantly differs from the ongoing task, it elicits an orienting response (OR; Sokolov, 1963). Novelty P3/P3a is considered to be the brain's electrical correlate of the OR induced by unexpected task-irrelevant deviant stimuli (see more details about P3a and oddball paradigms in the General introduction section).

Stimulus complexity is an important factor of the OR (Berlyne, 1958) and is characterized by variability across multiple stimulus dimensions, such as color, texture and spectral composition. Stimulus complexity is highly related to the respective processing demands in the brain and is positively correlated with subject response time to that stimulus. Furthermore, complex events are more likely to capture attention and elicit an OR.

3.1.1.2 Present study

The main purpose of the present study was to assess the influence of complexity of the unexpected rare (task-irrelevant stimuli in the laboratory oddball paradigm) events compared those of the regular environmental events in the elicitation of the OR, in other words the mobilization of attentional processes. The original figure of Berlyne (1958) illustrates the complexity relationship between two stimuli (Figure 1). According to the results of Berlyne (1958), who found that the fixation time for the more complex figures is greater than for the less complex figures, we hypothesized that, unlike complex events in a simple environment,

⁶ Barkaszi, I., Czigler, I., & Balazs, L. (2013). Stimulus complexity effects on the event-related potentials to task-irrelevant stimuli. *Biological Psychology*, *94*(1), 82-89. doi:10.1016/j.biopsycho.2013.05.007

simple, unexpected events presented in a complex environment draw attention to a lesser extent.

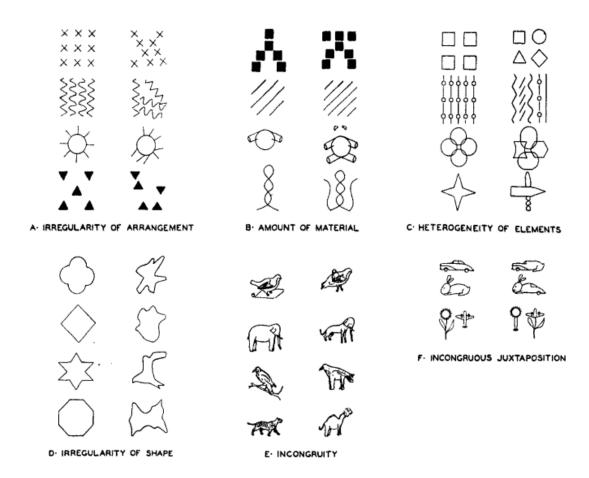


Fig. 1. Stimuli in an experiment of Berlyne (1958). The left column of each category (A, B, C, D, E and F) illustrates the less complex figures and the right column of each category illustrate the more complex figures (The original figure of Berlyne, 1958).

In the present study, we upturned the traditional oddball paradigm in terms of the complexity relations between relevant and irrelevant stimuli. Here, simple irrelevant stimuli were presented in sequences of complex, task-relevant stimuli. In this paradigm, the two consequences of the OR can be separated and investigated independently. The simple, irrelevant stimuli are still capable of disrupting the sequence of standard and target stimuli and therefore interfere with the task-set. However, the simple irrelevant stimuli require less processing than the complex, task-relevant stimuli.

In addition to studying the effects of stimulus complexity, we investigated the role of irrelevant stimulus variability in attentional processing. We employed the traditional 'novelty' paradigm in addition to a modified version of this paradigm to test the effects of stimulus

variability on ERPs. In the 'novelty' task, the standards and targets presented were simple stimuli, whereas the irrelevant stimuli were relatively more complex and variable. The modified version of this paradigm differed only in the variability of the irrelevant stimuli. Specifically, in the modified novelty paradigm, the irrelevant stimuli presented were always identical. We predicted that subjects would pay more attention to the variable irrelevant stimuli and, consequently, that these stimuli would elicit a larger P3a than identical, irrelevant stimuli.

We investigated the effects of stimulus complexity and variability in both visual and auditory modalities. Because the functionality and underlying neural systems of visual and auditory modalities differ, we predicted that these differences could be reflected in modality-specific elicitation of P3a and N2b by irrelevant stimuli (Neumann, van der Heijden, & Allport, 1986).

Our study is not the first to apply simple, irrelevant stimuli and complex, unusual standard and target stimuli in a visual oddball task. Indeed, Daffner, Mesulam, et al. (2000) and Daffner, Scinto, et al. (2000) previously administered this type of task. However, the procedure utilized in the previous studies differs from the present study in at least three important aspects. First, unlike in typical oddball designs, subjects in the Daffner, Mesulam, et al. (2000) and Daffner, Scinto, et al. (2000) studies were able to regulate stimulus duration and, consequently, the onset of subsequent stimuli. Thus, because all trials in these studies required some activity of the subject, the irrelevancy of rare, non-target stimuli was diminished. Second, the simple irrelevant stimuli employed in the current study were identical within a given sequence. Therefore, the relative novelty of these irrelevant stimuli was reduced compared with the variable simple irrelevant stimuli presented by Daffner and colleagues. Additionally, the contrast between the complex standards and targets and the irrelevant stimuli was augmented in the present study. If P3a emerges as a result of differences between the task-related and task-irrelevant stimuli, P3a would be expected to emerge in our study. Third, the complex stimuli presented in the current study were meaningful patterns that could be classified into recognizable categories (e.g., butterflies, environmental noises). Accordingly, long-term novelty of these complex stimuli was relatively reduced compared with the long-term novelty of the uncategorizable stimuli presented in the Daffner, Mesulam, et al. (2000) and Daffner, Scinto, et al. (2000) studies.

3.1.2 Materials and methods

3.1.2.1 *Subjects*

Twenty-three young adults (9 female and 14 male; 20–26 years of age, mean 22.13 years; 1 left handed, 22 right handed) participated in the experiments. Based on self-reporting, subjects were without any major neurological, psychiatric or other medical problems and had either normal or corrected vision. Subjects had normal hearing. All subjects signed informed consent and received payment for their participation. The study was approved by the Joint Psychological Research Ethics Committee of the Hungarian Psychology Faculties and Research Labs.

3.1.2.2 Stimuli

3.1.2.2.1 Visual stimuli

Visual stimuli were presented in the center of the computer screen. Fig. 2 summarizes the visual stimuli utilized in this study. The background color of the screen was light gray. The duration of stimulus presentation was 100 ms. In Conditions 1 and 2, the standards were gray circles $(3.77 \times 3.77^{\circ})$, the targets were gray ellipses $(3.43 \times 3.77^{\circ})$, and the complex stimuli were either identical (Condition 1) or variable (Condition 2) color pictures of butterflies $(3.77 \times 2.76^{\circ})$. In Condition 3, the standards were color pictures of various butterflies, the targets were color pictures of peacock butterflies, and the irrelevant stimuli were gray squares $(3.77 \times 3.77^{\circ})$.

3.1.2.2.2 Auditory stimuli

Three types of auditory stimuli were utilized in this study. Fig. 3 summarizes the auditory stimuli. Sounds were presented binaurally via earphones/headphones (Sennheiser, HD 600). The duration of tones was 110 ms, including 5 ms rise and fall times. The tones were presented with an intensity of 60 dB SL (individually adjusted for each subject). In Condition 1 and 2, the standards were low tones (comprising a 887 Hz fundamental frequency [f] and the second and third harmonics [2f,3f]), the targets were high tones (comprising a 938 Hz fundamental frequency [f] and the second and third harmonics [2f,3f]) and the complex stimuli were either identical (Condition 1) or variable (Condition 2) environmental noises (e.g., glass breaking, engine starting, water splashing, bicycle bell ringing, brakes squeaking,

clock ringing). In Condition 3, the standards were variable environmental noises, the targets were variable phone rings, and the irrelevant stimuli were simple identical tones (450 Hz).

3.1.2.3 Procedures

All subjects were presented with 6 task conditions (3 visual and 3 auditory). Stimulus conditions were defined according to the modality of the task and the complexity and variability of the non-target, irrelevant stimuli. In the Visual Variable (VV), Auditory Variable (AV), Visual Identical (VI) and Auditory Identical (AI) conditions the tasks consisted of simple standards (80%) and targets (10%) and complex, task-irrelevant stimuli (10%). In the Visual Identical and Auditory Identical conditions, the presented complex stimuli were identical. However, in the Visual Variable and Auditory Variable conditions, the presented complex stimuli were different for each trial. In contrast, in Visual Simple (VS) and Auditory Simple (AS) conditions, the standards and targets were more complex than the task-irrelevant infrequent stimuli, which were identical in each trial and relatively simple (see Figs. 2 and 3).

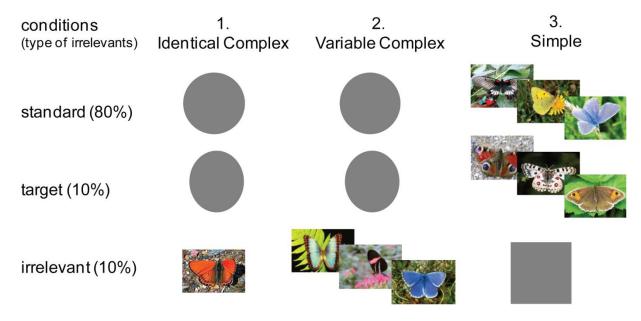


Fig. 2. Characteristics of visual stimuli for each task condition.

EEG activity of subjects was recorded during 12 blocks. Each condition comprised 2 measured stimulus blocks (1 and 2). In the first block of each condition, subjects were presented with 280 stimuli (30 practice and 250 non-practice stimuli), and the second block of each condition consisted of 250 non-practice stimuli. The SOA was random in the 1100–1300 ms range.

conditions	1.	2.	3.	
(type of irrelevants)	Identical Complex	Variable Complex	Simple	
standard (80%)	identical low tone	identical low tone	variable noise	
target (10%)	identical high tone	identical high tone	variable phone rings	
irrelevant (10%)	identical noise	variable noise	identical tone	

Fig. 3. Characteristics of auditory stimuli for each task condition.

1...

During the trials, subjects were seated in a comfortable chair in a sound-attenuated room. Prior to the first block of each condition, we introduced the targets and standards to the subjects. Subjects were instructed to press the response button with their dominant hand when they detect the target stimuli i.e., whenever they see an ellipsoid (not a circle) or a peacock butterfly (not any butterfly) or they hear the high tone (not the low tone) or a phone ring (not any other noise). Subjects were instructed to respond in a fast, accurate manner. Subjects were not informed of the occurrence of irrelevant stimuli prior to the trials.

Subjects were divided into 2 groups, which were presented with different stimuli sequences. The order of the conditions and blocks for subject group 1 was AI1, VS1, AV1, VV1, AS1, VI1, VI2, AS2, VV2, AV2, VS2, and AI2. For subject group 2, the sequence of the conditions and blocks was VI1, AS1, VV1, AV1, VS1, AI1, AI2, VS2, AV2, VV2, AS2, and VI2.

3.1.2.4 EEG recording and data analysis

EEG was recorded with Ag/AgCl electrodes mounted in an electrode cap (EASYCAP GmbH) with a Synamps-2 amplifier (Neuroscan Inc.). Data were online filtered at DC-200 Hz with 12dB per octave. The sampling rate was 1000 Hz. 63 scalp electrodes were placed using the extended 10–20 system: AF7, Fp1, Fpz, Fp2, AF8, AF3, AFz, AF4, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FT7, FC5, FC3, FC1, FCz, FC2, FC4, FC6, FT8, T7, C5, C3, C1, Cz, C2, C4, C6, T8, TP7, CP5, CP3, CP1, CPz, CP2, CP4, CP6, TP8, P7, P5, P3, P1, Pz, P2, P4, P6, P8,

PO7, PO3, PO2, PO4, PO8, O1, Oz, O2, PO9 and PO10. Horizontal eye-movements were monitored using two electrodes placed lateral to the outer canthi of each eye; vertical eye-movements were monitored with one electrode placed below the right eye and the AF8 electrode. Right mastoid reference was used for all recordings.

EEG was band-passed filtered (0.1–40 Hz, 24 dB/oct) offline. Epochs of 1200 ms were extracted (–200 to 1000 ms) and baseline corrected (–200 to 0 ms). To achieve comparable signal-to-noise ratios across experimental conditions, the total number of standard trials was reduced to 50 trials, preceded and followed by standards, to equalize the number of stimuli for each condition. Only trials with correct responses (target) and without responses (standard and novel) were analyzed.

Extended ICA was performed on individual data sets to remove eye blink artifacts from EEG recordings (Delorme & Makeig, 2004). Components representing eye blink artifacts were identified by inspecting the component scalp map, time course and ERP-image (visualization of event-related signal variations across single trials) and were rejected from further analysis. Eye blink-free EEG data were obtained by backprojecting the remaining ICA components to the time domain.

In the current study, we focused on the P3a and N2 components elicited by irrelevant stimuli. P3a peak latency was identified as a positive peak at the Cz electrode site within the 300–450 ms range for complex visual irrelevant stimuli or within the 270–420 ms range for complex auditory irrelevant stimuli. Mean P3a amplitude was evaluated in a 100 ms time window centered at peak latency. N2b latency was identified at the Cz location within the 210–300 ms range for complex visual irrelevant stimuli. N2b amplitude was evaluated in a 50 ms time window centered at peak latency. The mean amplitude values of the latency ranges were measured at the midline electrodes (Fz, Cz, Pz, Oz). The amplitude values were analyzed using Electrode Locations (4) × Stimulus Conditions (3) repeated measures ANOVA. Separate ANOVAs were calculated for visual and auditory stimulation. Peak latency values were analyzed by a paired t-test comparing the two complex conditions at the Cz electrode site for both visual and auditory stimulation paradigms. Greenhouse–Geisser correction was applied for all repeated measures with greater than 1 degree of freedom. Uncorrected degrees of freedom and corrected p-values are reported. Two a priori hypotheses were tested with planned comparisons (contrasts): (a) P3a amplitude is larger in the two conditions with complex irrelevants (variable or identical) compared to simple irrelevants, (b)

P3 amplitude is larger to variable as opposed to identical complex irrelevant stimuli. Bonferroni correction was applied in post hoc comparisons where appropriate.

Reaction time (RT) for targets was calculated as the mean duration between the stimulus onset and button press within the 150–1100 ms time range. Hit rate for targets was also analyzed.

3.1.3 Results

Table 4. Mean reaction time (ms) and performance rates for each task condition.

Modality	auditory			visual		
conditions (type of irrelevants)	1. Identical Complex	2. Variable Complex	3. Simple	1. Identical Complex	2. Variable Complex	3. Simple
Reaction time (ms)	467.66	479.31	466.89	496.23	511.75	476.92
Target hits (%)	96.0	96.4	97.6	91.1	90.0	97.6
False alarms (%)	0.18	0.12	0.43	0.23	0.10	0.22

3.1.3.1 Behavioral performance

Behavioral data are summarized in Table 4. A two-factor (Modality (2) × Stimulus Conditions (3)) ANOVA was performed on subjects' reaction time (RT) data. A significant main effect of modality (F(1,22) = 5.59, p < 0.05, η_p^2 = 0.20) and condition (F(2,44) = 6.04, p < 0.01, η_p^2 = 0.21) were obtained. The RT for visual tasks was longer than RT for auditory tasks. Post hoc tests revealed that RT for Simple conditions was shorter than RT for Variable conditions (p < 0.01). A similar two-factor (Modality (2) × Stimulus Conditions (3)) ANOVA was calculated for hit rate. Significant main effects of modality (F(1,22) = 19.57, p < 0.001, η_p^2 = 0.47), condition (F(2,44) = 10.89, p < 0.001, η_p^2 = 0.33), and interaction between the modality and condition factors (F(2,44) = 7.53, p < 0.01, η_p^2 = 0.25) were obtained. Follow-up

simple effects tests indicated that the Visual Variable and Identical conditions were more difficult than their auditory counterparts (p < 0.01 for both), however there was no modality difference between the Simple conditions (p = 0.95). As to the conditions main effect the only significant simple effects occurred in the visual modality; the tasks in the Variable and Identical conditions were more difficult than that of the Simple condition (p < 0.01 for both). There were no significant differences between the tasks performances in the auditory modality in the three different conditions. Table 4 also demonstrates that false alarm rates were very low in all tasks (less than 0.5%).

3.1.3.2 ERP results

3.1.3.2.1 *P3a amplitude*

The present study focused on elucidating the effects of the relative complexity of task-irrelevant stimuli. Therefore, only the P3a and N2b components elicited by these irrelevant stimuli are reported. Figs. 4 and 5 illustrate the grand-mean ERPs for each stimulus type in each condition recorded at the midline electrode sites for visual and auditory modalities, respectively. Fig. 6 demonstrates the topographic distributions of the grand-mean P3a and N2b components for the complex irrelevant stimuli. In both modalities, the infrequent complex irrelevant stimuli elicited the P3a component. However, no recognizable P3a was elicited by the simple irrelevant stimuli. The mean amplitude values of P3a are shown in Fig. 7.

