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DOES SELECTIVE ATTENTION HAVE AN IMPACT ON THE PERCEPTION OF AMBIGUOUS FIGURES?

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AR SELEKTYVUS DĖMESYS TURI ĮTAKOS DVIPRASMIŲ VAIZDŲ SUVOKIMUI?

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CONTENTS

ABBREVIATIONS

C3/C4 – central electrodes

EEG – electroencephalography

EOG – electro-oculography

ERP – event-related potential

F3/F4 – frontal electrodes

FRP – frontal reversal positivity

fMRI – functional magnetic resonance imaging

ISI – inter-stimulus-interval

LP/LPC – Late Positivity or Late Positive Component

MEG – magnetoencephalography

N2pc – N2 posterior contralateral component

P3/P4 – parietal electrodes

O1/O2 – occipital electrodes

RN – Reversal Negativity

RP – Reversal Positivity

SD – standard deviation

SN – Selection Negativity

T5/T6 – temporal electrodes

VAN – Visual Awareness Negativity

1. INTRODUCTION

Vision is undoubtedly the most dominant of human senses and is by no means essential in order to successfully behave in the everyday world. But does our visual system really provide pure and unaltered interpretation of the external environment? Most of the psychophysicists would say that it doesn't. There are multiple examples showing how our vision, or other senses (and consecutively our brain) may be tricked simply by providing insufficient amount of information required in order to make the correct decision.

One of the many available examples on such matters is an intriguing phenomenon of ambiguous figures. Ambiguous figure is an image typically containing two mutually exclusive percepts that are constantly interchanging each other. Explanations of their reversibility patterns could clarify the issue of perspective formation in the brain. They are important in research of developing (Mitroff et al., 2006) and aged brain (Heath and Orbach, 1963). Perception of ambiguous figures varies with age, as children under five years old (Rock et al., 1994; Gopnik and Rosati, 2001, Holt and Matson, 1976) and the majority of older (i.e., 65-90 years old) people (Heath and Orbach, 1963; Holt and Matson, 1976), especially those suffering from dementia (Heath and Orbach, 1963) or Alzheimer's disease (Shimada et al., 2006), have considerable difficulties in perceiving ambiguous figure reversals. Perception of ambiguous figures can be impaired by some neurological diseases, such as, schizophrenia (Hunt and Guilford, 1933), or brain injuries, for example, frontal lobe damage (Ricci and Blundo, 1990; Meenan and Miller, 1994; Windmann et al. 2006), or hemispatial neglect (Bisiach et al., 1999). However, the perceived reversal rate of the Necker cube, reported by people suffering from depression is found to be almost equal to that of controls (Weckowicz et al., 1978).

Ambiguous figures is an invaluable research tool in electroencephalographic research (or other brain imaging methods, e.g., fMRI, MEG etc.), since they help to separate perceptual mechanisms from stimulus engaged mechanisms. When a person is viewing such image, his/her brain constantly tries to choose "the correct alternative" from at least two available interpretations. It is possible to perceive only one interpretation at a given time and the interpretations constantly alternate. Therefore, the participant is experiencing a change, although physical properties of the stimulus remain the same.

Recently, a new paradigm of electroencephalographic research has been introduced (Kornmeier and Bach, 2004) to investigate the perception of ambiguous figures. The main finding of almost all current experiments includes Reversal Negativity – a negative deflection of event-related potentials related to perceptual reversals, and elicited around 200-300 ms after the onset of the stimulus. Reversal Negativity has been found to reflect ambiguous figure reversals and also it is susceptible to task requirements (e.g., voluntary modulation of the perceived reversal rates) (Pitts et al., 2008). However, it is still not clear whether Reversal Negativity is mainly determined by mechanisms of visual selective attention, or those of visual awareness. In this thesis, the methods selected from studies of visual selective attention were applied in the electroencephalographic research of ambiguous figure perception, in order to find out whether Reversal Negativity is susceptible to the attentional manipulations of the given tasks.

1.1. Aim and objectives

Clarification of the cognitive interpretation of Reversal Negativity: whether it depends on mechanisms of attention, awareness of a change, or is it a response specific to ambiguous figure reversal.

Objectives:

a) Clarification whether Reversal Negativity is functionally related to N2 posterior contralateral component;
b) Clarification wthether Reversal Negativity is a subtype of Visual Awareness Negativity;

c) Clarification of impact of high or low perceptual load tasks on the reversals of the ambiguous stimuli.

1.2. Actuality and scientific novelty

Several methodical innovations for electroencephalographic research were used for the first time:

a) two ambiguous figures presented simultaneously;
b) performance of tasks unrelated to perceptual reversals while performing the reversal task;
c) introduction of extremely short presentation (200-400 ms) and inter-stimulus (200 ms) intervals;
d) introduction of unambiguous – ambiguous lattice presentation mode in a single experimental trial.

Selective attention related tasks were used for the first time to explore ambiguous figure perception in order to test whether Reversal Negativity, elicited by the perceptual reversals of the ambiguous figures, is a response related to selective attention.

1.3. Available practical applications

Several methodical innovations for electroencephalographic research of ambiguous stimuli were created and tested. Currently, other researchers working in the same area may apply them in their studies.

1.4. Defended statements

- Reversal Negativity is the non-attentional event-related potentials correlate of the perceptual changes in the presented ambiguous object:

a) it is not reflected by event-related potential component N2 posterior contralateral;
b) it is completely suppressed when subjects are simultaneously performing the task of ambiguous figure perception and the task of either high or low perceptual load.

- It is highly likely that Reversal Positivity is an attentional event-related potentials correlate of the perceptual changes in the presented ambiguous object, but it does not necessarily depend on selective attention.
- Late Positivity is not directly related to the perceptual changes of the presented ambiguous object.

2. LITERATURE REVIEW

2.1. Principal theories explaining the perception of ambiguous figures

Ambiguous figures are images that strikingly change their appearance during extended viewing and can be seen in two (or more) perspectives. The proposed explanations for bistability of these figures tend to fall into two general classes, suggesting that their analysis is mostly governed by either bottom-up, or top-down perceptual processes. Neural satiation theory (based on bottom-up processes) suggests that figures reverse because the cortical organization corresponding to one representation satiates (or adapts) and then perception shifts to another possible interpretation (e.g., Cohen, 1959). Cognitive theory (top-down processes) emphasizes perceptual ability to interpret visual information and suggests that reversals are caused by feedback relationships of central mechanisms with the lower level sensory mechanisms (e.g., Girgus et al., 1977).

There is a quite considerable amount of data available both for support or rejection of the above mentioned theories. For example, a participant is able to decrease or increase the reversal rate of viewed ambiguous figure by means of intentional control (Toppino, 2003; Pelton and Solley, 1968), or the perceived reversal rate is influenced by a secondary task, for example, performance of mental arithmetic exercises while viewing ambiguous stimulus significantly decreases perceived reversal rate of the presented ambiguous figure (Reisberg and O'Shaughnessy, 1984; Wallace and Priebe, 1985). These effects clearly show the operation of higher order activities. But the perceived reversal rate also can be influenced by size, brightness or the intermittent presentation sequence of the stimulus (Orbach et al., 1963; Babich and Standing, 1981; Leopold et al., 2002; Maier et al., 2003), and that indicates the operation of lower level sensory activities. Due to these facts, several alternative theories have been proposed as possible explanations of the interpretation of ambiguous stimulus in the brain: perceptual alterations might occur due to common activation of bottom-up and top-down perceptual processes during ambiguous figure perception (Long and Toppino, 2004), also percepts might interchange due to continuous shifts in visual attention (Leopold and Logothetis, 1999), or because of interhemispheric switching (Miller et al., 2000). An elaborate review on the phenomenon and theoretical explanations can be found in Long and Toppino (2004).