In the visual modality significant main effects of condition (F(2,44) = 18.33, p < 0.001, η_p^2 = 0.45) and electrode location (F(3,66) = 10.74, p < 0.002, η_p^2 = 0.32), and interaction between the condition and electrode location factors (F(6,132) = 6.75, p < 0.001, η_p^2 = 0.23) were obtained. Planned comparisons verified that P3 amplitudes were larger in the two conditions with complex deviants (variable or identical) compared to the simple condition (p < 0.001) at Cz, Pz and Oz (with similar tendency at Fz, p = 0.084) as predicted by our initial hypothesis. Contrary to our expectation P3a was larger to the identical deviants compared to the variable ones (p < 0.005) at each electrode location. This unexpected result was confirmed by post hoc tests controlled for multiple comparisons at Fz, Cz,and Pz (p < 0.001).

In the auditory modality, we observed a main effects of task condition (F(2,44) = 113.80, p < 0.001, η_p^2 = 0.83) and electrode location (F(3,66) = 24.67, p < 0.001, η_p^2 = 0.52), and we additionally observed a significant interaction effect between electrode location and

task condition (F(6,132) = 41.67, p < 0.001, $\eta_p^2 = 0.65$). Planned comparisons verified that P3 amplitudes were larger in the two conditions with complex deviants (variable or identical) compared to the simple condition (p < 0.001) and larger to the variable deviants compared to the identical ones (p < 0.005) at each electrode location.

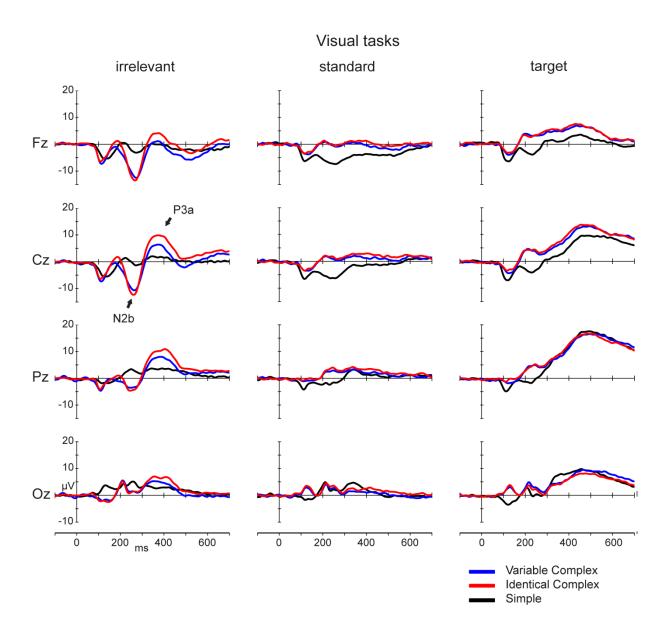


Fig. 4. Grand-mean event-related potential plots in response to task-irrelevant stimuli (left column), standard stimuli (middle column) and target stimuli (right column) in the visual modality recorded at the midline (Variable Complex condition, blue lines; Identical Complex condition, red lines; Simple condition, black lines).

3.1.3.2.2 *P3a latency*

In both visual and auditory modalities, the complex irrelevant stimuli elicited a P3a component. However, no recognizable P3a was elicited by the simple irrelevant stimuli. Thus, the analyses of P3a latency were restricted to complex irrelevant stimuli.

P3a latency data for each modality were assessed using a paired t-test comparing the ERP elicited by two conditions (2 Complex irrelevant stimulus types) at the Cz electrode. Based on our analysis, P3a peak latency did not vary significantly across conditions in either modality.

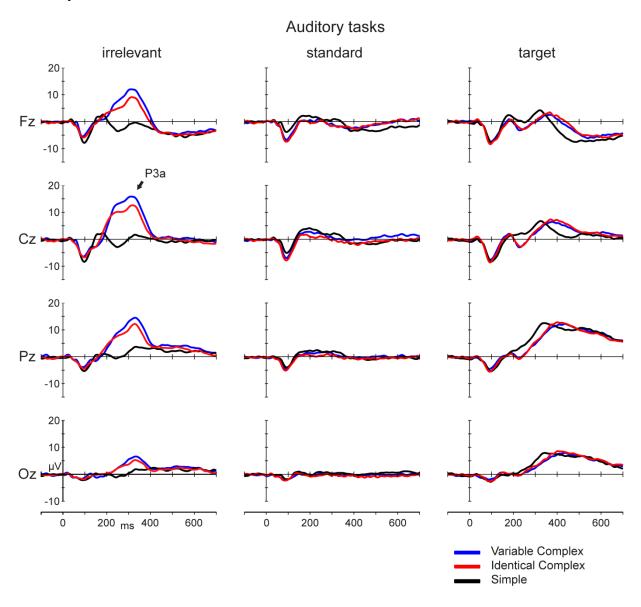


Fig. 5. Grand-mean event-related potential plots in response to task-irrelevant stimuli (left column), standard stimuli (middle column) and target stimuli (right column) in the auditory modality recorded at the midline (Variable Complex condition, blue lines; Identical Complex condition, red lines; Simple condition, black lines).

3.1.3.2.3 N2 amplitude

In the auditory modality, the presented stimuli did not elicit N2b.

Fig. 7 illustrates the mean N2b amplitudes elicited by the visual irrelevant stimuli. We observed a significant main effects of task condition (F(2,44) = 53.46, p < 0.001, η_p^2 = 0.70) and electrode location (F(3,66) = 32.83, p < 0.001, η_p^2 = 0.59). We also observed a significant interaction between the task condition and electrode location (F(6,132) = 22.38, p < 0.001, η_p^2 = 0.50). The simple effect analysis shows that the N2b elicited by both variable and identical butterflies was significantly larger than the N2b elicited by the identical squares at each electrode site (p < 0.05) and no significant differences were observed between the N2b elicited by various and identical butterflies.

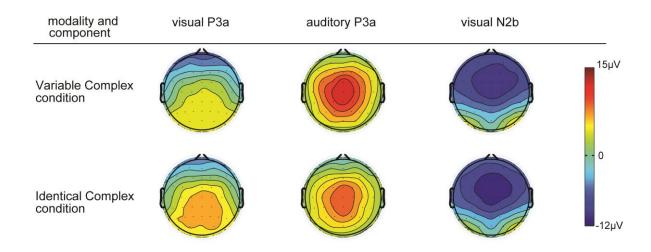


Fig. 6. Topographic distributions of the grand-mean P3a and N2b components (in μV) for complex irrelevant stimuli.

3.1.3.2.4 N2 latency

N2b latency data were assessed using a paired t-test comparing the ERP evoked by two conditions (2 Complex irrelevant stimulus types) at the Cz electrode. N2b peak latency did not vary significantly across conditions.

3.1.4 Discussion

In the present study, we investigated the effects of irrelevant stimuli complexity on the novelty P3/P3a and N2b event-related potential components. The goal of the present study was to assess the effects of the complexity of unexpected events compared with the complexity of

regular environmental events in eliciting the OR. Specifically, we examined the mobilization of attentional processes reflected by the late positive ERP component (P3a). We assumed that unlike complex events in a simple environment, simple unexpected events in a complex environment do not capture attention.

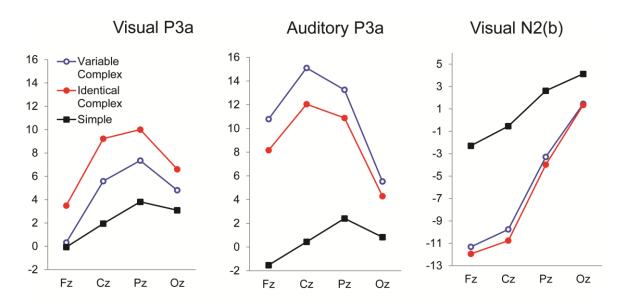


Fig. 7. Mean visual P3a and N2b and auditory P3a amplitude for the irrelevant stimuli for each task condition as a function of the midline electrode site.

3.1.4.1 Processing irrelevant stimuli and the relative complexity of stimuli

Previous studies (Sawaki & Katayama, 2007, 2008a) have reported that the P3a reflects attentional capture by stimulus deviance, rather than response inhibition or cognitive interference with maintaining the representation of the standard stimuli. Furthermore, (Sawaki & Katayama, 2008b, 2009) has shown that top-down attention to a certain stimulus feature or location modulates bottom-up attention to irrelevant deviations.

In this study, we also investigated the attentional mechanisms involved in processing of irrelevant stimuli. The major goal of the present study was to elucidate whether P3a is associated with elaborative processes, like evaluation and categorization of the irrelevant stimuli or it is rather the consequence of the interference with the task-set. By utilizing task-irrelevant stimuli which are clearly less complex than the stimuli comprising the task we attempted to separate the two possible consequences of the OR. The simple irrelevant stimuli are still capable of disrupting the sequence of standard and target stimuli and therefore interfere with the task-set, but do not require elaborate processing. We speculated that if the

P3a reflects the interference with the task-set, simple irrelevant stimuli in context of complex stimuli will elicit the P3a. In contrast, if the P3a reflects elaboration of the irrelevant stimuli, the simple irrelevants will not elicit the P3a. Similar to data from previous studies (Conroy & Polich, 2007; Courchesne et al., 1975), the findings of the present study demonstrate that *variable complex* infrequent irrelevant stimuli (variable colorful pictures of butterflies or environmental noises) elicit P3a in both auditory and visual modalities. In addition, complex irrelevant stimuli (independent of variability) also elicited the N2b component, but only in the visual modality. A similar result was observed for *identical complex* task-irrelevant stimuli (repeated, identical pictures and noises).

As predicted by our initial hypothesis, simple irrelevant stimuli within a sequence of complex task-relevant stimuli elicited neither anterior late positivity (P3a), nor N2b. It is important to note that similar simple irrelevant stimuli were reported to elicit P3a in classical *three-stimulus oddball* tasks where the complexity level of the task-relevant and irrelevant stimuli was within a similar range (Comerchero & Polich, 1999; Hagen et al., 2006; Katayama & Polich, 1999; Polich, 2007; Polich & Comerchero, 2003).

Polich (2003) provided evidence that the difficulty of target-standard perceptual discrimination may be an important determinant of P3a elicitation; P3a was larger and has a more central scalp distribution in tasks where targets were more similar to standards. In the present experiments, the tasks in conditions with complex and simple irrelevant stimuli were obviously incomparable in difficulty. If we compare our study with other studies (Frank, Yee, & Polich, 2012; Sawaki & Katayama, 2008a, 2008b) we can declare that the difficulty levels of our tasks were easy or medium. Nevertheless it is unlikely that the lack of detectable P3a (and N2b) in the Simple conditions resulted from differences in task difficulty. Although the performance data indicated that the visual tasks in the Complex (Identical and Variable) conditions were more difficult than in their Simple counterpart, no such difference existed in the auditory modality. According to Sawaki and Katayama (2006), the stimulus context (i.e. perceptual distinctiveness of targets and standards) determines whether non-target stimuli are processed as task-relevant or distractor information and consequently the distribution of the P3 complex. However, in our study the simple irelevants did not elicit any late positivity, i.e. these simple stimuli are not processed either as task-relevant or distractor information. The simple irrelevant stimuli of the present study had two important characteristics. First, these simple stimuli within the sequence of complex, task-related stimuli did not require elaborate processing such as evaluation and categorization. Second, these stimuli were extremely different from the task-related (standard and target) stimuli. The relative characteristics of the simple, irrelevant stimuli are important to consider, especially with regard to the characteristics of stimuli that elicit P3a.

P3a emerges at least in four conditions. (1) P3a is elicited by the irrelevant stimuli of the three-stimulus oddball paradigm (Comerchero & Polich, 1998; Hagen et al., 2006; Katayama & Polich, 1999; Polich, 2007; Polich & Comerchero, 2003). In the typical version of the oddball paradigm, the irrelevant stimuli differ from the standard and target stimuli (i.e., differ from the task-set) but are within the same range of complexity (e.g., standards are circles, targets are smaller circles, and the irrelevant stimuli are squares; standards are 2000 Hz frequency tones, targets are 1940 Hz frequency tones, and irrelevant stimuli are 500 Hz frequency tones; Comerchero & Polich, 1999). Therefore, because of the similar levels of perceptual processing, it seems to be difficult to avoid the elaborate processing of the irrelevant stimuli. (2) P3a is also elicited by the irrelevant stimuli of the novelty oddball paradigm (Courchesne, 1978; Courchesne et al., 1975; Grillon et al., 1990) in which the irrelevant stimuli differ greatly from the relevant stimuli, thus diverging from the task-set. In typical variants of this paradigm, the irrelevant stimuli are more complex than the task-related stimuli, which requires elaborate processing of the irrelevant stimuli (e.g., standards are letters A, targets are letters B, and irrelevant stimuli are variable, unrecognizable, colored patterns; Courchesne, 1978; standards are 900 Hz tones, targets are 1600 Hz tones, and irrelevant stimuli are a collection of variable buzzes, filtered noises, etc.; Grillon et al., 1990). (3) P3a is elicited not only by irrelevant events but also by the target stimuli of the oddball task (Goldstein et al., 2002), even if P3b masks the P3a component. Target stimuli are part of the task-set. Thus, the target stimuli are evidently processed, because they have to be discriminated from the standards, and their representations have to be transferred to the structures of motor organization. (4) Finally, P3a was also elicited in the visual modality in the 'mixed stimuli' condition in studies by Daffner and his colleagues (Daffner, Mesulam, et al., 2000; Daffner, Scinto, et al., 2000). The appearance of P3a in these studies seemingly contradicts the results of the present study. The irrelevant stimuli were simple shapes, and the standard and target stimuli were complex meaningless figures. The irrelevant stimuli were less complex than the task-relevant ones, although a different (i.e., novel) irrelevant stimulus was presented in each trial. Accordingly, such novel, irrelevant stimuli may require elaborate processing. As a specific feature of the paradigm, stimuli were presented by the participants. The self-initiated action may enhance the task-involvement of each stimulus, even if such stimuli were simple shapes. These features of the paradigm might contribute to the similar scalp distribution of the P3a components elicited by the irrelevant stimuli and the targets. On

the contrary, in the present study the simple irrelevant stimuli in the context of complex task-relevant stimuli remained in the background, imposing no substantial load on the processing system.

Emergence of P3a has been attributed to involuntary attentional distractions (Escera et al., 1998). Our results are not at variance with such claim. The probability of an attentional shift is relatively high for 'salient' stimuli. Several studies (Combs & Polich, 2006; Frank et al., 2012) demonstrated that the saliency is a key factor for eliciting P3a. However, 'saliency' is often context dependent. Complex stimuli attract attention when presented in the background of simple stimuli, but the opposite is not true. In this view attentional shift to the irrelevant stimuli and the processing demand of the irrelevant stimuli are 'two sides of the same coin'.

In the tasks presented in the current study, only the visual complex irrelevant stimuli elicited the N2b component. Falkenstein, Koshlykova, Kiroj, Hoormann, and Hohnsbein (1995) observed a similar modality difference in their go/no-go study. However, explaining the functional significance of N2b is beyond the scope of the present study.

3.1.4.2 Stimulus variability

As to the effect of stimulus variability on ERPs our study provided mixed results. In the auditory modality, variable complex stimuli elicited larger P3a than the identical stimuli. However, in the visual modality, we observed the opposite result. The identical complex visual stimuli elicited larger P3a than the variable stimuli. This result was unexpected, and we can only propose a post hoc explanation. There was a substantial difference between the sets of the auditory and visual stimuli utilized in the current study. In the Visual Variable condition stimuli belonged to the same category, whereas in the Auditory Variable condition, stimuli were selected from a wide array of categories. Therefore, category level identification was not needed in the Visual Variable condition. In contrast, the repeated presentation of the same complex visual stimulus may have resulted in an increasingly elaborate coding scheme (Gibson, 1969), and this process may have contributed to an increased P3a.

3.1.4.3 Conclusion of the present study

In conclusion, simple task-irrelevant visual and auditory stimuli do not elicit P3a or N2b components in the context of complex task-related stimuli. Polich and Comerchero (2003) had previously emphasized the importance of stimulus context, which was highlighted

by the results of the current study. Polich and Comerchero (2003) demonstrated that the context of the task (discrimination difficulty between standard and target), rather than stimulus novelty, modulated P3a in a set of three-stimulus oddball tasks. In our study, an alternative aspect of stimulus context, specifically the complexity relationships between task-related and task-irrelevant stimuli, determined elicitation of P3a. Based on results from the current study, we propose that the OR and P3a occur only if the irrelevant stimuli require elaborate processing. The processing requirement for irrelevant stimuli, however, also depends on their complexity relative to that of the standards and targets. It is reasonable to conclude that P3 is reflecting the elaborate processing of irrelevant stimuli.

3.2 Study 2. Extreme environment effects on cognitive functions: a longitudinal study in high altitude in Antarctica⁷

3.2.1 Introduction

The aim of this study was to investigate cognitive activity in Antarctic conditions. On this end we introduced an auditory distraction task (Schröger & Wolff, 1998), and the attention network paradigm (Fan et al., 2009). Beside the behavioral data in both tasks event-related brain potentials (ERPs) were measured. We compared 6 measurements (so-called cycles) that were completed during the campaign.

Participants of the present study were members of the over-wintering crew at Concordia Antarctic Research Station, which is a joint French-Italian research facility. The station is located on the Antarctic Plateau 3233 m above sea level. It is one of the coldest places on Earth, in 2011 the average air temperature was -51.2 °C (min. -76.4 °C, max. -19 °C). The air temperature of that year was -35.8 °C in summer and -64.4 °C in winter. The sun disappears completely during winter (from 2-3 of May to 9-10 of August). The over-wintering crewmembers (13 participants) had to adapt to this harsh environment. The main stressors of this environment are hypoxia, fluctuation of sunshine duration, isolation and confinement.

At the Concordia station (3233 m altitude) the average air pressure was 482.5 Hgmm between February and December 2011 (this value corresponds to 3880 m along the Equator). Due to the reduced partial pressure of oxygen, this condition caused moderate *hypoxia*. The average nocturnal oxygen saturation (Sp₀₂) measured by pulse-oximetry was 85.1-87.9% during the campaign (Tellez et al., 2014). Our data on diurnal Sp₀₂ exhibits slightly higher values, 89-94% during the stay, still noticeably under the normal Sp₀₂ of 96-100% (see exact numbers in Results). Additionally, Tellez et al. (2014) reported, for most of the participants, clinically severe level of periodic breathing all through the year-long campaign without any improvement. The heart rate, frequency of respiration and length of periods with periodic breathing remained stable during the campaign. Another study Abeln et al. (2015) investigated the cognitive performance and mood in the same crewmembers in 2011. They separated subjects into active and inactive groups based on their training load during the campaign. Subjects did not show changes in cognitive performance during their stay.

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⁷ Barkaszi, I., Takacs, E., Czigler, I., & Balazs, L. (2016). Extreme Environment Effects on Cognitive Functions: A Longitudinal Study in High Altitude in Antarctica. *Frontiers in Human Neuroscience*, *10*, 331. doi:10.3389/fnhum.2016.00331

Concerning the mood state, they measured the physical well-being and the perceived psychological state (perceived psychological strain and perceived motivational state). The deterioration of mood was observed in the inactive group which means that they felt physically worse, their motivation decreased and they became more strained. The mood of the active group remained stable. They also registered eyes closed resting EEG. Alpha and beta bands decreased in the active group during the campaign and alpha band increased in the second session and remained in this level in the inactive group during their stay.

In this range of altitude (3880 +/- 500 meters) compromised psychomotor functions, arithmetical skills (Shukitt-Hale, Banderet, & Lieberman, 1998), impairments in short-term memory (Bartholomew et al., 1999), multi-task performance (Adam, Fulco, & Muza, 2008), logical reasoning (Green & Morgan, 1985) have been observed in response to acute exposure. Long-term sojourn in high altitude locations affected long-latency event-related potentials in several studies (Ma, Wang, Wu, Luo, & Han, 2015; Singh et al., 2004; Thakur, Ray, Anand, & Panjwani, 2011).

Besides the direct effect of systemic hypoxaemia on brain, hypoxia might impact waking neurocognitive functions through the deterioration of sleep quality. Sleep in high altitude becomes more superficial with frequent awakenings. The proportion of REM sleep and slow-wave sleep (deep sleep; stages 3 and 4) decreases and the proportion of light sleep (stages 1 and 2) increases (Wickramasinghe & Anholm, 1999). The occurrence of periodic breathing during the campaign in question (Tellez et al., 2014) may indicate deteriorated sleep quality. However, the relationship of periodic breathing with sleep fragmentation and decrease of slow-wave sleep is controversial (P. L. Johnson, Edwards, Burgess, & Sullivan, 2010; Nussbaumer-Ochsner, Ursprung, Siebenmann, Maggiorini, & Bloch, 2012) and lacking data on chronic exposures. Still, Stadelmann et al. (2014) suggest that central apneas during periodic breathing initiate previously undetected sleep microarousals. Sleep fragmentation in turn might lead to daytime sleepiness, vigilance decrement and cognitive impairments (Bonnet & Arand, 2003).

Accordingly, Collet et al. (2015) observed compromised sleep quality in a different cohort of subjects at Concordia station. Total sleep time was shorter, sleep efficiency was lower and wake periods after sleep onset were longer at Concordia station compared to sea level station Dumont d'Urville, highlighting the role of hypoxia in sleep disruption.

Beyond hypoxia, the fluctuation of sunshine duration is another main stressor in this environment. Collet et al. (2015) found that constant *sunlight* exposure during summer has

initiated sleep fragmentation at both high-altitude and sea-level stations. Moreover, the disappearance of sun for the winter triggers affective problems in some subjects (Palinkas & Suedfeld, 2008).

As for other stressors of this environment, crewmembers stay in complete physical *isolation* and *confinement* during the winter with minimal or no chance of evacuation in emergency. Isolation and confinement are traditionally thought to impact mood, motivation and interpersonal relations (Palinkas & Suedfeld, 2008) so they might exert influence on cognition and attention through these factors, although exact pathomechanisms are little-known.

Based on the negative effects of stressors, we expected deterioration of cognitive functions mainly during the winter (third and fourth measurements) because of several factors. First, the sun disappeared completely in these measurement periods which might exacerbate sleep problems (Bhargava, Mukerji, & Sachdeva, 2000) and might trigger affective problems. Second, crewmembers had already spent a few months in Antarctica and according to Reed et al. (2001) three months residence in Antarctica had detrimental effect on cognition. Furthermore, few months of the mission in isolation and confinement have passed and the end of the mission is too far away that might also increase emotional and interpersonal problems (so called third-quarter phenomenon; Bechtel & Berning, 1991) in the fourth measurement.

However, due to successful coping with stress, a polar expedition may induce also positive (so-called salutogenic, Antonovsky, 1987) effects, like enhanced self-efficiency and personal growth (Palinkas, Gunderson, Johnson, & Holland, 2000; Palinkas & Suedfeld, 2008) that may counteract the detrimental effects of stressors.

The results of cognitive performance investigations on Antarctica are controversial (see more details in the General introduction). To settle the controversy, in our Antarctic study, participants had to perform two cognitive tasks while brain electrical activity (EEG) had been recorded. Occasionally event-related brain potentials (ERP) might be more sensitive to slight changes of brain activity than behavioral measures (Czigler, Csibra, & Ambró, 1994). We hypothesized that attentional functions become impaired in Antarctica as these abilities are particularly sensitive to stressors, such as *hypoxia* (Virues-Ortega, Buela-Casal, Garrido, & Alcazar, 2004), *mental fatigue* (Lorist et al., 2000), *sleep loss* (Jones & Harrison, 2001) and *sleep quality* (Schapkin et al., 2006), therefore we selected tasks capable to assess these functions.

The auditory distraction paradigm (Schröger & Wolff, 1998) .consists of a durationdiscrimination task with infrequent, task-irrelevant changes. Typical findings regarding the irrelevant changes include prolonged reaction time and higher error rate accompanied by a series of ERP components (see more details in the General introduction section). The Attention Network Test (ANT) combines cued detection task (Posner, 1980) with a flankertype paradigm (Eriksen & Eriksen, 1974) and the effect of warning signal. The attention system comprises three anatomically and functionally separate networks (alerting, orienting and executive control functions; Fan, McCandliss, Sommer, Raz, & Posner, 2002; Posner & Petersen, 1990) and these networks are calculated as reaction time differences of specified task conditions. The alerting network is responsible for a state of arousal. The orienting network is involved in the selection of information among multiple sensory inputs or locations, while executive control involves a set of operations including detecting and resolving conflicts (Fan et al., 2009). Only few studies investigated the event-related potentials (ERPs) in the ANT task (Neuhaus et al., 2010). We expected changes in those ERP components which are related to attentional functions and known to be influenced by stressors described above. Such components are the N2 and the late positivity (P3 complex).

N2 component. Several studies investigated the effect of hypoxia and mental fatigue on the N2 component elicited in flanker tasks and in other tasks that require cognitive control (such as the Simon task) and on the no-go N2 component elicited in go/no-go tasks. Ma et al. (2015) found delayed latency of no-go N2 and larger go and no-go N2 amplitude in the high-altitude group compared to the low-altitude group. N2 amplitude and latency are also sensitive to *mental* fatigue (Boksem, Meijman, & Lorist, 2006; Kato, Endo, & Kizuka, 2009). In a study by Boksem et al. (2006) fatigue resulted in diminished N2 amplitude difference between congruent and incongruent trials which indicative of impaired executive control. Others reported increased no-go N2 latency with time on task in a go/no-go task (Kato et al., 2009).

P3 complex. The effect of hypoxia, mental fatigue, sleep deprivation and disturbed sleep on P3 components were also investigated. In hypoxia P3a amplitude diminished (Balázs et al., 2001). Fowler and Prlic (1995) observed an inverted U function of P3b amplitude as a function of degree of hypoxia. Thakur et al. (2011), Singh et al. (2004), Fowler and Lindeis (1992) and Fowler and Prlic (1995) found delayed P3b latencies. Ma et al. (2015) obtained decreased P3b and no-go P3 amplitude in the high-altitude group compared to the low-altitude group. As for other stress effects, Boksem et al. (2006) obtained increased P3b latency as a result of mental fatigue. Kato et al. (2009) also found increased latencies for both

no-go P3 and P3b, and no-go P3 amplitude deterioration in a go/no-go task. Additionally, Massar, Wester, Volkerts, and Kenemans (2010) found decreased P3a amplitude after a cognitively demanding task. In *sleep deprivation* amplitude of P3a decreased in an auditory oddball task (A. Gosselin et al., 2005) and in a modified ANT task P3b amplitude decreased (Trujillo et al., 2009). Additionally, Schapkin et al. (2006) obtained decreased no-go P3 amplitude after disturbed sleep.

Beyond the N2 and P3 components (likely connected to frontal functions), we also investigated the effect of extreme environment on early stages of information processing, reflected by the *N1/MMN* and *N1* components. There are several results showing that these components are also sensitive to stressors. For example, in a study by Yang, Xiao, Liu, Wu, and Miao (2013) MMN amplitude decreased as a result of *mental fatigue* and in another study by Raz et al. (2001), MMN amplitude decreased after total *sleep* deprivation. In an ANT study by Trujillo et al. (2009) parietal N1 amplitude decreased after sleep deprivation.

3.2.2 Materials and methods

3.2.2.1 *Subjects*

A total of thirteen male adults participated in the experiments (six French, six Italians and one British). ERP data from 3 participants and behavioral data from 2 participants had to be excluded from the data analysis because of one or more missing sessions in the ANT task and distraction data of one additional participant had to be excluded because of low performance.

The remaining 10/11 participants (10 subjects had ERP data and 11 subjects had behavioral data) in the ANT task were 37.09/36.70 years old and the remaining 9/10 participants (9 subjects had ERP data and 10 subjects had behavioral data) in the distraction task were 37.30/36.88 years old (20-55 years of age) and all reported normal hearing. Participants were members of the over-wintering crew at Concordia Antarctic Research Station in 2011. During their stay, they performed these tasks on 7 occasions (Cycles) from mid-February to mid-November, once approximately every six weeks. ERP data from seventh session had to be excluded from the analysis because only a few subjects performed this session. Each subject participated in a 4-day-long fixed-sequence measurement at approximately every 6 weeks (SD 0.5). Supplementary Table 1 shows the measurement intervals. After some tests of other researchers, they performed our tasks on the second day.

On each occasion, they performed the ANT task right after the distraction task. Participants performed the experiment in the same room under the same circumstances.

All subjects gave written informed consent. The study was approved by the Ethics Committee of the Department of Psychology of the University of Rome "La Sapienza".

3.2.2.2 Stimuli and procedure of distraction task

Subjects performed a sound duration discrimination task. For each tone presented, the subjects were asked to indicate by button presses whether it was short (200 ms) or long (400 ms). The frequency of sounds was either 440 Hz (86%, Standard) or 480 Hz (14%, Deviant). The task was composed of equal number of long and short tones to be responded to by pressing left/right mouse key. Assignment of left and right hand responses was counterbalanced between subjects. Participants were instructed to hold the mouse with both hands and operate it with two thumbs. Infrequent changes in frequency were irrelevant for the task; subjects were instructed to attend the duration information only.

The task comprised 4 stimulus blocks. In the first block (practice block), subjects were presented with 20 practice stimuli. The second block consisted of 150 non-practice stimuli and the third and fourth blocks consisted of 170 non-practice stimuli. All stimuli were presented binaurally via headphones (Sennheiser PMX 60). In the first block, subjects were given a "Correct" or "Incorrect" feedback displayed after each trial. SOA was random in the 1200-1400 ms range. Subjects were instructed to respond as quickly and accurately as possible.

3.2.2.3 Stimuli and procedure of ANT task

The test features a cued reaction time task. Fig. 8 summarizes the stimuli and procedure. Each trial begins with a central fixation cross of variable duration (500 ms to 1500 ms). The fixation cross is followed by one of three cue types, that were equally likely to appear: No cue, Center or Spatial cue. Cues were presented for 100 ms, and consisted of an asterisk. Center cues appeared at the location of fixation cross, informing the subjects about the timing of the stimulus. Spatial cues appeared above or below the fixation cross and provided information about the timing as well as the location of the stimulus. A target display appeared 400 ms after the offset of the cue. The stimulus comprised five arrows. The subjects had to press buttons according to the direction of the central arrow. The other four arrows (flankers) could point to the same (congruent condition) or to the opposite direction

(incongruent condition). The arrows could arrive above or below the fixation cross with equal probability. Each flanker type was equally likely. The target display remained on the screen until a response was made or 1000 ms elapsed.

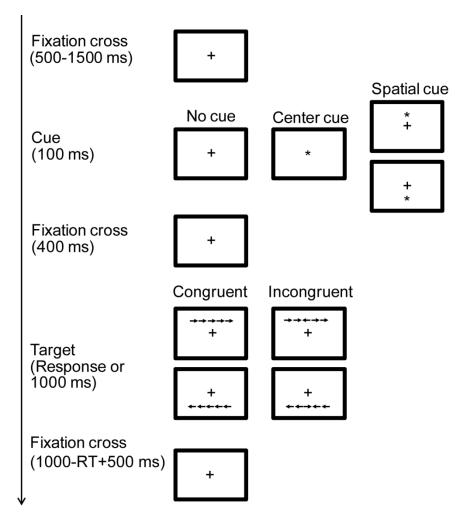


Fig. 8. Task design of Attention Network Test. Each trial begins with a central fixation cross (+) followed by one of three cue types: No Cue, Center or Spatial Cue. After the cue (*) five arrows appeared. The subjects had to press buttons according to the direction of the central arrow. The other four arrows (flankers) could point to the same (congruent condition) or to the opposite direction (incongruent condition). The arrows could arrive above or below the fixation cross. Timing information of the events is in the left side of the figure.

The task comprised 240 trials divided in 3 blocks. Subjects were given an auditory feedback (beep) of incorrect responses during the entire task. Participants held the mouse with both hands and operated it with two thumbs. They were instructed to respond only to the

direction of the central arrow in the target display as quickly and accurately as possible. Participants were told to maintain fixation at the fixation cross all the time.

3.2.2.4 EEG recording and data analysis

EEG was recorded with BrainAmp amplifier and actiCap electrode cap (BrainProducts) using 29 (Fp1, Fp2, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, TP9, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, O1, Oz, O2) electrodes according to the extended 10-20 system referenced to FCz. AFz was used as ground. Data were online filtered at 0.5-70 Hz with 12dB per octave. Sampling rate was 250 Hz.

Extended ICA was performed on individual data sets to remove eye movement artifacts from EEG recordings (Delorme & Makeig, 2004; Onton & Makeig, 2006). Components representing eye blink and horizontal eye movement artifacts were identified by inspecting the component scalp map, time course and ERP-image (visualization of event-related signal variations across single trials) and were deleted. Eye movement-free EEG data were obtained by back-projecting the remaining ICA components to the time domain. EEG was low-passed filtered (20 Hz; Kaiser windowed sinc FIR filter) and re-referenced to TP9 offline. Supplementary Image 1 shows the electrode locations.

3.2.2.5 Data analysis of distraction task

Reaction times (RTs) were calculated as the median duration between stimulus onset and button press within the 150-1000 ms time range. Median RTs were computed separately for Standards and Deviants. Correspondingly, the overall percentages of correct responses were computed. To assess the effect of stimulus type and cycle on both RTs and accuracy, data were analyzed by two-factor (Stimulus Type (Deviant, Standard) x Cycle (1-6)) repeated measures ANOVA.