In this thesis, perception of ambiguous figures was investigated by applying two different kinds of methods, namely, by recording psychophysical and psychophysiological data. In two (out of three) studies multiple-figure presentation technique (Flügel, 1913; Babich and Standing, 1981; Long and Toppino, 1981; Long, Toppino and Kostenbauder, 1983; Toppino and Long, 1987) was applied, that is, participants had to view two ambiguous stimuli presented simultaneously either during short term presentation intervals, or during extended viewing periods. In the third study, the participants had to reverse the presented ambiguous figure and simultaneously perform a secondary task unrelated to ambiguous figure perception.

2.2. Perceptual bias in the multiple-figure presentation

Multiple-figure presentation is one of the methods applied in order to study perception of ambiguous figures, with an aim to clarify the issue what kind of strategy participants will use while selecting the available interpretations from the presented stimuli, when there are more than one perceptual alternative available at a given time. For this reason, at least two ambiguous figures are used in that sort of experiments (Adams and Haire, 1958; Babich and Standing, 1981; Flügel, 1913; Long and Toppino, 1981; Long et al., 1983; Toppino and Long, 1987).

In the pilot study of this doctoral dissertation multiple-figure presentation paradigm was combined with extended viewing of ambiguous stimuli. Corrozi et al. (1993) found that viewing of two simultaneously presented Necker cubes for an extended period (i.e., 180 sec) lead to fatigue-like effects, as the independence of perceived reversals of the stimuli increased when the viewing time was extended. It is also known, that the proportion of 'different' percepts perceived in both figures is susceptible to high inter-individual differences, as the mean values of independent percepts can range from 13% to 51% depending on the individual variations (von Grünau et al., 1984; Flügel, 1913).

While viewing a single ambiguous figure, it is possible to choose the interpretation only from two available percepts; therefore, the changes are perceived only in a mutually exclusive manner. But what if there are more than two available percepts for a subject to select from? That kind of a design might answer the question about the pattern of the changes of reversible figures. Is there any kind of a pattern, or maybe the interpretations will simply interchange each other in a random fashion? Burton's (2002) experiments with the four-state ambiguous figure revealed that observers were capable to perceive and report their percepts while viewing the ambiguous figure which had more than two available interpretations. However, no studies so far were conducted when the simultaneously presented ambiguous stimuli are not identical. How an observer will perceive reversals of ambiguous figures when one of them is slightly biased towards one (or another) of possible alternatives?

Only studies with sequentially presented biased and ambiguous stimuli are available in the literature (von Grünau et al. 1984; Long et al. 1992; Long and Olszweski 1999; Long and Moran 2007). In these studies participant first views the unambiguous figure (adapting stimulus) which corresponds to one of the interpretations of successively presented ambiguous figure. After extended inspection of adapting stimulus (i.e., from 60 to 150 sec), subjects typically report the version of the presented ambiguous figure which is incompatible to the adapting stimulus (von Grünau et al. 1984, Long et al. 1992, Long and Olszweski 1999; Long and Moran 2007). If the inspection period is brief (i.e., 1–5 sec) participants usually perceive ambiguous figure in the same interpretation as previously presented adapting stimulus (Long et al. 1992; Long and Olszweski 1999).

Hence, it was hypothesized that observers can use at least two different strategies while viewing ambiguous and biased stimuli simultaneously: introduction of a bias to one of the presented figures should either significantly increase the possible randomness of perceptual changes (i.e., participants will more often perceive ambiguous figures in different interpretations), or alternatively, the changes will start to follow some sort of a unifying pattern (i.e., participants will start to perceive both figures significantly more often according to the biased interpretation).

2.3. Electroencephalographic studies on perception of ambiguous figures

Event-related potentials (ERPs) are the electrophysiological measurements calculated from the electroencephalographic recording by the means of averaging technique. Electroencephalography (EEG) provides an online measure of brain activity during cognitive, perceptual, sensory and motor tasks and it can be comfortably recorded from human subjects. EEG is constantly measured during the experiment and there are several ways to select the appropriate time window from each trial for averaging (Luck, 2005). The reference point for it may either be the onset of the stimulus, or the response provided by the subject (Picton et al., 2000). After the averaging of ERPs, it becomes possible to analyse which parts of the stimulus processing sequence are influenced by particular experimental manipulation (Luck, 2005). Therefore, ERPs may provide information on the neurocognitive mechanisms and the temporal characteristics associated with the perceptual reversals of ambiguous stimuli.

The first ERP study with bistable stimuli was conducted by O'Donnell et al. (1988). They used an intermittent presentation sequence for the presentation of the Necker cube, and reported P3-like effects in their study. They implemented the behavioural design created by Orbach et al. (1963), who developed and refined (Orbach et al., 1966) an intermittent Necker cube presentation design, which led to an immediate reversal of the figure at stimulus onset. This design largely depends on the presentation durations of the stimulus and inter-stimulus intervals, that is the shorter the inter-stimulus interval (i.e., usually from 200 to 400 ms), the more reversals participants will report (Orbach et al., 1966). The study was successfully replicated by Leopold et al. (2002). They showed that extremely long inter-stimulus intervals have a deteriorating effect on the ambiguity of the Necker cube. Maier et al. (2003) further examined this phenomenon in order to understand its underlying mechanisms and claimed that such disambiguation of the stimuli is related to the effects of perceptual memory.

Electrophysiological studies on the perception of ambiguous figures conducted between 1990 and 2004 (Basar-Eroglu et al., 1993; Isoglu-Alkac et al., 1998; Klemm et al., 2000; Strüber et al., 2001) did not use the intermittent presentation sequence for the demonstration of the stimuli, instead they employed the method of backward-averaging, that is, the subject's response was used as the temporal reference point of a perceptual reversal. They have also obtained Late Positivity (LP) as the correlate of perceptual reversals, in comparison to non-reversals. It was observed in P3 time window (positive potential difference occurring approximately from 300 to 700 ms post-stimulus) over the central-posterior (Basar-Eroglu et al., 1993) and frontal (Strüber et al., 2001) areas of the head. According to the recent literature (Kornmeier and Bach, 2004; Pitts et al., 2007), these studies have several disadvantages from the methodological point of view, that is, due to this kind of averaging process smaller ERP effects might be obscured, as the observer's reaction (indicated by the button press) vary from trial to trial, and ERPs might be also diminished by the motor activity related to the button press.

Recent ERP studies are employing intermittent presentation sequence for the presentation of the Necker lattices (composed of several Necker cubes) as such procedure optimally induces perceptual reversals at stimulus onset. Due to this paradigm, the onset of stimulus can be used as a reference point for averaging and much sharper and more clearly defined ERP components have been found (Kornmeier and Bach, 2004, 2005, 2009; Kornmeier et al., 2007;

Pitts et al., 2007; Pitts et al., 2008; Britz et al., 2009; Qiu et al., 2009) in comparison to data of older backward-averaging studies.

There are three main findings observed in the current EEG experiments exploring the perception of ambiguous stimuli (Fig. 2.1):

(a) Reversal Positivity (RP),

(b) Reversal Negativity (RN),

(c) Late Positivity (LP), or (Late Positive Component).