Epochs of 1200 ms were extracted (-100 to 1100 ms) and baseline corrected (-100 to 0 ms). Only trials with correct responses were analyzed. Epochs with the signal range exceeding 70 μ V on frontal channels and 100 μ V on non-frontal channels were discarded from the analyses. Grand-means were computed from the individual subject averages. Difference waves were formed by subtracting Standard ERPs from Deviant ERPs to evaluate the N1/MMN, P3a and RON components. N1/MMN peak latency was identified as a negative peak at the Fz electrode site within the 130-300 ms range, P3a peak latency was identified as a positive peak at the Cz electrode site within the 250-500 ms range and RON peak latency

was identified as a negative peak at the Fz electrode site within 450-750 ms range. Mean N1/MMN amplitude was measured as the average in a 40 ms time window, P3a and RON in 70 ms time windows centered at peak latencies. Mean amplitude values were calculated at the Fz, Cz and Pz electrode sites. The amplitude values were analyzed using Electrodes (Fz, Cz, Pz) x Cycle (1-6) repeated measures ANOVA.

3.2.2.6 Data analysis of ANT task

RT and precision measures were calculated as above. Attention network effects were calculated as reaction time differences of the following conditions: alerting= RT_{nocue} - $RT_{centercue}$; orienting= $RT_{centercue}$ - $RT_{spatialcue}$, inhibition= $RT_{incongruent}$ - $RT_{congruent}$.

To assess the effect of the target type, cue type and the cycle on RTs data were statistically evaluated by three-factor (Target Type (Incongruent, Congruent) x Cue Type (No Cue, Center Cue, Spatial Cue) x Cycle (1-6)) repeated measures ANOVA and three separate single-factor (6 Cycles) repeated measures ANOVAs, one for each attention network difference score (alerting, orienting and inhibition).

Epochs of 2000 ms were extracted (500 ms pre-cue to 1000 ms post-target including 500 ms cue-target interval) and baseline corrected (100 to 0 ms pre-cue). We identified 3 ERP components after the target stimuli: N1, N2 and P3. Trials were collapsed over all target conditions to analyze the effect of Cue type on N1. Target type (congruency) effects were analyzed by collapsing all cue conditions to identify N2 and P3.

N1 latency was identified at Oz electrode site within 120-280 ms range after the onset of target stimuli. N1 amplitude was collapsed across P7, P3, Pz, P4, P8, O1, Oz and O2 electrode sites. Mean N1 amplitude was evaluated in a 40 ms time window centered at peak latency. The amplitude values of N1 were analyzed using Cue Type (No Cue, Center Cue, Spatial Cue) x Cycle (1-6) repeated measures ANOVA.

N2 component peak latency was identified as a negative peak at Fz electrode site within 200-380 ms after target stimuli. N2 amplitude was collapsed across FP1, FP2, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, C3, Cz and C4. Mean N2 amplitude was evaluated in a 80 ms time window. The amplitude values were analyzed using Target Type (Incongruent, Congruent) x Cycle (1-6) repeated measures ANOVA.

This component exhibits a centro-parietal scalp distribution with a peak stimulus latency between 300 and 600 ms. Target-locked P3 component peak latencies were identified as a positive peak at Cz and Pz within the 300-600 ms range after the onset of target stimuli.

Mean P3 amplitude was evaluated in a 100 ms time window centered at peak latencies. The mean amplitude values were measured at Fz, Cz and Pz. The amplitude values were analyzed using Electrode (Fz, Cz, Pz) x Cycle (1-6) x Target Type (Incongruent, Congruent) repeated measures ANOVA.

Greenhouse-Geisser correction was applied for all repeated measures with greater than 1 degree of freedom. Uncorrected degrees of freedom and corrected p-values are reported. Partial eta squared was computed as an estimate of effect size. Significant effects were further specified by Tukey-HSD post hoc tests.

3.2.3 Results

3.2.3.1 Results of the distraction task

3.2.3.1.1 Behavioral performance

The Stimulus Type x Cycle ANOVA of reaction time showed a significant main effect of Stimulus Type (F(1,9)=11.38, p<0.01, η_p^2 =0.55) and Cycle (F(4,55)=3.37, p<0.05, η_p^2 =0.27). RT for deviants was longer than RT for standards (p<0.05). RT significantly decreased from cycle 1 to cycle 6 (significant pairs: cycle1 – cycle6).

The Stimulus Type x Cycles ANOVA of the percentages of correct responses showed a significant main effect of Stimulus Type (F(1,9)=8.32, p<0.05, η_p^2 =0.48). Accuracy for Standards was better compared to Deviants (p<0.05).

Table 5 summarizes the behavioral data.

3.2.3.1.2 *ERP results*

3.2.3.1.2.1 N1/MMN

A significant main effect of Electrodes (F(2,16)=7.87, p<0.05, η_p^2 =0.49) was obtained. N1/MMN amplitude was larger at Fz than Pz electrode site (p<0.05).

3.2.3.1.2.2 P3a

A significant main effect of Electrodes (F(2,16)=5.99, p<0.05, η_p^2 =0.42) was obtained. P3a amplitude was smaller at Pz compared to Cz electrode site (p<0.05).

3.2.3.1.2.3 RON

A significant main effect of Electrodes (F(2,16)=5.93, p<0.05, η_p^2 =0.42) was obtained. This component was larger at Fz than Pz site (p<0.05).

Table 5. Mean reaction time (ms) and hit rate for Deviant and Standard stimuli in each cycle (with standard error of mean).

Cycle	1.	2.	3.	4.	5.	6.
Reaction time (ms) for Deviant	617.70	618.10	595.75	609.90	599.05	589.90
	(7.17)	(14.16)	(10.02)	(10.61)	(15.84)	(13.79)
Hits (%) for Deviant	85.42	88.57	88.88	88.71	90.8	90.57
	(3.86)	(3.04)	(4.14)	(2.19)	(1.89)	(1.43)
Reaction time (ms) for Standard	614.50	598.10	588.10	596.00	587.70	581.70
	(11.12)	(11.77)	(11.32)	(9.72)	(14.72)	(11.81)
Hits (%) for Standard	91.30	93.30	90.15	93.19	94.45	93.78
	(1.65)	(1.40)	(3.28)	(1.48)	(1.28)	(1.19)

Fig. 9 illustrates the grand-mean deviant-minus-standard difference waveforms for the six cycles at Fz, Cz and Pz electrode sites. Fig. 10 demonstrates the topographic distribution of the overall mean N1/MMN, P3a and RON components averaged across subjects and cycles. Supplementary Image 2 shows the grand-mean deviant-minus-standard difference waveforms for all electrodes for the six cycles.

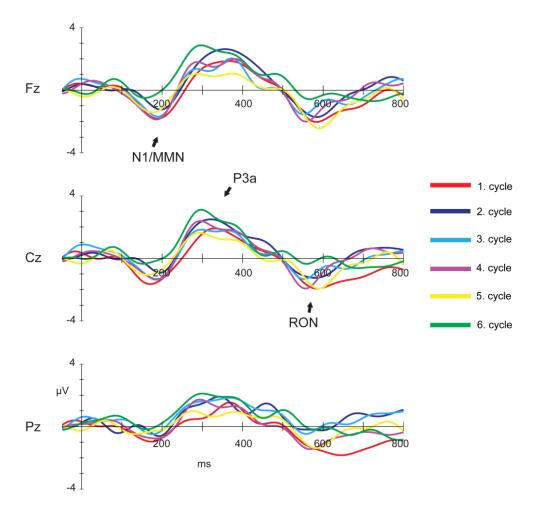


Fig. 9. Grand-mean difference waves (deviant ERPs – standard ERPs) for the six cycles depicted at electrode positions Fz, Cz and Pz (filtered with a 10-Hz low-pass) in the distraction task. In all cycles deviant stimuli elicited MMN, P3a and RON components.

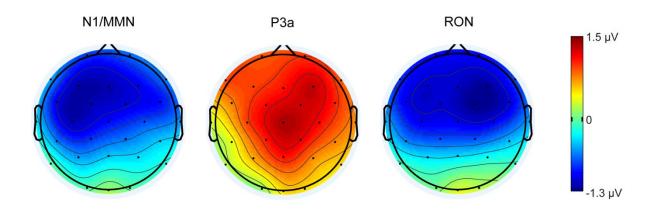


Fig. 10. Topographic distributions of the overall mean N1/MMN, P3a and RON components (in μ V) averaged across subjects and cycles presenting in 40 ms time window for MMN and in 70 ms time window for P3a and RON centered at peak latency. Dots indicate electrode positions on the scalp.

3.2.3.2 Results of the ANT task

3.2.3.2.1 Behavioral performance

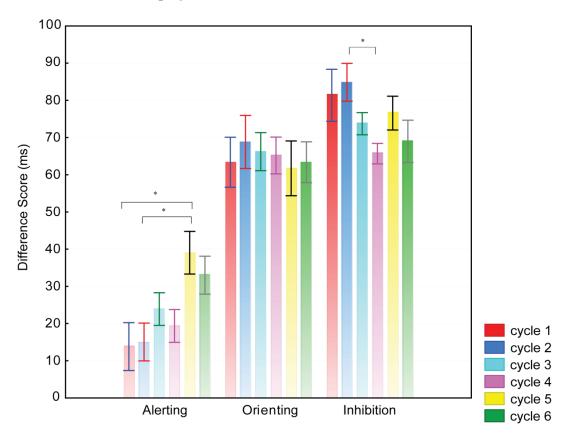


Fig. 11. Mean difference scores and standard errors for each of the three attention networks and six cycles. Attention network effects were calculated as reaction time differences of the following conditions: alerting= RT_{nocue} - $RT_{centercue}$; orienting= $RT_{centercue}$ - $RT_{spatialcue}$, inhibition= $RT_{incongruent}$ - $RT_{congruent}$. Asterisks indicate the significant differences.

For the RT data, a main effect of Cue Type (F(2,20)=256.41, p<0.001, η_p^2 =0.96) and Target Type (F(1,10)=839.89, p<0.001, η_p^2 =0.98), and an interaction between these two variables (F(5,50)=2.63, p<0.05, η_p^2 =0.46) replicated earlier results (Fan et al., 2009). Participants were faster to correctly categorize targets in Spatial Cue trials than in No Cue or Center Cue trials (p<0.001) and were also faster in Center Cue than No Cue trials (p<0.001). RTs were longer to Incongruent than to Congruent targets (p<0.001) and this effect was greatest for Center Cue.

A main effect of Cycle (F(5,50)=9.78, p<0.001, η_p^2 =0.49) shows that RT decreased monotonically from cycle 1 until cycle 5 (significant pairs: cycle 1 – cycle 3,4,5 and cycle 2 – cycle 4). A marginally significant Target Type x Cycle (F(5,50)=2.63, p=0.08, η_p^2 =0.20) and

a significant Cue Type x Target Type x Cycle (F(10,100)=3.55, p<0.05, η_p^2 =0.26) interactions were also obtained.

Analysis of alerting difference scores demonstrated an effect of cycle (F(5,50)=4.04, p<0.05, η_p^2 =0.28). Post-hoc tests revealed an increasing alerting effect from cycle 1 until cycle 5 (significant pairs: cycle 1 – cycle 5 and cycle 2 – cycle 5). Analysis of inhibition difference scores demonstrated a marginal effect of cycle (F(5,50)=2.63, p=0.08, η_p^2 =0.20). A decreasing inhibition effect was found (significant pair: cycle 2 - cycle 4). Fig. 11 shows the mean difference scores and standard errors for each of the three attention networks and six cycle levels. Supplementary Table 2 summarizes the behavioral data.

3.2.3.2.2 *ERP measures*

3.2.3.2.2.1 N1

A significant main effect of Cue Type (F(2,18)=7.15, p<0.05, η_p^2 =0.44) and a marginally significant main effect of Cycle (F(5,45)=2.45, p=0.07, η_p^2 =0.21) were obtained. Smaller N1 component emerged for No Cue than for Center and Spatial Cue (p<0.05). The amplitude of N1 was decreasing from cycle 1 to cycle 6 (significant pair: cycle 1 – 6).

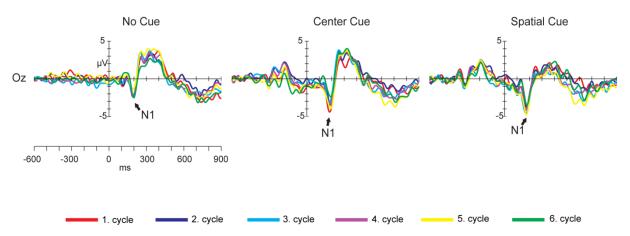


Fig. 12. Grand-mean event-related potential plots stratified by cue condition (No Cue, Center Cue and Spatial Cue) for Oz electrode site in the ANT task. Arrows indicate the peaks of the N1 waveforms.

Fig. 12 illustrates the grand-mean mean event-related potential plots stratified by cue condition (No Cue, Center Cue and Spatial Cue) for Oz electrode site. Fig. 13 shows the

topographic distributions of the overall mean N1 component (in µV) averaged across subjects and cycles presenting in 40 ms time window centered at peak latency.

Supplementary Images 3, 4 and 5 show the grand-mean event-related potential plots stratified by cue condition for all electrodes for the six cycles.

3.2.3.2.2.2 N2

The Target Type x Cycle ANOVA did not show any significant effect. Congruent and Incongruent trials evoked similar N2 component.

Fig. 14 illustrates the grand-mean event-related potential plots stratified by target condition (Congruent and Incongruent) for Fz, Cz and Pz electrode sites.

Fig. 13 shows the topographic distributions of the overall mean N2 component (in μV) averaged across subjects and cycles presenting in 80 ms time window centered at peak latency.

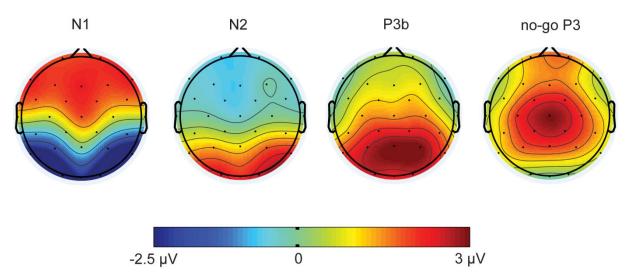


Fig. 13. Topographic distributions of the overall mean N1, N2, no-go P3 and P3b components (in μ V) averaged across subjects and cycles presenting in 40 ms time window for N1, in 80 ms time window for N2 and 100 ms time window for no-go P3 and P3b centered at peak latency. Dots indicate electrode positions on the scalp.

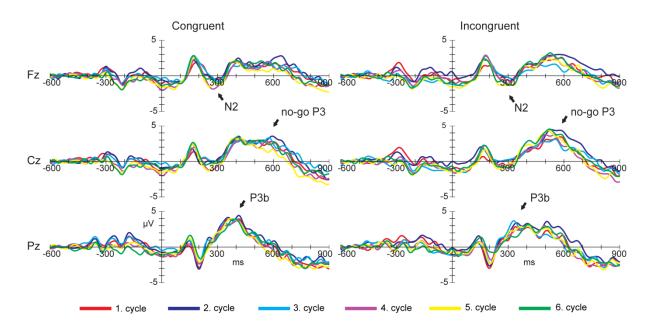


Fig. 14. Grand-mean event-related potential plots stratified by target condition (Congruent and Incongruent) for Fz, Cz and Pz electrode sites in the ANT task. Arrows indicate the peaks of the ERP waveforms.

A main effect of Target Type (F(1,9)=12.00, p<0.05, η_p^2 =0.57), Electrode (F(2,18)=13.53, p<0.001, η_p^2 =0.60) and a significant Target Type x Electrode interaction (F(2,18)=11.50, p<0.001, η_p^2 =0.56) were obtained for the earlier P3 subcomponent, indicating a larger earlier P3 response for Congruent versus Incongruent trials and smaller P3 response at Fz versus Cz and Pz and Cz versus Pz electrodes for Congruent and Incongruent trials. The difference between Congruent and Incongruent earlier P3 response was smaller at Fz compared to Cz and Pz electrode sites. The later peak of P3 was measured at Cz electrode. A main effect of Target Type (F(1,9)=6.48, p<0.05, η_p^2 =0.41) and Electrode (F(2,18)=10.31, p<0.05, η_p^2 =0.53) indicated that the later P3 response was smaller for Congruent versus Incongruent trials and larger at Cz versus Fz and Pz electrodes. No other main or interaction effects were significant for the early or late P3. Most importantly, there was no effect of Cycle.

Fig. 14 illustrates the grand-mean event-related potential plots stratified by target conditions (Congruent and Incongruent) for Fz, Cz and Pz electrode sites.

Fig. 13 shows the topographic distributions of the overall mean no-go P3 and P3b components (in μV) averaged across subjects and cycles presenting in 100 ms time window centered at peak latency.

Supplementary Images 6 and 7 show the grand-mean event-related potential plots stratified by target condition for all electrodes for the six cycles.

3.2.3.3 Diurnal SpO2 values

Table 6. shows the mean diurnal Sp_{O2} values for each subject and 5 cycles. The Sp_{O2} values of cycle1 are missing.

Table 6. Mean diurnal Sp_{O2} value for each subject and 5 cycles. The Sp_{O2} values of cycle1 are missing. Some cells are empty because of missing data.

subject	cycle2	cycle3	cycle4	cycle5	cycle6	
1	89	90	94	96	89	
2	96	90	96	93	94	
3	94	90	92	93	89	
4	91	88	95	94	88	
5	88	93	94	93	86	
6	90	86	86	91	90	
7		91	95	98	96	
8		89	95	95	94	
9	88	88	94		88	
10	89	88	93	93	88	
11	88	88	89	92	87	
12		87	88	93	86	
13	87	88	94	95	87	

3.2.4 Discussion

3.2.4.1 Typical findings

Our results show typical effects both in the distraction task and in ANT task. In the distraction task reactions to Deviants were prolonged and less accurate compared to the reactions to Standards. Typical ERP responses to the task irrelevant changes were also obtained; N1/MMN, P3a and RON were elicited for the deviating tones.

In the ANT task we replicated earlier results (Fan et al., 2009). The RT was smaller for Spatial Cue than for No Cue or Center Cue conditions and were also smaller for Center Cue than No Cue condition. RTs were faster for congruent than incongruent stimuli. Similarly to Neuhaus et al. (2010) and Galvao-Carmona et al. (2014), target-related N1 amplitude increased during alerting, and an amplitude increase of target-related N1 was found in Center Cue trials relative to No Cue trials. Contrary to the results of Neuhaus et al. (2010), no amplitude increase of target-related N1 was found in Spatial Cue trials relative to Center Cue. Our results do not support the idea of many other studies that spatial attention influences this component (Luck et al., 1994). The attention related later ERP components N2 and P3 in the ANT task show similar results to those observed by Neuhaus et al. (2010) and Neuhaus et al. (2007). No congruency effects were obtained on the N2 component, although we expected higher N2 amplitude for incongruent compared to congruent trials as this component might be related to the response monitoring and control of preparation for incorrect response (Folstein & Van Petten, 2008). Wendt, Heldmann, Munte, and Kluwe (2007) actually found higher N2 amplitude to incongruent compared to congruent trials in an Eriksen flanker task.

We identified two target-locked P3 subcomponents, the earlier P3 response with parietal amplitude maximum and a later P3 response with central amplitude maximum (frontal in article of Neuhaus et al., 2010). We labeled the earlier subcomponent as P3b and the later subcomponent as no-go P3. P3b amplitude reduced and no-go P3 increased for the incongruent trials compared to congruent condition (similarly to Neuhaus et al., 2010). P3b reduction suggests increased decision uncertainty, because flanking arrows in incongruent trials induce ambiguity which is thought to decrease P3b amplitude (R. J. Johnson, 1986; Luck, 2005). On the other hand, larger no-go P3 amplitude presumably reflects inhibition of conflicting response tendencies in incongruent trials (Pfefferbaum et al., 1985).

3.2.4.2 Results of repeated testing in Antarctic conditions

The RTs were sensitive to the passage of time in both tasks. The decreasing RT in distraction and ANT tasks could be attributed to sustained effect of practice. Furthermore, two of the calculated attention network scores, specifically the alerting and inhibition effects also changed as a function of time. The alerting effect increased, which could indicate that participants better utilized central cues that alert them to trial onset. In accordance with a previous study (Ishigami & Klein, 2010) the inhibition effect decreased due to the repeated execution of task, which may derive from the better inhibition of the influence of surrounding flankers.

Contrary to our expectations the late ERP components (N2, P3, RON) related to frontal attentional functions did not show any significant changes.

As to the effect of time in the Antarctic environment on the early stage of information processing reflected by N1 and N1/MMN our study provided mixed results. Contrary to our expectations we only obtained a marginally significant decrease of N1 in the ANT task, but the N1/MMN component in the distraction task was not sensitive to the passage of time. Most likely the N1 amplitude reduction in the ANT task could be attributed to practice effect, as every other measure (RT and accuracy) shows that subjects improved constantly during their stay.

3.2.4.3 Adaptation to Antarctic environment

The lack of detectable cognitive deterioration might be attributed to the inappropriate sensitivity of the method, however, evidence shows that the cognitive functions which can be measured in these tasks are sensitive to stressors, such as *hypoxia* (Virues-Ortega et al., 2004), *mental fatigue* (e.g. Lorist et al., 2000) *sleep loss* (see review Jones & Harrison, 2001) and *impaired sleep quality* (Schapkin et al., 2006), but these studies are diverse concerning the baseline data and control group. Despite the limitations of the present study (the lack of baseline data collection before the expedition and the lack of control group), based on the results described above, it is more likely that the Antarctic conditions had no negative influence on the neurocognitive functions. Although the lack of detrimental effects seems clear from our results, the possible explanations for this result must be very cautious. As a tentative account, we summarize a few likely factors, that might have counteracted the negative influence of hypoxia, fluctuation of sunlight, isolation, confinement and other stressors.

First, several factors could influence crewmembers' sleep positively that might reduce the *sleep problems*. Crewmembers could take a nap in their free time. Research has shown that the amount of sleep per day is the most important factor of cognitive performance, irrespectively whether it is attained totally during the night or partly during the day in the form of napping (Mollicone, Van Dongen, Rogers, & Dinges, 2008). Moreover, they had the opportunity to exercise and according to Arendt (2005) sleep quality improves after physical activity. Indeed Abeln et al. (2015) have shown that the mood of physically active crewmembers remained steady through the campaign compared to inactive.

Second, *slight deterioration of mood* that might affected some subjects (for example, physically inactive crewmembers, Abeln et al., 2015) does not necessarily lead to cognitive problems as previous studies have shown (Chepenik et al., 2007). Third, from a more psychological point of view, Antarctic missions also have positive aspects (Suedfeld, 2001, 2005) which counteract the impact of stressors. These *positive characteristics of the mission* are related on one hand to the environment (outside and inside, e.g. beauty of nature, comfortable and cozy habitat; Atlis, Leon, Sandal, & Infante, 2004; Suedfeld, 2001, 2005). Moreover, crewmembers often experience personal growth (Kjærgaard, Leon, Venables, & Fink, 2013; Palinkas, 1986) and enjoy social life (Suedfeld, 2001, 2005).

Furthermore, *humans are adaptive beings* and can adapt successfully to the negative attributes of a long-duration mission. In extreme situations people are able to manage stress and stay well (Antonovsky, 1987).

In acute hypoxia, especially when it is probed in laboratory settings devoid of other confounding factors as cold, fatigue and high level of physical exertion, the altitude of up to 3880 (+/- 500) meters have not produced reliable cognitive deterioration in numerous studies (for no effect see Crow & Kelman, 1973; Gustafsson, Gennser, Ornhagen, & Derefeldt, 1997; Hewett, Curry, Rath, & Collins, 2009; M. A. Paul & Fraser, 1994; Takagi & Watanabe, 1999). In longer sojourns, hypoxia attenuates with long-term acclimatization on various physiological levels, for example, red blood cell count increases in the first 5-6 weeks (Zubieta-Calleja, Pauley, Zubieta-Calleja, & Zubieta-Castillo, 2007).

Two studies reported results of the Antarctic overwintering at the Concordia station in 2011 without control group and baseline data collection, similarly to our study. In accordance with our results a study of Abeln et al. (2015) did not obtain any effect of Antarctic conditions on behavioral responses in cognitive tasks. Another study of Tellez et al. (2014) measured decreased nocturnal Sp_{02} all through the campaign. Based on our results and those of Abeln et

al. (2015) it seems that this mild systemic desaturation have not impaired brain oxygenation as compensatory processes (for example, red blood cell mass increase or cerebral vasodilation) effectively neutralized it.

The results of the present study might be regarded as additional evidence that it is possible to adapt to hypoxic conditions on long-term exposures, at least we have not detected any sign of detrimental effects by using tasks measuring mostly attentional functions.

Further research is needed to determine which factors play crucial role to counteract the stressors. Mapping these factors would be important in order to prevent deterioration of cognitive functions in future missions to extreme environments.

3.3 Study 3. Human cognition in space: impacts of space environment on attentional functions

3.3.1 Introduction

During the past 55 years of manned spaceflight, many studies investigated effects of this environment on cognitive functions. The majority of results show that these functions do not deteriorate in space (see the General introduction section).

In space, many stressors could influence cognitive performance adversely. Microgravity has a direct effect on vestibular, sensory-motor and cardiovascular systems which could deteriorate cognitive functions (e.g. Bock et al., 2010; Glasauer & Mittelstaedt, 1998; Kanas & Manzey, 2008; Lipnicki & Gunga, 2009; Manzey et al., 1998; Manzey et al., 1993, 1995). Nonspecific stressors also occur during the whole spaceflight, such as high workload and sleep loss (Barger et al., 2014; Mallis & DeRoshia, 2005), furthermore the ISS is an isolated and confined environment which can also worsen cognitive performance. Furthermore, the elevated ambient level of CO₂ and radiation can also negatively impact cognition (Cucinotta et al., 2014; Strangman et al., 2014).

In the present study, two tasks were applied that require visuospatial perception and working memory. In these tasks complex, colorful task-irrelevant stimuli were presented occasionally in the sequence of target stimuli. These irrelevant stimuli typically elicit the P3a ERP component, which can be considered as a brain electrical correlate of the orienting response (see more details in the General introduction section). Many studies demonstrated that this component is sensitive to several stress factors, such as sleep deprivation (A. Gosselin et al., 2005), mental fatigue (Massar et al., 2010) and hypoxia (Balázs et al., 2001).

In this investigation, subjects performed these tasks three times before launch, two times during the flight and four times after returning from space. The mean of the three preflight and two late post-flight measurements was regarded as the baseline for the evaluation of the effects of spaceflight (in-flight) and readaptation (early in-flight) conditions. We hypothesized that attentional functions connected to irrelevant stimuli diminish in space due to direct effects of microgravity, nonspecific and other stress factors. We also assume that the readaptation, i.e. the recovery of attentional functions takes some time after returning from space. Furthermore, we were also interested in the following factors: are there any differences between the pre-flight and late post-flight measurements; does the very early post-flight

measurement differ from the baseline; are there any differences between the two in-flight measurements; does the second early post-flight measurement differ from the baseline.

In the present study, we focus on the ERP component elicited by irrelevant stimuli. The description and explanation of behavioral data and other ERP components are beyond the scope of the present report.

3.3.2 Materials and Methods

3.3.2.1 *Subjects*

Five male astronauts participated in this experiment. Each astronaut took part in a long-duration mission on the International Space Station. At the time of their launch, the mean age of the subjects was 52.6 years (48-56 years of age). This study was conducted during four missions (expeditions 20/21, 26/27, 30/31, 34/35). They performed the experimental tasks on nine occasions. Data were collected at regular time intervals. The preflight data were collected 55-78, 41-46 and 27-29 days before launch. The in-flight data were collected 6-12 and 49-59 days after the launch. The post-flight data was collected 2-3, 5-8, 15-17 and 18-22 days after return to Earth. Pre-flight and post-flight experiments were conducted at the Gagarin Cosmonaut Training Center (Star City, Russia), European Astronaut Center (Cologne, Germany) and Johnson Space Center (Houston, USA).

The Ethics Committee of the Institute for Psychology of the Hungarian Academy of Sciences, the Institutional Review Board (IRB) of ESA and the IRB of NASA approved the experimental protocol, which complied with all guidelines stated in the Declaration of Helsinki. All astronauts signed an informed consent form.

3.3.2.2 Stimuli and procedure

The Neurospat experiment consists tasks devised by two science teams. In order to reduce fatigue, tasks were presented in 5-8 minute blocks with short breaks in-between. The total execution time was 70 minutes. The order of task blocks was as follows: Control measurements, Lines task, Clock NoFrame task, Clock Frame task, four blocks of Visuomotor Tracking task, Clock Frame task, Clock NoFrame task, Lines task. We will present here the results of the Lines and Clock tasks.

During the whole task, a cylindrical tunnel with a form-fitting facemask was affixed to the screen of the laptop computer (Fig.15.). This equipment served to exclude external visual cues and providing circular viewing field. The distance between the eyes and the screen of the computer was 25 cm. The tunnel had a diameter of 22 cm. The background color of the screen was dark gray.

On Earth, subjects performed the experiment while sitting in a chair and looking straight ahead through the tunnel. The computer with the tunnel and mask was placed on a table. In space, subjects performed the experiment in quasi-free floating posture without any rigid contact with the station structure. They held the computer with the tunnel and mask in their hands and strapped their head to the mask of the tunnel with an adjustable head belt.

Subjects and assisting crewmembers were trained to perform the in-flight measurements themselves.



Fig.15. Computer with the tunnel and mask.

3.3.2.2.1 Lines task

Fig. 16 summarizes the stimuli and procedure. First, a simple yellow line appeared on the screen for 100 ms. This defined the *reference* stimulus orientation, which was to be remembered by the observer. Following a 500 ms blank screen a second *probe* stimulus (a blue line) was presented for 100 ms. Subject had to indicate as quickly as possible, by pressing buttons on a gamepad, whether the probe stimulus was at the same orientation as the reference stimulus. The position of reference and probe lines was different. They were asked to push the button with the index finger if the lines were the same direction and with the

thumb if directions are different. Subjects had 800 ms to react after the offset of stimuli. The next trial appeared 1000 ms after the offset of stimuli. The SOA (reference stimulus onset to reference stimulus onset interval) was 1700 ms. The probe stimuli could be of three types, which were equally likely to appear: Same, Hard or Easy. In the Same trials, the probe line was at the same orientation as the reference line. In the Easy trials, the differentiation was easy as the difference in angle between the reference and probe lines was relatively large; 60 degrees. In the Hard trials, the difference in angle between reference and probe lines was small; 30 degrees, making discrimination hard. In the remaining 20% of the trials, task-irrelevant stimuli (pictures) of 100 ms duration were presented in the place of the probe stimulus. Subjects should not press either button when presented with these Irrelevant stimuli. The lines were 2.1 cm length and 0.2 cm thick. Task-irrelevant stimuli were variable colorful, circular (so-called fisheye) pictures (e.g. buildings, statues, everyday objects) with a diameter of 4.7 cm. The task has 450 trials divided into two blocks. In the first ten trials of the first block, an auditory feedback (beep) was provided when the subject responded erroneously.

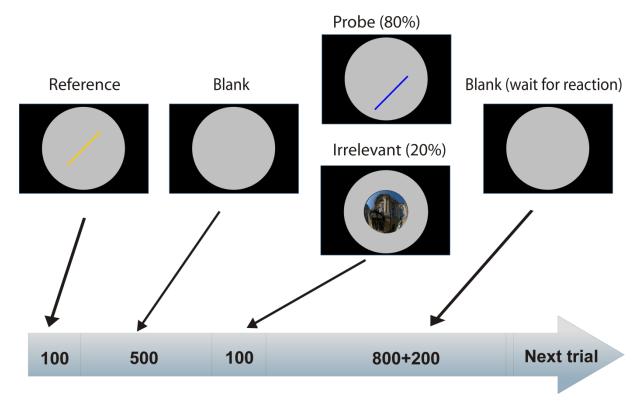


Fig. 16. The design of Lines task. Each trial begins with a yellow reference line followed by a blank screen. After the blank screen, a probe line or an irrelevant stimulus appeared followed by another blank screen. Subjects had to press buttons according to the relative direction of the probe and reference lines. Timing information of the events is in the bottom of the figure.

(Subjects had 800 ms to react after the offset of stimuli, but the next trial appeared 1000 ms after the offset of stimuli).

3.3.2.2.2 Clock tasks

Fig. 17 summarizes the stimuli and procedure. Each trial began with a black number (digital clock - reference stimuli) on a light gray disk of 100 ms duration. The diameter of the disk was 1.1 cm. The following numbers were used as stimuli: 1, 2, 4, 5, 7, 8, 10 and 11. Numbers were rotated randomly $\pm 60^{\circ}$, $\pm 30^{\circ}$, or 0° compared to vertical in order to avoid reference to the vertical direction. Following a 500 ms blank screen a white dot (probe stimuli) was displayed on the perimeter of an invisible circle (an imaginary analog clock face) for 50 ms. The diameter of the dot was 0.4 cm. Subject had to indicate as quickly as possible, by pressing pushbuttons on a gamepad whether the dot was at the location corresponding to the hour indicated by the digital clock. Subjects were asked to press the button with the index finger if the dot was at the given hour and with the thumb if the dot is not at the right time. Subjects had 850 ms to react after the offset of probe stimuli. The next trial appeared 1050 ms after the offset of stimuli. The SOA (reference stimulus onset to reference stimulus onset interval) was 1700 ms. The dot stimuli could be of three types, which were equally likely to appear: Same, Hard or Easy. In the Same trials, the dot appeared at the hour indicated by the numerical reference stimuli. In the Easy trials, the differentiation was easy as the difference in hour between the reference and probe stimuli was relatively large, 2 hours. In the Hard trials, the difference in hour between reference and probe stimuli was small, 1 hour, making discrimination hard. As in the Lines task, Irrelevant stimuli were occasionally presented (in the 20% of the trials) in the place of the dot stimuli. Subjects should not press either button when presented with these stimuli.