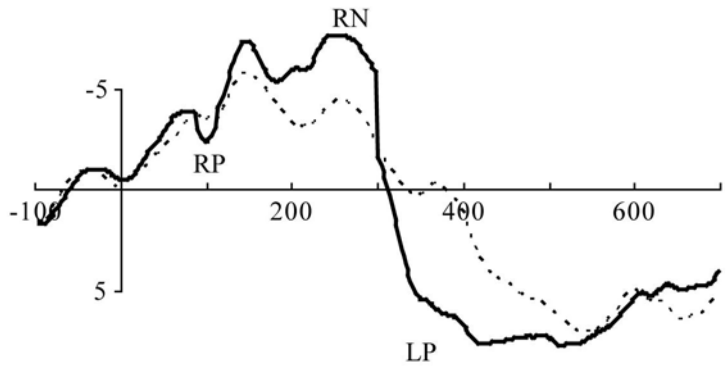


Figure 2.1 ERP components typically elicited in response to ambiguous figure reversals: Reversal Positivity (RP), Reversal Negativity (RN) and Late Positivity (LP). Black line signifies event-related potentials in response to perceived changes, dashed line – in response to no-changes.

Most of the current studies found that perceptual reversals elicit an enhanced positivity (RP) around the P1 component in occipital electrodes (Kornmeier and Bach, 2005; Kornmeier and Bach, 2006; Kornmeier et al., 2007; Pitts et al., 2007; Schoth et al., 2007; Britz et al., 2009; Qiu et al., 2009). Kornmeier and Bach (2006) hypothesize that RP reflects the early instability of the perceptual system, as it is obtained only with Necker lattices, but not with unambiguous lattices. However, Pitts et al., (2007) propose that RP signifies initial changes in the spatial selective attention.

The majority of the contemporary studies of visual bistability, except Kornmeier and Bach (2009), have also revealed an enhanced negative difference between reversals and non-reversals around 250 ms after stimulus presentation, peaking at occipital and parietal electrode locations (Kornmeier and Bach, 2004, 2005, Kornmeier et al., 2007; Pitts et al., 2007; Pitts et al., 2008; Schoth et al., 2007; Qiu et al., 2009; Britz et al., 2009). This component was termed Reversal Negativity (RN), and it possible that RN reflects either the top-down attentional selection processes related to perceptual reversal (Pitts et al., 2007; Pitts et al., 2008), or it is an “early” ERP correlate of the perceptual reversal (Kornmeier and Bach, 2004; Kornmeier and Bach, 2005).

However, neither the Reversal Positivity, nor Reversal Negativity was obtained in the first intermittent Necker cube presentation ERP study conducted by O’Donnell et al. (1988). Kornmeier and Bach (2004) argue that the inter-stimulus intervals chosen by O’Donnell et al. (1988) were too long (i.e., 3300 ms) and, therefore, they did not obtain ERP components occurring earlier than P3 time window. Kornmeier and Bach (2004) suggested that the percept obtained with such long inter-stimulus intervals presumably diverges from the typical Necker reversal. Interestingly, O’Donnell et al. (1988) found a small deflection in their grand averages around N2 time window, but since it was not identified reliably in the averaged waveforms obtained from each subject, they decided not to include those results in their analyses.

Almost all recent ambiguous figure-related ERP experiments (Kornmeier and Bach, 2004, 2005; Kornmeier et al. 2007; Pitts et al., 2007; Pitts et al., 2008), except Kornmeier and Bach (2009), found the enhanced positivity, that is, late positive component (LPC) in the time range of P3, around 470 ms after presentation of ambiguous stimulus. In some of the studies, two distinct LPC components were observed: one around 340-410 ms post-stimulus at frontopolar locations and another one around 410-470 ms at parietal locations (Kornmeier and Bach, 2005; Kornmeier and Bach, 2006; Kornmeier et al., 2007). Kornmeier and Bach (2006) conclude that this component reflects the subsequent cognitive analysis of reversals, but not the perceptual reversal as such.

2.4. Perception of ambiguous figures in relation to selective attention

There are several theoretical explorations on the impact of selective attention in ambiguous figure perception (Leopold and Logothetis, 1999; Pitts et al., 2008). So far there are no studies exploring what role this type of attention has on the perception of ambiguous stimuli.

2.4.1. Implementation of multiple-figure presentation in the EEG study: N2 posterior contralateral

Despite the extensive investigation already conducted with the electroencephalography in order to find out the main mechanism(s) responsible for perception of ambiguous stimuli, the cognitive interpretation of RN still remains unresolved, and various researchers suggest different underlying mechanisms for the generation of the RN response. According to previous electrophysiological studies on visual attention and visual awareness, several negative ERP components, detectable over the posterior areas of the cortex and appearing about 150-300 ms after stimulus onset, might be related to RN:

(a) Selection negativity (SN) (Hillyard and Anllo-Vento, 1998) – negative amplitude difference in ERPs, between attended and unattended stimuli, visible around 200-300 ms after the stimulus onset at posterior electrode sites;

(b) Visual awareness negativity (VAN) (Koivisto and Revonsuo, 2003) – an electrophysiological correlate of visual awareness occurring in the posterior areas of the head approximately 120-260 ms after the stimulus;

(c) N2pc component (i.e., N2 posterior contralateral) (Eimer, 1996) – contralateral negativity in the relation to the position of the unilateral change in the bilateral stimulus display, visible over posterior electrodes and indicating the deployment of attention.

As RN (Kornmeier and Bach, 2004) is visible at the same latencies with SN (Hillyard and Anllo-Vento, 1998) RN may reflect changes in selective attention that may be fundamental for the generation of perceptual reversals (Pitts et al., 2007). In accordance with this view, Pitts et al. (2008) demonstrated that RN was modified by top-down intentional control, when observers were asked to (a) speed up perceptual reversals; (b) slow down perceptual reversals; or (c) maintain a neutral approach. Their data showed that RN was lateralized to the right posterior scalp locations, and amplitude of RN was enhanced in the condition where participants were asked to speed up perceptual reversals, in comparison to the condition where they were asked to slow down the perceived reversal rates. The data provided support for the hypothesis that RN is modulated by attention. Since latencies and scalp distributions of RN and SN are quite similar, Pitts et al. (2008) suggest that common mechanisms might generate those responses. They have also obtained a possible inverted polarity frontal equivalent of RN, and termed it frontal reversal positivity (FRP). Authors suggested that if RN is equivalent to SN, FRP might be an equivalent of selection positivity, which was also found in the previous studies employing the methods of attended versus unattended targets (Anllo-Vento and Hillyard, 1996). Interestingly, LPC was restricted to central locations and also was delayed in the condition when participants were asked to slow down perceptual reversals in comparison to other two conditions. In addition, Slotnick and Yantis (2005) conducted a functional magnetic resonance imaging (fMRI) study in order to compare voluntary shifts of attention (left vs. right) between voluntary shifts of reversals of the Necker cube. The obtained data showed increased activities in the parietal areas contralateral to the attended spatial location for both attentional and perceptual shifts in the perceived orientation of the cube.

While viewing bistable stimulus, the perceptual reversal is clearly represented in subjective visual awareness. Therefore, RN might be an electrophysiological correlate of the subjective perceptual experience. Visual awareness negativity (VAN), an electrophysiological correlate of visual awareness, was found in studies using various manipulations of perception (e.g., Koivisto et al., 2008; Koivisto and Revonsuo, 2003, 2008; Koivisto et al., 2006). This negativity has been shown to be unrelated to SN (Koivisto et al., 2005; Koivisto and Revonsuo, 2007, Koivisto et al., 2009). As RN and VAN occurs in similar time windows, and perceived changes are reflected in the contents of subjective visual awareness, RN might be an instance of VAN (Koivisto and Revonsuo, 2010).

Studies on change detection have revealed that successful detection of a unilateral change between two stimulus displays elicits enhanced posterior negativity, termed N2pc, contralateral to the position of the target (Eimer, 1996; Eimer and Mazza, 2005). It resembles the RN elicited during ambiguous figure reversals, as it occurs at the same time window and has similar amplitude. N2pc component is typically observed in visual search experiments. It is observed after the creation of difference waves – as activity observed in left/right posterior electrode site is subtracted from activity observed in the right/left posterior electrode site of the contralateral hemisphere (e.g. O1-O2 and O2-O1).

Having in mind the studies of Pitts et al. (2008) and Slotnick and Yantis (2005) that found the lateralization both of RN, and reversal (vs. non-reversal) related activity investigated with fMRI, it is reasonable to hypothesize that RN might be susceptible to lateral changes in the presented bilateral stimuli.

In this dissertation Necker lattices composed of 9 Necker cubes (Kornmeier and Bach, 2004) (Fig. 5.2), and two unambiguous lattices created from the ambiguous lattice after biasing each of the available interpretations (Fig. 5.1) were used. The experimental paradigm was designed so that it became feasible to study the relationship between RN, attention, and awareness. Since this study was the first one to explore both the N2pc response and ERP responses to multiple-figure presentation paradigm, unambiguous control stimuli were presented as targets in order to compare the electrophysiological effects elicited by real changes to changes in the perception of ambiguous stimuli. The bilateral displays in the present study not only help to examine the multiple-figure presentation paradigm with ERPs for the first time, but also allow measuring the N2pc component. They were used in order to test whether, or not RN and N2pc reflects the operation of the same attentional mechanism. If unilateral perceptual reversals induce RN only or more strongly over the hemisphere contralateral to the side of occurring change in comparison to the ipsilateral one, then RN is probably generated by the engagement of attentional mechanisms operating during perceptual reversals. Conversely, if RN and N2pc turn out to be unrelated, then perceptual reversals cannot be related to (or explained by) the same attentional processes as N2pc.

In previous ambiguous figure related ERP research, stimuli were presented for 800 ms (Kornmeier and Bach, 2004; Pitts et al., 2007; Britz et al, 2009), or even longer durations (i.e., 1500 ms) (Qiu et al., 2009). In this study, short presentation durations were chosen for both displays in order to facilitate the detection of N2pc, as it is known that this potential is extremely susceptible to increased stimulus duration, since longer stimulus presentation intervals significantly decrease the magnitude of N2pc (Brisson and Jolicoeur, 2007).

It is known that amplitudes of RP, RN and LP are susceptible to the duration of inter-stimulus-interval (ISI). Kornmeier et al. (2007) were investigating the impact of various ISIs on the amplitudes of RP and RN. The amplitudes of all components were susceptible to different ISIs (i.e., 14, 43, 130 and 390 ms), as amplitude of RP was reduced at longest ISI, although during other intervals, it stayed in the similar range. The amplitude of RN, conversely, was highest during longest ISI and also was extended to frontal and central areas, in comparison to earlier studies (Kornmeier and Bach, 2004; Kornmeier and Bach, 2005). The amplitude of LPC was higher for both longest ISIs in comparison to shorter ones. In other studies, the ISIs were set for 400 (Kornmeier and Bach, 2004; Kornmeier and Bach, 2005; Pitts et al., 2007; Pitts et al., 2008), 600 ms (Britz et al., 2009), or even 1000 ms (Qiu et al., 2009), therefore, shorter ISIs used in the present study might also have an impact on the obtained data.

Multiple-figure presentation (Long and Toppino, 1981; Long et al., 1983; Toppino and Long 1987) was chosen for this research for two main reasons:

1) It was inevitable to use it as an N2pc is a lateral effect, that is, it is usually obtained when there is a unilateral change in the display of at least two laterally presented stimuli;
2) This presentation type was quite convenient in order to test the hypothesis whether RN is related to the subjective awareness of the perceptual reversal, as two conditions with different types of perceived change could be compared, namely, ERP response to the unilateral reversal of the single Necker lattice (out of two lattices presented in the display) was compared with the response to the common reversal of two simultaneously presented Necker lattices.

Thus, if RN is a perceptual correlate of the processes of selective attention occurring each time the percept of ambiguous figure is regarded as changed; in the case of unilateral change it should resemble N2pc.

As perceptual experience of two simultaneous reversals is, subjectively, stronger than that of single change (Long et al., 1983), differences between the amplitudes of unilateral and bilateral change ERPs may be obtained, and due to them, it should be possible to indicate if RN directly correlates with the content of perceptual awareness. If RN is related to the change in the content of visual awareness, then it should depend on the number of reversing images, and differences between obtained RNs should be obtained. In that case, RN may be a subtype of VAN indicating the changes in bistable stimuli in visual awareness.

2.4.2. Ambiguous figure perception and perceptual load

The second experiment was designed in order to further clarify the possible relationship between selective attention and RN. It is known, both from behavioural (Toppino, 2003) and neuroimaging studies, applying EEG (Pitts et al., 2008) or fMRI (Slotnick and Yantis, 2005) that perception of ambiguous figures is susceptible to tasks of sustained attention. Nevertheless, there are no studies directly testing the possibility that ambiguous figure perception might be related to selective attention, although this idea has already been explored theoretically by several researchers (Pitts et al., 2008; Leopold and Logothetis, 1999).

One of the possible ways to investigate the relationship between the ambiguous figure perception and selective attention, would be to test whether RN (ERP negativity observed in response to perceived changes in ambiguous stimuli) is identical to SN (ERP negativity related to selective attention and visible in the similar time window and location as RN, but only in response to attended vs. unattended targets).

Another way is to manipulate the perceptual capacity of human brain with the help of varying amounts of perceptual load. Lavie (1995) proposed a theory of perceptual load which is based on a hypothesis that perception has a limited capacity, but it proceeds automatically between those limits. Therefore, our perception highly depends on the complexity of the target task. For example, if perceptual load is high, this would leave no free capacity for perception of distractor stimuli. Under the conditions of low perceptual load, on the contrary, only some parts of the available capacity are engaged in the processing, therefore, more perceptual resources would still be available for load-irrelevant distractors.

The theory of perceptual load was proposed as a hybrid model for the early and late selection debate in the research of selective attention (Lavie 1995; Lavie and Tsal, 1994). Early selection view proposes that focused attention prevents all the perceptual processing of the distractor stimuli, while late selection view claims that attention can influence only late post perceptual processes, (i.e., those occurring after the identification of the stimulus). Lavie and Tsal (1994) conducted a review of the early and late selection studies, and found out that studies supporting late perceptual selection applied low perceptual load tasks (e.g., Duncan, 1980), whereas studies supporting early selection applied high perceptual load tasks (e.g., Treisman, 1969). Such tasks normally differ either in the number of different items that need to be perceived, or under high load the same number of items require more attentional efforts (Lavie, 2006). As to the brain activity recorded under the high perceptual load, the activity related to load-irrelevant distractors is largely diminished and under low perceptual load, this activity stays in the usual range (Mohamed et al., 2009; Rees et al., 1997).

Perceptual load is a critical determinant of whether irrelevant distractors (or any other tasks that are not directly related to the presented load) are perceived (late selection) or not (early selection). Perceptual load is not only a convenient method to measure the attentional capacity of human brain, but also it is useful for studying the perception of load-irrelevant visual stimuli, especially those that rely on completely different psychological processes than tasks of perceptual load.