This task was presented in four blocks. In half of the blocks a spatially orienting rectangular frame was presented around the visible workspace on the screen (Frame condition; the size of the frame was 10.5 cm x 10.5 cm). In the other half of the blocks, the frame was circular (NoFrame condition; the diameter of the circle was 12.1 cm). Each condition had 300 trials (80 Same, 80 Hard, 80 Easy and 60 Novel trials). In the first ten trials of the first block of the Frame and NoFrame conditions, an auditory feedback (beep) was provided when the subject pushed the wrong key.

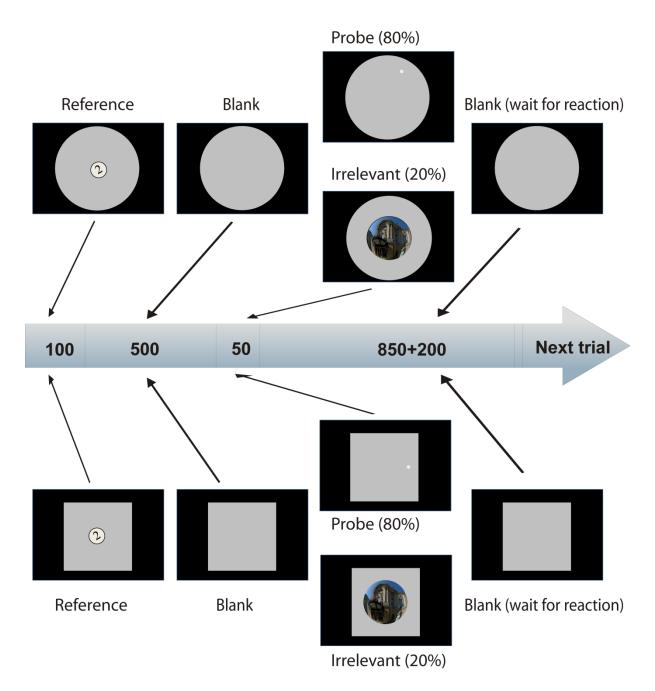


Fig. 17. The design of Clock tasks. Characteristics of the stimuli for NoFrame/Frame conditions is in the top/bottom of the figure. Each trial begins with a number (reference stimulus) followed by a blank screen. After the blank screen, a dot (probe stimulus) or an irrelevant stimulus appeared followed by another blank screen. Subjects had to press buttons according to the location of the dot corresponding to the hour indicated by the reference stimulus. Timing information of the events is in the middle of the figure. (Subjects had 850 ms to react after the offset of stimuli, but the next trial appeared 1050 ms after the offset of stimuli).

3.3.2.3 EEG recording and data analysis

In space, the experiment used the European Physiology Module (EPM), and the Multi-Electrodes Encephalogram Measurement Module (MEEMM). The same MEEMM module with ECI electrode cap was used in Star City and Cologne. The sampling frequency was 1116 Hz. 58 scalp electrodes were placed using the extended 10-20 system, and the ground electrode was on the forehead. In Houston, EEG was recorded with ANT system at a sampling frequency of 1024 Hz. 59 scalp electrodes were placed using the extended 10-20 system and an additional scalp electrode, the AFz functioned as ground. Right ear reference was used for all recordings.

Horizontal eye-movements were monitored using two electrodes placed lateral to the outer canthi of each eye; vertical eye-movements were monitored with one electrode placed below the left eye. EEG was band-passed filtered (0.5-30 Hz, Kaiser windowed sinc FIR filter) offline and downsampled to 512 Hz. Data segments containing paroxysmal artifacts (but not pure eye-movements) and bad channels (channels with extreme amplitude noise or isoelectric lines during most of the recording) were removed by visual inspection. Extended ICA was performed on individual data sets to remove eye blink artifacts from EEG recordings (Delorme & Makeig, 2004; Onton & Makeig, 2006). Components representing eye blink and horizontal eye movement artifacts were identified by inspecting the component scalp map, time course and ERP-image (visualization of event-related signal variations across single trials) and were deleted. Eye movement-free EEG data were obtained by back-projecting the remaining ICA components to the time domain.

Missing channels were interpolated using spherical spline interpolation. EEG was rereferenced to the average of all cortical electrodes.

Epochs of 1000 ms were extracted (100 ms pre-probe stimuli to 900 ms post-probe stimuli in each task) and baseline corrected (100 to 0 ms pre-probe stimuli). Only trials with correct responses were analyzed. Epochs with a signal range exceeding 70 μ V on frontal, central and temporal channels and 100 μ V on parietal and occipital channels were discarded from the analyses. Grand-means were computed from the individual subject averages.

In the current study, we focused on the P3a component. We identified the P3a ERP component as a positive peak within 280-480 ms range after the onset of Novel stimuli. As the P3a components elicited by Line, Clock Frame, and Clock NoFrame Irrelevants showed similar waveforms and peak latencies (382,8 ms for Line Irrelevants, 386,7 ms for ClockFrame Irrelevants, 384,7 ms for ClockNoFrame Irrelevants), the P3a latency was

measured on the grand mean ERP waveforms averaged across subjects, sessions and tasks at Cz electrode. P3a amplitude was evaluated in a 50 ms time window centered at this averaged peak latency. The mean amplitude values were measured at the F3, Fz, F4, C3, Cz, C4, P3, Pz and P4 electrode sites. The amplitude values were analyzed using Session (9) x Task (Line, Clock Frame, Clock NoFrame) x Region (Frontal, Central, Parietal) x Laterality (Left, Midline, Right) repeated measures ANOVA. In this analysis, we focused on the planned comparisons of the sessions described in Table 7 (baseline measurements: pre-flight1, pre-flight2, pre-flight3, post-flight4).

Table 7. Planned comparisons for P3a amplitude.

contrast	pre- flight1	pre- flight2	pre- flight3	in- flight1	in- flight2	post- flight1	post- flight2	post- flight3	post- flight4	p- value
1	2	2	2	-5	-5	0	0	2	2	0.0205
2	1	1	1	0	0	-5	0	1	1	0.0027
3	0	0	0	1	1	-2	0	0	0	0.5255
4	0	0	0	1	-1	0	0	0	0	0.4946
5	2	2	2	0	0	0	0	-3	-3	0.0177
6	1	1	1	0	0	0	-5	1	1	0.0920
7	2	2	2	-3	-3	0	0	0	0	0.0162

Fig. 19 shows that the topography of P3a is changed in space in contrast to baseline measurements. In order to examine whether this topography change is significant or not, we carried out an additional analysis of P3a amplitude with baseline and in-flight sessions (preflight, in-flight and late post-flight measurements) using Session (7) x Task (Line, Clock Frame, Clock NoFrame) x Region (Frontal, Central, Parietal) x Laterality (Left, Midline, Right) repeated measures ANOVA. In this analysis, we focused on the interaction of Session and Region.

Peak latency values were analyzed by Session (9) x Task (Line, Clock Frame, Clock NoFrame) repeated measures ANOVA at the Cz electrode site.

Greenhouse–Geisser correction was applied for all repeated measures with greater than 1 degree of freedom. Uncorrected degrees of freedom and corrected p-values are reported. Partial eta squared was computed as an estimate of effect size. Significant effects were further specified by Tukey-HSD post hoc tests.

3.3.3 Results

3.3.3.1 *P3a amplitude*

Fig. 18 illustrates the grand-mean ERPs for Novel stimulus for baseline, in-flight and early post-flight sessions in each task, recorded at F3, Fz, F4, C3, Cz, C4, P3, Pz and P4 electrode sites. Fig. 19 shows the topographic distributions of the P3a components (in μ V) averaged across subjects, tasks, and session types. Fig. 20 presents the mean P3a amplitude in each session.

The analysis of Session (9) x Task (Line, Clock Frame, Clock NoFrame) x Region (Frontal, Central, Parietal) x Laterality (Left, Midline, Right) repeated measures ANOVA for amplitude data shows a significant main effects of Session (F(8,32) = 7.37, p < 0.05, η_p^2 = 0.64) and Task (F(2,8) = 9.13, p < 0.05, η_p^2 = 0.69). Additionally a significant main effect of Region (F(2,8) = 6.98, p < 0.05, η_p^2 = 0.63) and a significant interaction between the Region and Laterality factors (F(4,16) = 4.82, p < 0.05, η_p^2 = 0.54) were obtained.

Planned comparisons verified that P3a amplitude was larger in ground baseline compared to in-flight (1. contrast, F(1,4)=13.80, p<0.05, $\eta_p^2=0.77$), but P3a amplitude did not change significantly from in-flight to very early post-flight (3. contrast), as predicted by our initial hypothesis. Furthermore, the amplitude of P3a was larger in ground baseline compared to very early post-flight (2. contrast, F(1,4)=43.08, p<0.05, $\eta_p^2=0.91$) and also larger in pre-flight than in late post-flight (5. contrast, F(1,4)=15.12, p<0.05, $\eta_p^2=0.79$). Additionally, there were no significant differences between the two in-flight (4. contrast) and between baseline and second early post-flight (6. contrast) measurements.

As there is a significant difference between pre-flight and late post-flight measurements, we also compare the in-flight data with pre-flight data. Planned comparison between pre-flight and in-flight measurements show that amplitude of P3a was larger in pre-flight compared to in-flight (7. contrast, F(1,4)=15.92, p<0.05, $\eta_p^2=0.79$). Post hoc tests

revealed that amplitude of P3a was larger in the Lines task than in the Clock tasks (p < 0.05). Additionally, amplitudes of P3a were larger at central and parietal electrodes compared to frontal sites (p < 0.05).

The analysis of Session (7) x Task (Line, Clock Frame, Clock NoFrame) x Region (Frontal, Central, Parietal) x Laterality (Left, Midline, Right) repeated measures ANOVA for amplitude data shows a significant main effects of Session (F(6,24) = 7.60, p < 0.05, η_p^2 = 0.65), Region (F(2,8) = 6.22, p < 0.05, η_p^2 = 0.60) and a significant interaction between the Session and Region (F(12,48) = 3.73, p < 0.05, η_p^2 = 0.48). Follow-up simple effects tests indicated that the amplitude of P3a was larger in ground baseline compared to in-flight at frontal (F(1,4) = 21.98, p < 0.01, η_p^2 =0.84) and central (F(1,4) = 21.98, p < 0.05, η_p^2 =0.71) regions. There was no significant difference between ground baseline and in-flight at parietal region.

3.3.3.2 *P3a latency*

P3a latency data were assessed using a repeated measures ANOVA comparing the ERP elicited by nine sessions and three tasks (Line, Clock Frame, Clock NoFrame) at the Cz electrode. Based on our analysis, P3a peak latency did not vary significantly across sessions and tasks.

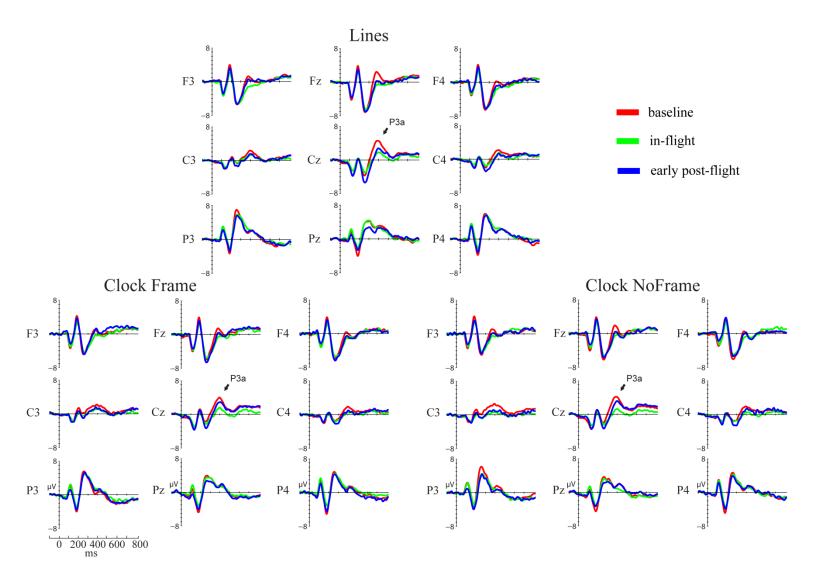


Fig. 18. Grand-mean event-related potential plots in response to task-irrelevant stimuli.

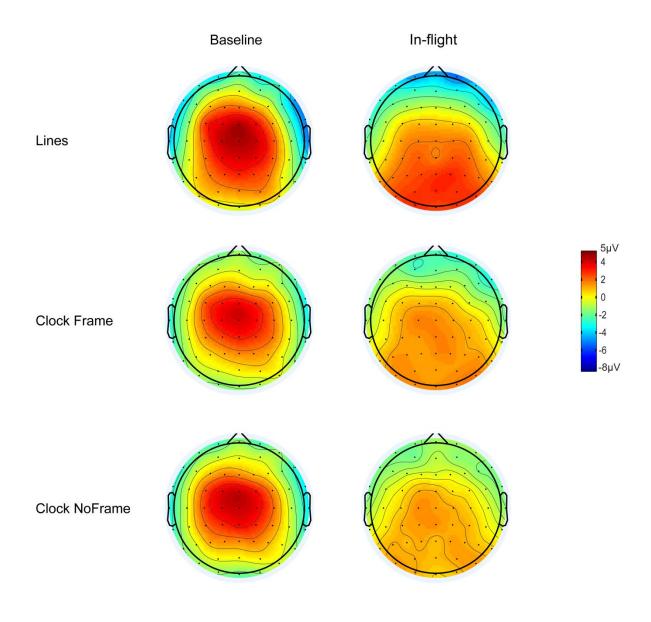


Fig. 19. Topographic distributions of the P3a components (in μV) averaged across subjects (baseline sessions: left column; in-flight sessions: right column).

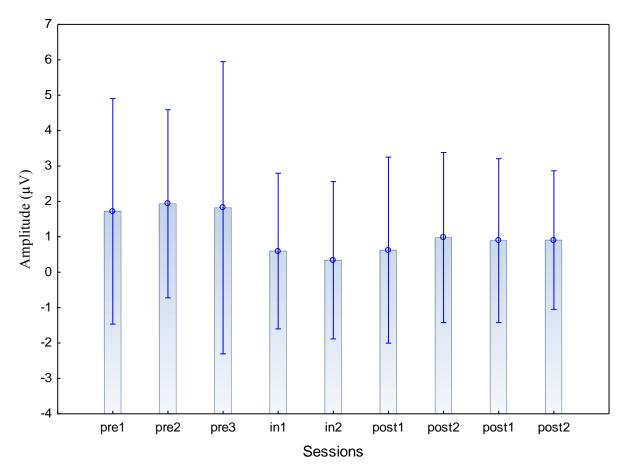


Fig. 20. Mean P3a amplitude in each session. Vertical bars denote the standard errors.

3.3.4 Discussion

In this study, we investigated the effects of microgravity, nonspecific and other stressors on cognitive functions. In the present analysis we examined the impact of this environment on P3a ERP component elicited by complex, task-irrelevant stimuli which reflect attentional functions. Although the description and explanation of behavioral data are beyond the scope of the present report, preliminary data analyses show that performance impaired in space compared to baseline. Preliminary behavioral data analyses also show that Clock tasks were more difficult than Lines task, that might have caused the higher P3a amplitude in Lines task compared to Clock tasks. As predicted by our initial hypothesis, P3a amplitude decreased in flight and in the first days after landing compared to baseline measurements. Additionally, the scalp distribution of P3a was also changed; amplitude of P3a diminished at frontal and central regions in space compared to ground baseline. This topography change could be attributed to the reduced activity of anterior cingulate cortex (ACC) which plays a role in the generation of P3a (Dien, Spencer, & Donchin, 2003).

Our results show that attentional functions related to processing of irrelevant stimuli are impaired in space. This impairment was observed not only in the early part of the flight, but also 1.5-2 month later which indicates that attentional functions of astronauts can not adapt to space circumstances even after many weeks in space. These attentional functions were sensitive to readaptation, as confirmed by the lack of significant difference between inflight and very early post-flight measurements and the significant contrast between very early post-flight and baseline measurements. Furthermore, there is no difference between the second early post-flight and baseline measurements which indicates that a few days on Earth after landing play a significant role in the readaptation. The difference between pre-flight and late post-flight measurements could be attributed to the fact that readaptation has not been fully completed yet.