Therefore, in this study it was decided to present the task of ambiguous figure perception under high (or low) perceptual load and to see if there is any difference in the obtained reversal-related ERPs of the observers, depending on the magnitude of the presented perceptual load. Subjects had to simultaneously perform two tasks, that is, to respond whether they perceive a change in the presented Necker lattice and also provide an answer about which target letter (out of two) was presented. It was hypothesized that (1) if RN is affected by selective attention, under high perceptual load RN will be completely suppressed, but under low perceptual load it will retain the comparable amplitudes as the RN which is usually obtained in the ERP experiments of ambiguous figure perception, or (2) if RN is unaffected by selective attention, ERPs elicited in response to perceived changes of ambiguous stimuli under high or low perceptual load, would not differ significantly.

There are also two other ERP responses related to ambiguous figure perception, namely Reversal Positivity and Late Positivity (for an extended description of these potentials see ‘Review of the literature’ section). As these components might also be affected by the manipulations of selective attention (Pitts et al., 2007; 2008), the results obtained in the time windows of these components, were also taken into consideration.

PILOT EXPERIMENT

3. METHODS

3.1. Participants

Twenty students (5 male) participated in the study (mean age=21.1 years, SD=0.45). Each participant had normal or corrected-to-normal vision and had no prior experience as a psychophysical subject. They were completely naïve to the hypotheses and goals of the study and received course credit for participation.

3.2. Stimuli

Necker cube was chosen as experimental stimulus (Fig. 3.1). Each of the figures was drawn in black on a white background and they were presented on an overall grey background. Two standard ambiguous figures or a pair of neutral-biased reversible figures were presented simultaneously, and they were viewed binocularly. Two types of neutral-biased pairs were used, namely, a pair with a modification towards one interpretation and a pair with a modification towards another interpretation. This comprised a total of three experimental trials. Everyone was tested with both biased versions of each ambiguous figure. One figure subtended a visual angle of 2.2° × 2.2° and the space between the two figures was approximately 0.6°.

The stimuli were displayed on a CRT monitor (diagonal 53 cm, resolution 1600 × 1200 pixels, frame-rate 80Hz) connected to a Pentium class computer. A computer program written in *Delphi 3* programming language was used to record the changing interpretations (i.e., rate of reversals) and the time spent on each interpretation (i.e., durations of percepts).

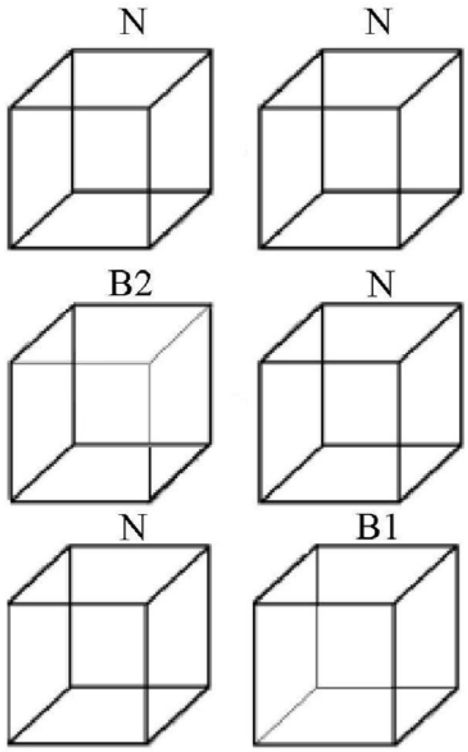


Figure 3.1 Illustration of the experimental trials with the Necker cube stimulus: N – neutral ambiguous figure; B1 – bias of 'down' orientation; B2 – bias of 'up' orientation.

3.3. Procedure

The experiment was conducted in a normal daylight environment. Participants sat approximately 60 cm away from a computer monitor. Before testing commenced, each participant was shown the Necker cube figure, and was allowed to watch it until reversals were perceived. A period of a few minutes generally sufficed for this.

At first, each participant viewed a pair of standard ambiguous figures and sequentially two neutral-biased pairs with each possible alternative of the biased figure. In the successively presented neutral-biased pairs, the left/right position of the biased figure was counterbalanced.

When figure pairs were presented, the participants were instructed to view them naturally, not to provoke perceptual reversals, and press three appropriate keys on the keyboard. They pressed 'Z' for the 'down' percept in both figures simultaneously (common reversals), 'C' – for the 'up' percept (common reversals), and ‘/’ (slash) – for different percepts perceived in both figures. Participants were instructed to make their judgments by looking at both cubes imultaneously and not to focus their attention on a single figure.

In all conditions, stimuli were presented for 150-sec and approximately 30-sec rest periods were provided between trials. For data analysis, the average number of key presses per minute was calculated as rate of reversals (i.e., reversal rate of percept ‘down’, percept ‘up’ and different percepts). The mean intervals between pressing one key or the alternative ones, was computed as durations of percepts. Each participant took part individually in a 30-min session.

4. RESULTS AND DISCUSSION

A 3 × 3 repeated measures ANOVA with the factors Bias (No-bias, Bias-1 and Bias-2) and Percept (Down, Up and Different percepts), was used to estimate the variability of the mean values of reversal rate and durations of each percept. The reversal rate and the durations of percepts data is presented in Fig. 4.1.

Results revealed a significant effect for Bias: perceived reversal rate of two Necker cubes presented simultaneously was significantly higher when bias of 'up' was introduced in comparison to bias of 'down' ($F(2,40) = 3.73$, $p < 0.04$) (Fig. 4.1A). Significant effect for Percept was also obtained ($F(2, 40) = 61.31$, $P < 0.0001$), with a greater number of reversals reported for percept 'down' in comparison to that of 'up' ($p < 0.0001$) and Different percepts ($p < 0.0001$). Significant Bias × Percept interaction ($F(4, 80) = 5.43$, $P < 0.006$) was observed and it was subsequently analysed by conducting separate Bias (3) ANOVAs for all conditions. Results revealed significant differences only when reversal rates of percept 'up' were compared, revealing that its perceived rate was highest in condition of up-bias: it was higher than the 'up' values in no-bias ($p < 0.04$) and down-bias ($p < 0.0001$) pairs. Thus, bias of 'up' increased frequency of 'up' percept, in comparison to its perception in a pair of neutral Necker cubes.

As to results concerning perceptual durations of available interpretations, a bias of 'up' orientation significantly shortened the perceived duration of 'down' orientation ($F(2,40) = 5.73$, $p < 0.02$) (Fig. 4.1B). Participants were able to view and perceive changes in both presented ambiguous stimuli, even though one of them was biased according to one or another of the available interpretations.

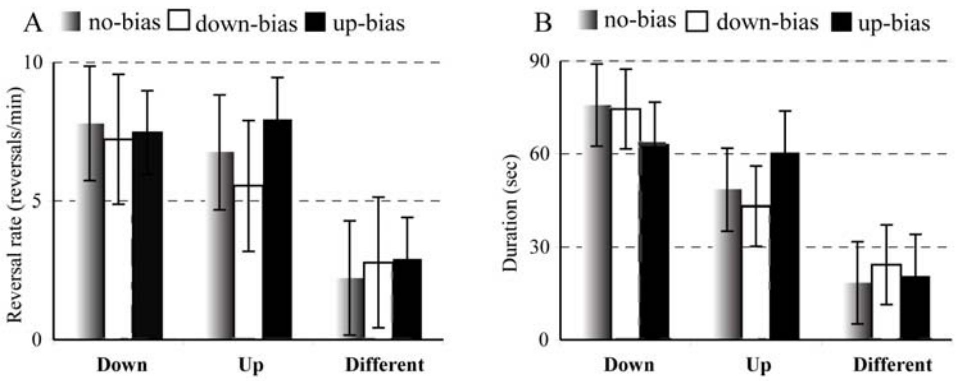


Figure 4.1 Results of the pilot study. A – differences in reversal frequencies from each percept to 'down' percept, from each percept to 'up' percept, and from each percept to different percepts for neutral (grey columns), down-bias (white columns) and up-bias (black columns) pairs. B – dominance durations of 'down', 'up', and different percepts for neutral (grey columns), down-bias (white columns) and up-bias (black columns) pairs. Error bars in the graphs represent SD.