There are several factors that could impair cognitive functions in space. (1) Cephaladfluid shift exists during the whole spaceflight and VIIP syndrome can also occur, which can impair cognitive functions confirmed by some bed rest studies and research of intracranial hypertension syndrome (Lipnicki & Gunga, 2009; Strangman et al., 2014). (2) Microgravity causes sensory-motor changes in space, but it has little chance to play a role in the deterioration of P3a. (3) Another factor is the modification of vestibular system in space. The most severe consequence of this alteration is the space motion sickness which usually lasts for 1-2 days at the beginning of spaceflight and after return from space (Williams et al., 2009). As the early flight measurements took place 6-12 days after launch, the chance of space motion sickness was minimal during this timeframe. It is more likely that this syndrome existed at the timeframe of very early post-flight measurements (2-3 days after return). Although, even if it would have existed, more studies show that the altered vestibular system does not necessarily lead to cognitive impairments (e.g. McIntyre et al., 2001). (4) The ambient CO₂ level is higher in ISS compared to Earth. Indirect evidence (e.g. CO₂ headache of astronauts) show that it can reach the level that may cause cognitive deterioration (Manzey & Lorenz, 1998; Strangman et al., 2014). (5) However adverse effects of radiation on cognitive functions are known from patients undergoing radiation treatments and from animal studies (Cucinotta et al., 2014), no direct evidence shows that radiation during spaceflight has negative influence on attentional functions of astronauts. (6) Sleep loss is an important stress factor in space. Barger et al. (2014) demonstrated that the average sleep amount of astronauts is 6.09 hours in the ISS which is less than that of 3 months before launch (i.e. 6.5 hours), and both values are below the recommended 8 hours (Evans-Flynn et al., 2016). Additionally, Barger et al. (2014) reported that astronauts slept less during the ISS mission than during the first 7 days after landing (6.95 hours). The summary of Alhola and Polo-Kantola (2007) shows that sleep loss has an adverse impact on attentional functions and additionally, more studies demonstrated that amplitude of P3a decreased after sleep deprivation (A. Gosselin et al., 2005; N. Gosselin et al., 2006). We have self assessment information about sleep quality and quantity of the night before the experiment and the current level of sleepiness and fatigue of astronauts (a total of 8 questions). We did not obtain any significant difference between in-flight and baseline measurements in any of these factors, but similarly to the results of Barger et al. (2014), data show that astronauts slept less during spaceflight (an average of 6.9 ± 0.42 hours) than in the ground (an average of 7.47 ± 0.99 hours in preflight, 7.8 ± 2.20 hours in early postflight and 7.4 ± 0.82 hours in late postflight). Furthermore, we have no information about the sleeping hours of the preceding days except for the night before the experiment and according to Van Dongen et al. (2003) insufficient sleep sums up. (7) The ISS is an isolated and confined environment, but there is no clear evidence that this impacts the cognitive functions adversely. (8) Astronauts experience to high workload which can lead to mental fatigue and impair attention. Indeed, more studies found performance decrement in space along with subjectively raised fatigue and/or workload (e.g. Eddy et al., 1998; Manzey et al., 1998; Manzey et al., 2000). Moreover, Massar et al. (2010) demonstrated that P3a is sensitive to mental fatigue. Although astronauts did not feel more tired during spaceflight than in the ground, however it is possible that the subjective feeling of mental fatigue does not coincide with the physiological state reflected by the ERP or behavioral data.

3.3.4.1 Strengths and limitations of the study

In the present study nine measurements were conducted, two of them in the ISS. Because of the design, we had an adequate number of reference points to investigate the impact of space mission, and to investigate the early (1. in-flight) and late (2. in-flight) effects in the ISS. Another strength of the design is the very early post-flight measurement which serves to estimate the impact of the readaptation process. On the other hand, we do not have follow-up measurements, as the last experiments took place 15-22 days after landing. So it cannot be clearly decided whether readaptation finished until the late post-flight measurements or not. Another limitation of the study is the small sample size.

It is common in the cognitive space research that post-flight measurements were conducted right after return to Earth (on the day of landing in several cases) (e.g. Benke, Koserenko, Watson, et al., 1993; Bock et al., 2001; Eddy et al., 1998; Kelly et al., 2005; Manzey et al., 1993; Ross et al., 1987). Among them, there are studies in which the impaired

performance in space remained at the same level after landing (Eddy et al., 1998) and also in which performance returned to pre-flight level (Manzey et al., 1993) after landing. It is also a result which shows that the impaired performance in space remained at the same level after landing but performance improved some days later, thus the first few days are essential concerning readaptation (Ross et al., 1987). In some research there are later post-flight data collection, too (Berger et al., 1997; Leone et al., 1995b; Manzey et al., 1998; Manzey et al., 2000; Matsakis et al., 1993; McIntyre et al., 2001; Pattyn et al., 2009; Semjen et al., 1998), although among them several studies merged the post-flight data, because of the huge interindividual differences concerning the timeframe and number of post-flight measurements (Berger et al., 1997; Leone et al., 1995b; Matsakis et al., 1993; McIntyre et al., 2001; Semjen et al., 1998). The latest post-flight measurements (compared to landing) were conducted by Manzey et al. (1998), Manzey et al. (2000) and Sangals et al. (1999). In these case studies, astronauts performed tasks 72-74 days (Manzey et al., 2000; Sangals et al., 1999) or 168 days (Manzey et al., 1998) after landing (so-called follow-up assessments) in addition to the earlier post-flight measurements. In the studies of Manzey et al. (1998) and Manzey et al. (2000), those tasks that demonstrated performance deterioration in some measurement points at the beginning of in-flight also showed impaired performance in some of the post-flight measurements, but the comparison of baseline and follow-up measurements revealed no performance decrement. Furthermore, Sangals et al. (1999) showed impaired performance in flight and in post-flight compared to the merged pre-flight and follow-up measurements. As only 3 astronauts participated in the studies with follow-up measurements and the results of post-flight data are not homogeneous, we can only conclude that it may occur that performance fluctuates in few week after landing.

Results of some studies (e.g. Manzey et al., 1998) demonstrated that performance could deteriorate a few days before launch, but not months earlier. Although we did not collect data few days before launch, the only disadvantage of the missing data is the lack of knowledge about how stress factors can influence attention in this period.

Taking together, we can conclude that attentional functions are impaired in space. Further research is needed to determine which factors play a crucial role in this deterioration. Nevertheless, we assume that it is the combined effect of several factors that caused the impairment of attentional functions. Sleep loss, mental fatigue caused by high workload, neurovestibular changes, elevated ambient CO₂ level, isolation, confinement, cephalad-fluid shift, the occurrence of VIIP syndrome and radiation could all play a role in the impaired performance during flight and right after returning to Earth.

4 General discussion

The main goal of two of the presented studies was to investigate effects of extreme environments on cognitive functions using the event-related potential technique. In each study, we focused on the impact of extreme environment or stimulus context, i.e. the complexity relationships between task-related and task-irrelevant stimuli on the mobilization of attentional processes reflected by the P3a ERP component. One of the advantages of using ERP technique is that it provides information about cognitive processes even when no behavioral data is available (e.g. task-irrelevant stimuli). Additionally, this method is more sensitive to slight changes of brain activity than behavioral indexes (Czigler et al., 1994). We targeted the P3a component due to its high sensitivity to stress factors, such as such as sleep deprivation (A. Gosselin et al., 2005), mental fatigue (Massar et al., 2010), and hypoxia (Balázs et al., 2001).

Although many studies investigated cognitive performance in space and Antarctica, results are controversial and have several limitations. Despite the advantages of using event-related potentials method in such extreme environments, only one study (in space; Cheron et al., 2014) investigated cognition using ERP prior to our experiments, but they only measured early (P1 and N1) visual evoked potentials. In the first study, we aimed to investigate the role of the complexity, variability and modality of the irrelevant stimuli compared to the complexity of standard and target events in mobilizing attentional functions, such as eliciting P3a and N2. The results confirmed our initial hypothesis that simple irrelevant stimuli within a sequence of complex task-relevant stimuli neither elicit P3a nor N2b.

Our second study aimed to investigate the effects of long-term Antarctic residence on cognitive functions. Contrary to our hypothesis, despite the presence of numerous stressors neither behavioral data nor ERP components including P3a have shown any sign of the adverse effect of this environment on cognitive functions, particularly on attention.

In the third study, we investigated the effects of long-duration space missions on attentional functions reflected by the P3a ERP component. As predicted by our initial hypothesis, attentional functions deteriorated in space. Additionally, the landing was followed by a short readaptation period with similar decrements in ERP.

4.1 Possible explanations of the contradicting results between space and Antarctica

Taking the results together of the three studies it can be said that elaborative processes (i.e. evaluation and categorization of irrelevant stimuli) reflected by the P3a component, are seems to be altered in space, but not in Antarctica. There are many possible factors that may cause this contradicting result. First, the stressors are not completely identical in the two environments. The isolation, confinement, alteration of the light-dark cycle, and sleep problems mainly caused by this extreme light condition are common stressors in both Antarctica and space. The different impact of the two extreme environments on cognitive functions may be -at least partly- attributed to microgravity-related factors. Concerning the ISS, microgravity results in cephalad-fluid shift, modification of neurovestibular and sensorymotor systems and it may cause VIIP syndrome. Other space-related factors are the elevated level of CO₂ and radiation. The high workload is also typical, especially in space and astronauts are frequently required to modify their sleeping schedule. Concerning Antarctica, due to the location of the research station (3233 m above sea level) the hypoxia is an additional stress factor in this environment. Second, the tasks used in these studies are different. We investigated P3a ERP component in both studies, however we used an auditory distraction paradigm in Antarctica, while modified visual novelty oddball tasks that require visuospatial perception in space. Third, in contrast to our space research, measurements before and after the mission were absent in the Antarctic study. Because of this missing data, we can only conclude that cognitive functions are not deteriorated during the Antarctic mission. Furthermore, it is not completely excluded that there were more positive aspects of the mission in Antarctica than in space, which counteracts the impact of stressors (Suedfeld, 2001, 2005). For example, in Antarctica the habitat is more comfortable, the number of crewmembers of the same nationality is larger, and there is less danger than in space.

4.2 The effect of irrelevant stimuli on attention

Irrelevant stimuli capture attention, but they can also cause an increase in arousal and mobilize further attentional processes (Schomaker & Meeter, 2015), which depends on several factors, such as attentional demands of the task and the context of task-irrelevant stimuli (Schomaker & Meeter, 2015). The P3a could be the indicator of these attentional processes. In our second study, the irrelevant feature of stimuli did not increase arousal and attention in the distraction paradigm, as in this task the irrelevant feature of the stimulus

impairs performance, but in the case of increased attention, a better performance would be expected. In our first study the attentional demands of tasks were low and irrelevant stimuli were more complex than standard ones, which could result in increased arousal and attention according to Schomaker and Meeter (2015). Thus, P3a in our first study could be an indicator of the increased attention, however this increased attention was most likely directed towards irrelevant stimuli and would not improve task performance as the time between irrelevants and targets was considerably longer than in Schomaker and Meeter (2014). Regarding our research in the ISS, since the relative complexity of task-irrelevant and task-relevant events were similar to the ones used in our first study and it was also not a difficult task (based on performance indicators), the irrelevant stimuli could increase arousal and attention in a similar way. It is possible that the tasks demanded more attention and thus the execution of tasks became more difficult in space and soon after return to Earth because of the environmental factors and other stressors (as evidenced by the decreased performance in space), which required more attentional resources to be allocated to the task (Kahneman, 1973). Consequently, less attention was available for irrelevant events which could result in a smaller increase of arousal and attention by irrelevant stimuli in space and soon after returning to Earth than in the baseline measurements. The impaired P3a amplitude in space and after landing can be the outcome of this process.

4.3 Conclusion

- 1. The results of the first study enriched the knowledge of attention switch by a new aspect. We demonstrated that the appearance of rare unexpected irrelevant stimuli during a task execution elicit attentional orientation and generate the brain electrical correlate of this response if these irrelevant events are at least as complex as the environment determined by task-relevant stimuli. The results also show that rare and unexpected complex events mobilize attentional processes even if these events are identical. Furthermore, our results show that interference with the task-set is not enough for mobilization of attention, it requires elaborative processes, like evaluation and categorization of the irrelevant stimuli. These results help to identify circumstances an unexpected event captures attention.
- 2. In the second study, results show typical effects both in behavioral and ERP data (e.g. reaction times for deviant events are slower than for standards). Performance of crewmembers improved and ERP components did not change significantly during the

campaign. Our results show that the overwintering crewmembers of Antarctica adapted to this environment, their cognitive functions did not change despite the presence of hypoxia and other stressors, such as isolation, confinement, altered light-dark cycle and sleep problems mainly caused by this extreme light condition. It is possible that some factors might have counteracted the negative influence of stressors. Since the amount of sleep per day is one of the most important factor of cognitive performance (Mollicone, Van Dongen, Rogers, & Dinges, 2008), the fact that crewmembers were allowed to take a nap may have affected their performance. The positive characteristics of the mission (e.g. beauty of nature) could also counteract the negative impacts of stressors (pl. Suedfeld, 2005). Moreover, numerous studies show that hypoxia do not necessarily produce cognitive impairment (pl. Gustafsson et al., 1997) and acclimatization to hypoxia is also possible during long-term sojourn on various physiological levels (Zubieta-Calleja, Paulev, Zubieta-Calleja, & Zubieta-Castillo, 2007).

3. The results of the third study, show that cognitive functions deteriorate during spaceflight. Recognizing these cognitive impairments and avoiding the resulting errors can be an important step in planning further successful spaceflights. The results also show that cognitive functions do not adapt to the extreme conditions during spaceflight and the readaptation is not immediate after return to Earth. We assume that the combined effect of several factors caused the impairment of attentional functions. According to the literature, sleep loss and mental fatigue caused by high workload may change that attentional indicator (P3a amplitude), which we also examined (A. Gosselin et al., 2005; Massar et al., 2010). The role of neurovestibular changes can not be completely excluded, especially during early readaptation and the higher ambient CO2 level in the ISS can also lead to cognitive impairment, although this has not been proved concerning attentional functions. Although the literature does not support that isolation, confinement and cephalad-fluid shift would negatively affect attentional functions, the role of these factors can also not be excluded as these studies investigated behavioral data only except for one or two cases. Two other factors, the ionizing radiation and the occurrence of VIIP syndrome in some astronauts could also affect attentional functions adversely.

4.4 Further investigations

As several factors can influence cognitive performance in these environments, further research is needed to determine which specific factors play crucial role in the deterioration of

cognitive functions. Therefore, future research shall investigate the effects of sleep loss, cephalad fluid shift and mental fatigue separately

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7 Publications

7.1 Articles related to the thesis

Barkaszi, I., Czigler, I., Balazs, L. (2013). Stimulus complexity effects on the event-related potentials to task-irrelevant stimuli. *Biological Psychology*, 94(1), 82-89. doi:10.1016/j.biopsycho.2013.05.007

Balázs, L., **Barkaszi, I.**, Czigler, I., Takács, E. (2015). Agyműködés súlytalanságban: Kísérlet a Nemzetközi Űrállomáson. *Magyar Tudomány 9*, 1045-1051.

Barkaszi, I., Takacs, E., Czigler, I., Balazs, L. (2016). Extreme Environment Effects on Cognitive Functions: A Longitudinal Study in High Altitude in Antarctica. *Frontiers in Human Neuroscience*, 10, 331. doi:10.3389/fnhum.2016.00331

7.2 Oral and poster presentations related to the thesis

Barkaszi, I., Czigler, I., Balazs, L. (2011). *The role of complexity of the infrequently presented irrelevant stimuli in orientation*. Poster session presented at the 13th Conference of the Hungarian Neuroscience Society (MITT), Budapest, Hungary

Barkaszi, I., Czigler, I., Balazs, L. (2011). *Influence of stimulus complexity and variability to the ERP response evoked by task irrelevant stimuli*. Poster session presented at the 51th Annual Meeting of Society for Psychophysiological Research Conference, Boston, United States

Barkaszi, I., Czigler, I., Balazs, L. (2011). *Az irreleváns, ritka ingerek komplexitásának szerepe az orientáció kiváltásában*. Oral presentation at Magyar Pszichológiai Társaság Jubileumi XX. Országos Tudományos Nagygyűlése, Budapest, Hungary

Barkaszi, I., Czigler, I., Balazs, L. (2011). *Stimulus complexity effects on the orienting response*. Poster session presented at XI International Conference on Cognitive Neuroscience (ICON XI), Palma, Mallorca, Spain

Barkaszi, I., Takacs, E., Czigler, I., Balazs, L. (2013). *The impact of Antarctic overwintering on cognitive processes*. Poster session presented at the 53th Annual Meeting of Society for Psychophysiological Research Conference, Florence, Italy

- **Barkaszi, I.**, Takacs, E., Czigler, I., Balazs, L. (2013). *Cognitive performance during Antarctic overwintering*. Poster session presented at 18th Meeting of the European Society for Cognitive Psychology (ESCOP), Budapest, Hungary
- **Barkaszi, I.**, Takacs, E., Czigler, I., Balazs, L. (2013). *Brain electrical activity and performance in a distraction task during Antarctic overwintering*. Poster session presented at the 19th IAA Humans in Space Conference, Cologne, Germany
- Takacs, E., **Barkaszi, I.**, Czigler, I., Balazs, L. (2013). Event related potentials and the Attention Network Test in Antartica a longitudinal study. Poster session presented at the 19th IAA Humans in Space Conference, Cologne, Germany
- Balázs, L., **Barkaszi, I.**, Czigler, I., Takács, E. (2014). *Spaceflight conditions influence event related brain electrical activity*. Oral presentation at the 6th International Congress of Medicine in Space and Extreme Environments (ICMS), Berlin, Germany
- Takács, E., **Barkaszi, I.**, Czigler, I., Balázs, L. (2014). *Processing of basic spatial orientation cues in microgravity*. Oral presentation at 6th International Congress of Medicine in Space and Extreme Environments (ICMS), Berlin, Germany
- Balázs, L., **Barkaszi, I.**, Cheron, G., Czigler, I., McIntyre, J.M., Takács, E. (2015). Spaceflight yields diminished perception of directions and increased reliance on external visual framework. Oral presentation at IAA-HIS-15 Conference, Prague, Czech Republic
- Takács, E., **Barkaszi, I.**, Czigler, I., Balázs, L. (2015). *Attention related brain responses reveal reduced activity in microgravity*. Oral presentation at IAA-HIS-15 Conference, Prague, Czech Republic