The data of the pilot experiment revealed that observers are capable to view and perceive alternating changes in the presented Necker cubes, when two cubes are presented simultaneously and one of them is biased according to one (or another) of the available interpretations. A bias had an effect on the perception of Necker cube pairs, as it increased the probability of different percepts perceived simultaneously in the presented cube pairs. Also, a bias of particular percept significantly increased the perceived frequency of it. On the basis of the data obtained in this experiment, experimental methods for an electroencephalographic (EEG) study were designed and created. The presentation of bias was incorporated with selective attention related task, in order to clarify the following issues:

1) Clarification of the potential relationship between the ambiguous figure perception and selective attention.

2) Exploration of the operation of the principal mechanisms responsible for the perception of ambiguous stimuli.

EXPERIMENT I

5. METHODS

5.1. Participants

Thirteen healthy students (five male) within age range from 20 to 35 years old, (mean age=24.2 years, SD = 4.5), participated in the study. They were completely naïve as to the specific experimental question and received course credits for the participation. Edinburgh handedness inventory (Oldfield, 1971) was used in order to assess the usage of a person's right and left hands in daily activities. Each individual was right-handed (mean handedness values = 0.77, SD = 0.30), as confirmed by this measurement scale. All participants reported normal or corrected-to-normal vision. The study was formally approved by the local ethical committee of University of Turku and written consent was obtained from each participant.

5.2. Stimuli

The subjects completed two conditions: the real change (hereafter RC) and Necker change (hereafter NC). RC condition included only unambiguous lattices (Fig. 5.1) constructed from nine unambiguous cubes, as stimuli, whereas NC included both unambiguous lattices and Necker lattices constructed of nine ambiguous Necker cubes (Fig. 5.2).

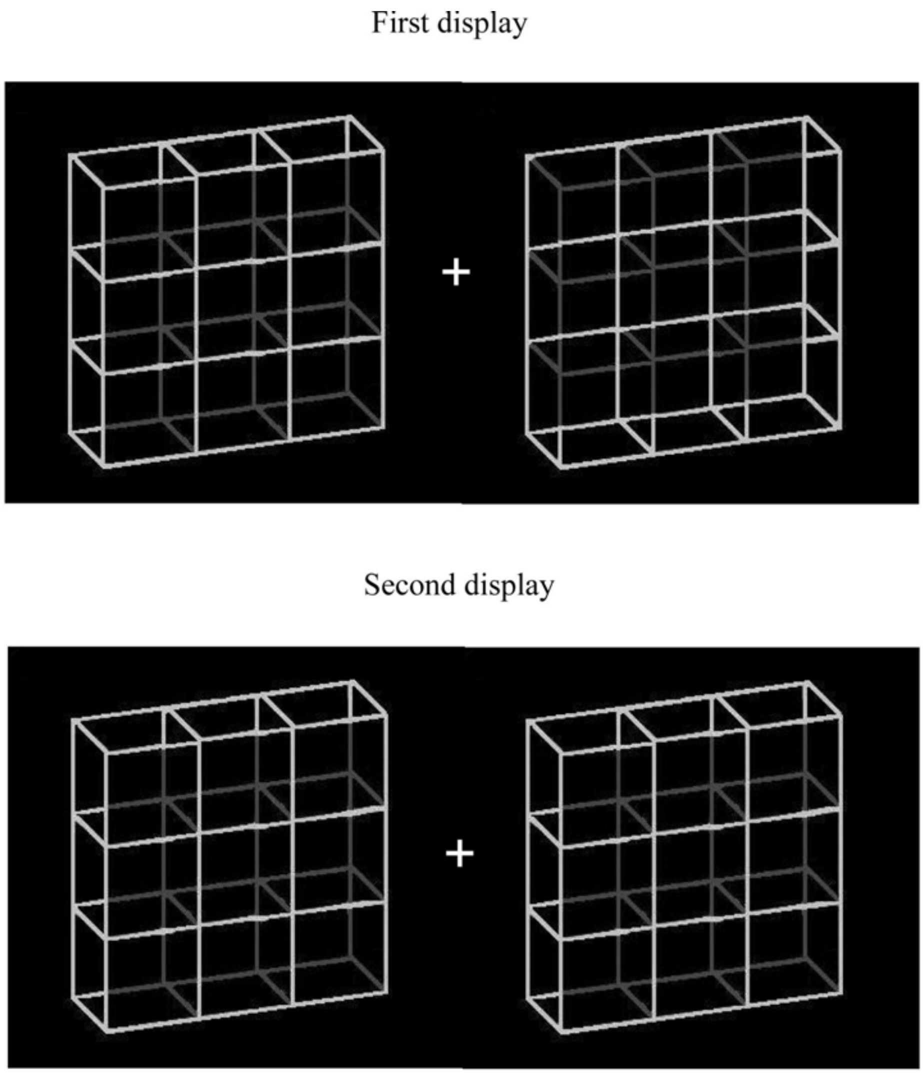
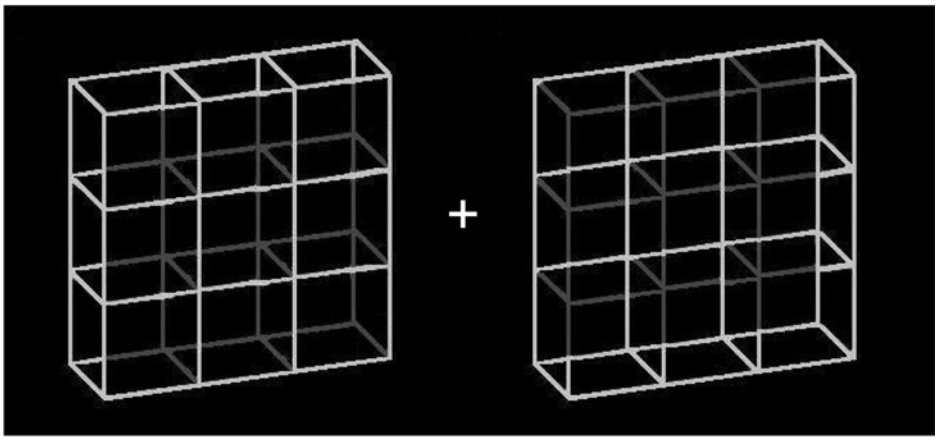


Figure 5.1 Stimuli display in the real change condition (example of unilateral right change in the orientation of unambiguous lattices).

For each type of stimulus a mirror image version with respect of the left-right orientation was created and shown on half of the trials. Each stimulus subtended a visual angle of 1.9° × 1.9° and was presented on a 21 inch computer screen with a frame rate of 60 Hz at a viewing distance of 150 cm. They were presented in white (20 cd/m²) on a black background (0.1 cd/m²). In all trials, a pair of lattices was presented, one on the left side, and one on the right side of the fixation cross. They were viewed binocularly. The inner edges of the lattices were placed on average 0.6° away from fixation. The location of the lattices between the first and second display in each trial was randomly jittered by small changes (about ± 0.3°) to avoid afterimages and trivial local cues.