7.3 Articles non-related to the thesis

- Kondé, Z., **Barkaszi, I.**, Czigler, I. (2009). Gátlási mechanizmusok és válaszszelekciós interferencia a feladatváltásban. *Pszichológia*. 29(2), 119-143.
- Takács, E., Sulykos, I., Czigler, I., **Barkaszi, I.**, Balázs, L. (2013). Oblique effect in visual mismatch negativity. *Frontiers in Human Neuroscience*, 7, 591. doi:10.3389/fnhum.2013.00591

7.4 Oral and poster presentations non-related to the thesis

Barkaszi, I., Czigler, I., Pató, L.G., Balazs, L. (2010). *A mentális fárasztás módszere, a mentális fáradás elektrofiziológiai és viselkedéses hatásai*. Oral presentation at Magyar Pszichológiai Társaság XIX. Országos Tudományos Nagygyűlése, Pécs, Hungary

Barkaszi, I., Czigler, I., Pató, L.G., Balazs, L. (2010). *Target P3 decrement as a result of mental fatigue*. Poster session presented at the 15th World Congress of Psychophysiology of the International Organization of Psychophysiology (IOP.), Budapest, Hungary

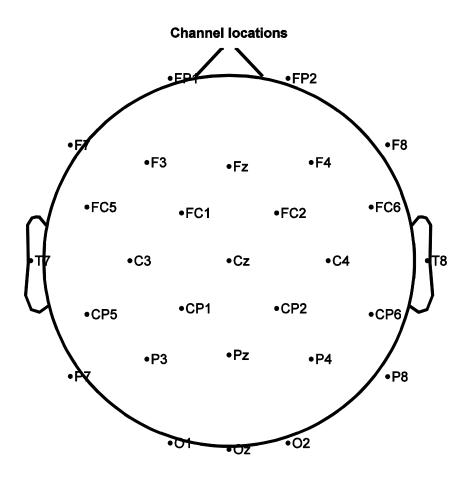
Balázs, L., **Barkaszi, I.**, Czigler, I., Sulykos, I., Takács, E. (2012). *Event related potential manifestations of the oblique effect*. Oral presentation at 6th World Congress of Psychophysiology of the International Organization of Psychophysiology (IOP) Pisa, Italy

Takacs, E., Sulykos, I., Czigler, I., **Barkaszi, I.**, & Balazs, L. (2013). *Oblique effect in visual mismatch negativity: change detection is more efficient when deviating from cardinally oriented stimuli*. Poster session presented at the 53th Annual Meeting of Society for Psychophysiological Research Conference, Florence, Italy

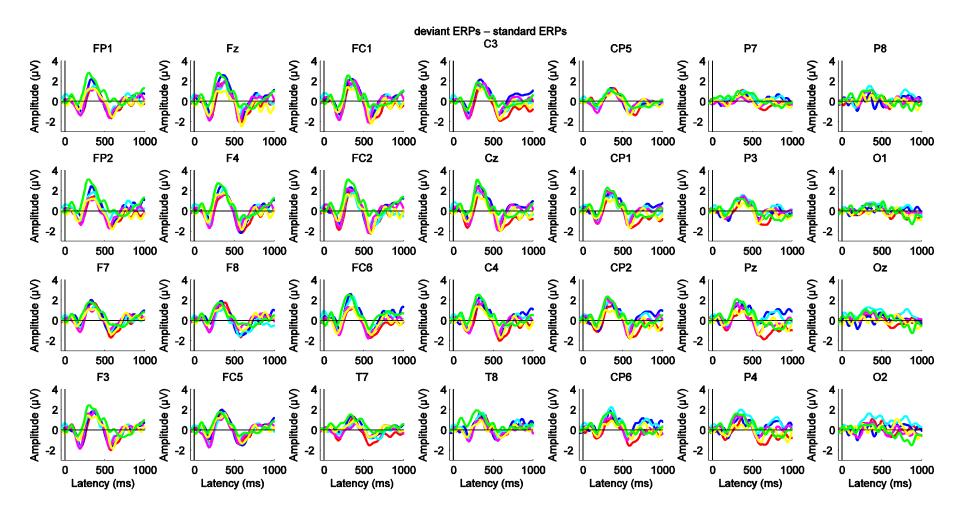
Takacs, E., Sulykos, I., Czigler, I., **Barkaszi, I.**, & Balazs, L. (2013). *Visual sensory memory demonstrates orientation anisotrophy*. Poster session presented at 18th Meeting of the European Society for Cognitive Psychology (ESCOP), Budapest, Hungary

8 Supplementary materials

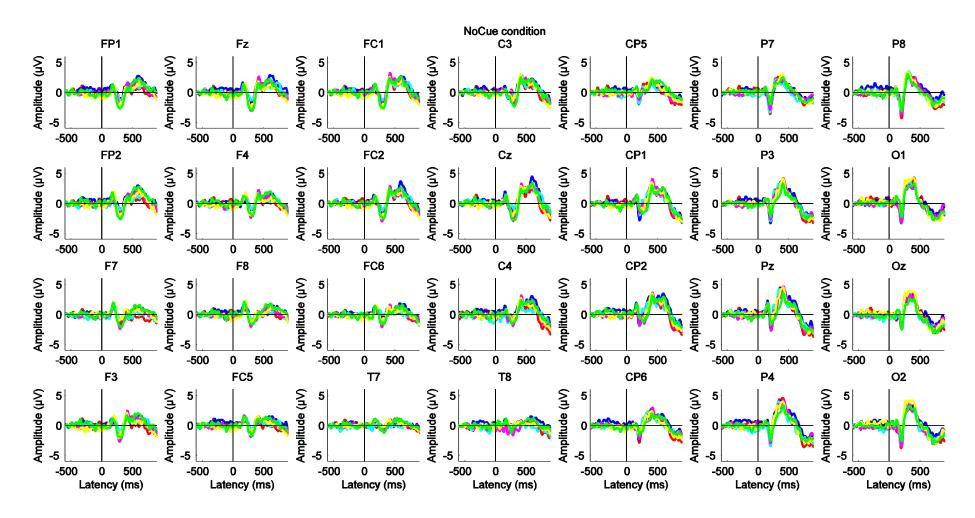
Supplementary Image 1. Electrode locations.



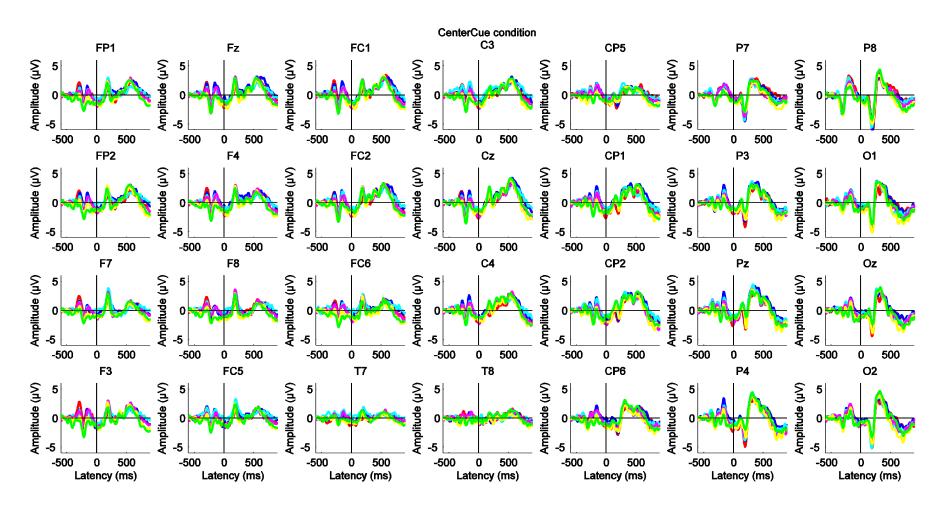
Supplementary Image 2. Grand-mean difference waves (deviant ERPs – standard ERPs) for all electrodes for the six cycles (filtered with a 10-Hz low-pass) in the distraction task (1.cycle-red, 2.cycle-blue, 3.cycle-cyan, 4.cycle-purple, 5.cycle-yellow, 6.cycle-green).



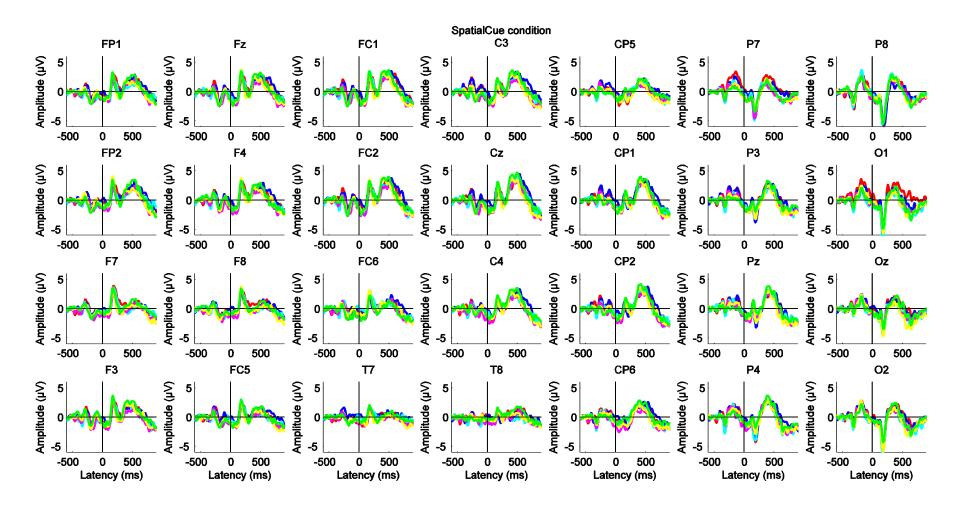
Supplementary Image 3. Grand-mean event-related potential plots for No Cue condition for all electrodes in the ANT task. (1.cycle-red, 2.cycle-blue, 3.cycle-cyan, 4.cycle-purple, 5.cycle-yellow, 6.cycle-green).



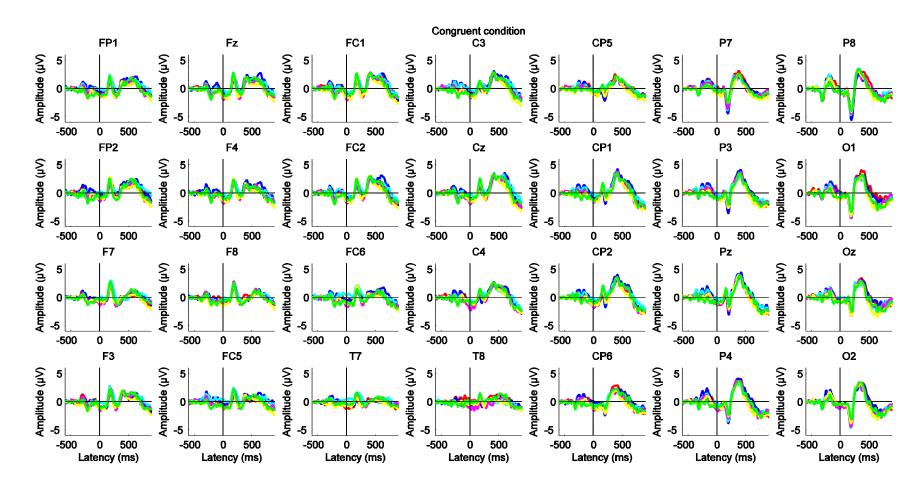
Supplementary Image 4. Grand-mean event-related potential plots for Center Cue condition for all electrodes in the ANT task. (1.cycle-red, 2.cycle-blue, 3.cycle-cyan, 4.cycle-purple, 5.cycle-yellow, 6.cycle-green).



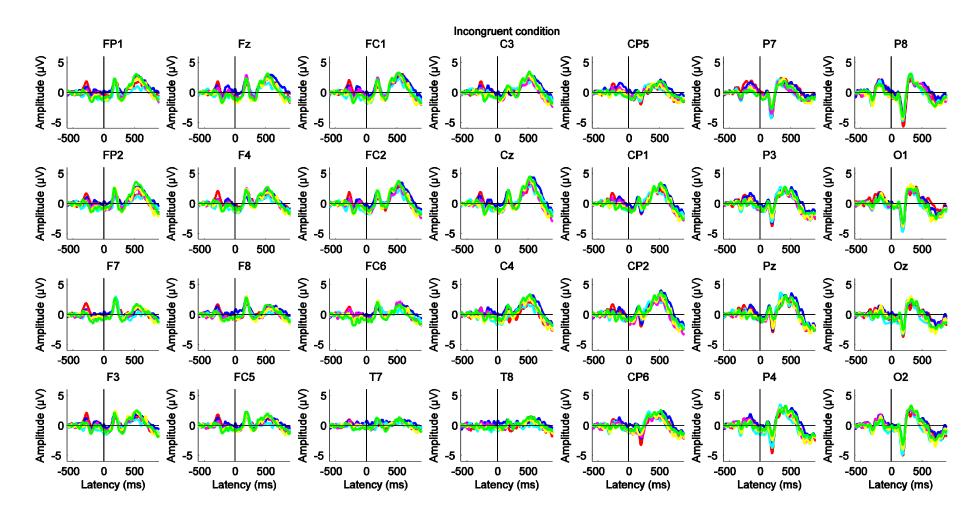
Supplementary Image 5. Grand-mean event-related potential plots for Spatial Cue condition for all electrodes in the ANT task. (1.cycle-red, 2.cycle-blue, 3.cycle-cyan, 4.cycle-purple, 5.cycle-yellow, 6.cycle-green).



Supplementary Image 6. Grand-mean event-related potential plots for Congruent condition for all electrodes in the ANT task. (1.cycle-red, 2.cycle-blue, 3.cycle-cyan, 4.cycle-purple, 5.cycle-yellow, 6.cycle-green).



Supplementary Image 7. Grand-mean event-related potential plots for Incongruent condition for all electrodes in the ANT task. (1.cycle-red, 2.cycle-blue, 3.cycle-cyan, 4.cycle-purple, 5.cycle-yellow, 6.cycle-green).



Supplementary Table 1.

Measurements intervals

cycle1	cycle2	cycle3	cycle4	cycle5	cycle6	
from mid-February	from late-March to	from mid-May to	from mid-June to	from early-August to	from mid-September	
to late-March	early-May	mid-June	late-July	mid-September	to mid-October	

Supplementary Table 2. Mean reaction time (ms) and standard error for No Cue Incongruent, No Cue Congruent, Center Cue Incongruent, Center Cue Congruent, Spatial Cue Incongruent and Spatial Cue Congruent stimuli and mean difference scores and standard errors for each of the three attention networks in each cycle.

	cycle 1	cycle 2	cycle 3	cycle 4	cycle 5	cycle 6
No Cue Incongruent Reaction time (ms)	561,59	545,09	528,36	505,09	516,32	526,18
standard error of mean	16,99	10,73	12,25	11,36	11,56	11,19
No Cue Congruent Reaction time (ms)	474,41	479,45	462,09	460,14	446,55	457,86
standard error of mean	13,15	13,37	8,86	13,21	13,37	12,70
Center Cue Incongruent Reaction time (ms)	547,23	539,27	517,05	498,82	492,09	500,14
standard error of mean	17,37	14,33	11,94	13,56	10,82	10,15
Center Cue Congruent Reaction time (ms)	462,23	443,64	425,00	417,05	406,64	428,73
standard error of mean	14,76	13,43	10,92	10,50	10,35	9,73
Spatial Cue Incongruent Reaction time (ms)	477,32	466,32	427,73	422,27	417,00	430,18
standard error of mean	18,33	15,96	9,42	14,17	9,42	12,56
Spatial Cue Congruent Reaction time (ms)	410,05	390,55	380,59	363,00	360,27	368,50
standard error of mean	16,46	14,11	12,49	11,92	10,48	10,04
Alerting Difference Score (ms)	13,82	15,05	23,91	19,36	39,05	33,00
standard error of mean	6,44	5,09	4,39	4,40	5,73	5,10
Orienting Difference Score (ms)	63,36	68,82	66,23	65,18	61,73	63,36
standard error of mean	6,72	7,14	5,12	4,95	7,36	5,49
Inhibition Difference Score (ms)	81,36	84,86	73,73	65,68	76,59	69,00
standard error of mean	6,99	5,10	2,97	2,76	4,55	5,67