First display



Second display

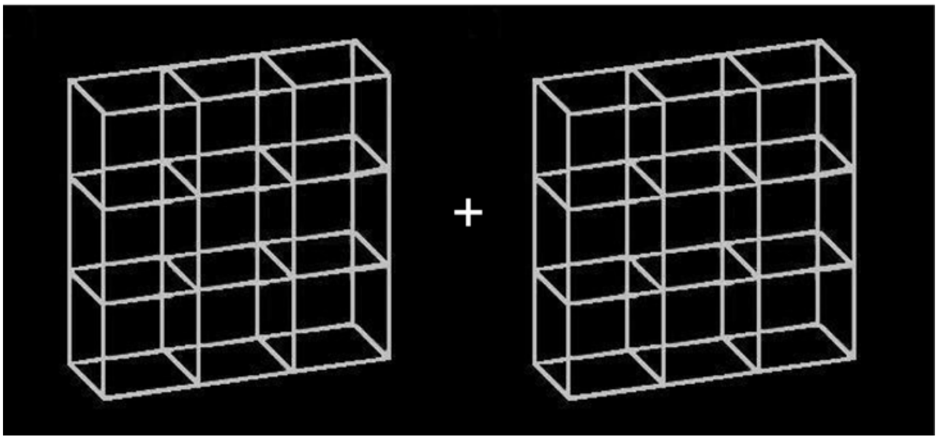


Figure 5.2 Stimuli display in the perceptual change condition including unambiguous lattices and Necker lattices (example of the possible unilateral change in the orientation of the left or right lattice).

5.3. Procedure

Prior to any recordings, observers were introduced to the concept of ambiguity as they viewed a Necker lattice. If an observer was initially unable to identify either one of the two possible interpretations of the figure, the experimenter accentuated the alternative orientation of the lattice for him/her, until the observer could easily perceive the ambiguity of the image.

Each participant performed four practice blocks, each composed of 32 trials, two for RC condition and two for NC condition. The practice trials served to familiarize the observers with the general performance of the task, the importance of fixating on the fixation cross and the usage of the response pad. The participants were asked to look at the central fixation cross, and not to move their eyes within trials. Eye movements and blinks were allowed after they have provided the response and were observed with the help of continuous electro-oculography (EOG) recording.

Each trial began with the appearance of the fixation cross for 500 ms. It was followed by the first display (always containing two unambiguous lattices) for 400 ms, after which a fixation cross was again introduced for 200 ms, and then the second display was presented for 200 ms (Fig. 5.3).

In the first display of both the RC and NC conditions one of four available stimulus configuration possibilities, each involving two unambiguous lattices, was presented:

1) Both lattices in ‘down’ orientations;
2) Both lattices in ‘up’ orientations:
3) Left lattice ‘up’ and right lattice ‘down’ orientations;
4) Right lattice ‘up’ and left lattice ‘down’ orientations.

It was decided to show unambiguous lattices in the first display of both the RC and NC conditions. This design of experiment was chosen for two main reasons:

1. Comparison of ERPs obtained from the ambiguous-ambiguous and unambiguous-unambiguous presentation conditions would introduce additional stimulus-related ERP confounding factors. It is impossible to have the RC condition without presentation of unambiguous stimuli in the first display.
2. During pilot experimentation, it was noticed that unilateral endogenous reversals could be induced more easily in the NC condition by using presentation manner when two unambiguous lattices in different orientations were presented in the first display. In

addition, by using only ambiguous-ambiguous presentation mode for the NC condition, it would be impossible to obtain a valid number of proper unilateral change experimental trials.

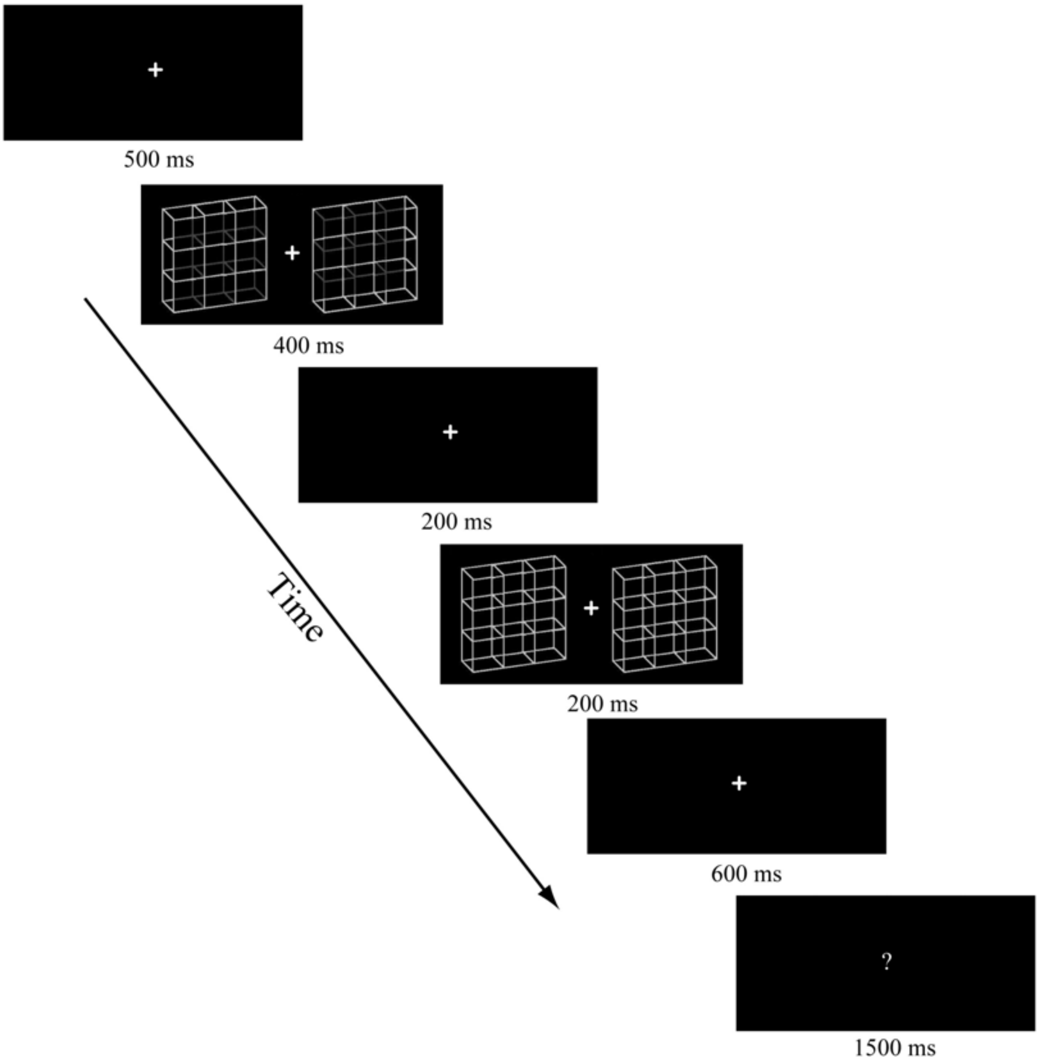


Figure 5.3 An example of a single experimental trial in the Necker change condition.

In the second display of the RC condition two unambiguous lattices having the same orientations were presented and in the second display of NC condition two ambiguous Necker lattices were presented. Such sequence of displays thus resulted in four possible real change configurations:

1) left lattice changed orientation,
2) right lattice changed orientation,
3) both lattices changed orientations,
4) neither of them changed orientation.

The unambiguous lattices reversed randomly in 75% of the trials in the RC condition, that is, in conditions 1-3, but not in condition 4.

After the second display a fixation cross was presented for 600 ms and after it the appearance of the question mark (?) indicated that the participant was allowed to respond on perceived changes between the first and second displays. The inter-trial interval between the observer's response and the beginning of the next trial was 1500 ms.

The participants compared the orientations of the stimuli in the second display with those in the preceding display. They were instructed to press the 'left' button when they saw a change of orientation in the left lattice, the 'right' button when they saw a change of orientation in the right lattice, and a button between the left and right buttons when they saw a change of orientation in both lattices. If the participants did not perceive any change, they were asked simply to wait for the next trial and not press any button. They were also asked not to provoke perceptual reversals, as it was stressed that they should press a button only when they really saw a change.

The RC condition included 320 trials and NC condition included 272 trials in total. For the RC condition four blocks of change were created: a change in the orientation of the left stimulus, a change in the orientation of the right stimulus, a change in the orientations of both stimuli and no change in the orientation of the stimuli. This resulted in 80 trials for each condition (320 trials in total). All the changes in the NC condition are entirely perceptual, so observers were able to select the 'no-change' answer in all provided trials. Therefore, there was no need to create a separate no-change block for NC condition. As the main aim of the experiment was to examine whether a selective attention related N2pc component is going to be observed in case of perceptual reversal of the Necker lattice stimulus, more experimental trials for unilateral reversals (i.e., trials when lattices presented in the first display had different orientations) were included in the experiment (192 trials in total) in comparison to bilateral change trials (i.e., trials when lattices presented in the first display had identical orientations) (80 trials in total).

Each of the two experimental conditions was divided into two blocks of trials. Each block was composed of half RC (or NC) trials arranged in random order. Every subject had to perform four stimulus blocks in order to complete the experiment. In the middle of the experiment there was a long break (approx. 10 min) provided for the participants and short 2 – 3 min breaks were given between the stimulus blocks. A complete experiment with one subject lasted approximately two hours. The response hand was counterbalanced: half of the subjects performed the first part of the experiment (i.e., one RC and one NC block) with the left hand, and the second part with the right hand. For the other half of the participants the order of response and the sequence of presentation of experimental blocks were reversed. When laterality of brain responses is explored in the experiment, changing hand in the middle of the study is essential. Otherwise, there is a risk to obtain a lateral effect (e.g., increased negative potential over the left hemisphere) that is determined by usage of only one (e.g., right) hand during an entire experiment.

On the basis of pilot work, unilateral perceptual reversals were verified to be rare in NC condition when the lattices in the first display had the same orientation and bilateral changes were verified to be rare when the lattices in the first display had different orientations; thus these kind of stimulus-response combinations served as fillers and ERPs in response to them were not analysed. In order for a participant’s data to be included in ERP analyses, at least 30 artefact-free single trials per change configuration were required (that is, trials without blinking, coughing, frowning etc.).

5.4. Electrophysiological recordings and analysis

EEG was recorded using Ag/AgCl electrodes from international 10/20 system sites Fp1, Fp2, F3, F4, F7, F8, Fz, P3, P4, Pz, C3, C4, Cz, T3, T4, T5, T6, O1, O2. An electrode between Fz and Cz was used as ground and electrode attached to the nose as reference. An electrode below the right eye was used for monitoring blinks and vertical eye movements and an electrode placed 1.5

cm to the right of right eye was used for monitoring horizontal eye movements. EEG was amplified by using a band pass of 0.15 to 100 Hz, with the sampling rate of 500 Hz. The impedance of electrodes was kept below 5 kΩ. Filtering (0.1 – 20 Hz) was also performed in order to attenuate high and low frequencies, caused by various sources of noise. Event-related potential (ERP) waveforms (sequences of positive and negative voltage deflections) were extracted from EEG recordings, using “BrainVision Analyzer” setup. ERPs were segmented and averaged separately for different types of changes (left change, right change, bilateral change and no-change), in the RC and NC conditions according to the response provided by the participant. Only correct response trials were analysed from the data of the RC condition. Baseline correction was performed to the activity in the -100 – 0 ms preceding the second display. Trials showing evidence of artefacts (> 70μV), occurring due to eye movements and blinks, or due to other reasons (e.g., movement of participant) in any of the electrodes were rejected off-line and discarded from analyses. After completion of all above mentioned steps, it was possible to create averages for each participant individually.

Consequently, the grand average waveforms were created by a common averaging of individually averaged ERPs of all participants. The time windows for P1, N1, P2, N2, and P3 potentials were determined by visually inspecting their latencies in the grand average waveforms (Picton et al., 2000). Mean amplitudes were statistically analysed in the P1 (100–150 ms), N1 (150–200 ms), P2 (200–250 ms), N2 (250–300 ms), and P3 (300–500 ms) time windows, beginning from the onset of the second stimulus display. On the basis of visual inspection, narrower P3 time window (in comparison to usual range from 400 to 700 ms) was chosen. When the degrees of freedom were greater than 1, Greenhouse and Geisser corrections were applied to the *p* values (Picton et al., 2000). RN is usually observed as enhanced negativity in response to perceptual reversals about 200 – 300 ms after the onset of the second display (e.g., Britz et al., 2009), so that it might overlap with N1, P2, and N2 waveforms. If RN reflects the work of the same system that is responsible for N2pc, then RN should be observed only in the contralateral electrode relative to the side of unilateral reversal (e.g., as larger negativity over the right hemisphere in comparison to that of the left one, in response to reversals on the left side). In addition, a more focused analysis on the mean amplitudes of N2pc was performed by applying the method of difference waves (contralateral minus ipsilateral, in relation to the side of real change in RC or perceived change in NC condition) in the time window of 270– 320 ms, calculated from occipital (O1/O2) and posterior temporal (T5/T6) electrodes, as previous research indicate that the N2pc was most clearly observable in this time window and in these electrodes (Girelli and Luck, 1997).

6. RESULTS AND DISCUSSION

6.1. Behavioural performance

Table 6.1 shows the number of correct (the RC condition) and perceptual (the NC condition) responses calculated as a percentage. The total number of trials, from which the percentage values were computed, is provided in brackets.

Table 6.1 The percentage values of reported unilateral, bilateral and no-changes in both conditions. The total numbers of trials provided for each condition are presented in brackets.

Left change	Right change	Bilateral change	No change
REAL CHANGE CONDITION			
79% (80)	84% (80)	88% (80)	94% (80)
NECKER CHANGE CONDITION			
33% (192)	36% (192)	42% (80)	27% (272)

A two repeated measures ANOVA with a factor Change location (left change, right change) was performed separately for RC and NC condition, but no statistically significant differences in performance between the change locations neither for the RC condition ($F(1,12)=2.86$; $p=0.12$), nor for the NC condition ($F(1,12)=0.88$; $p=0.37$) were observed.

6.2. Electrophysiological data

In the analyses of ERPs, only significant main effects or interactions which have Response (left change, right change, bilateral change and no-change) as a factor were reported. Thirty single artefact-free trials per change configuration were selected as a threshold number for calculation of ERPs. Since some of the subjects did not perceive the required number of changes (i.e., one subject for the unilateral changes and two subjects for the bilateral changes), their data were excluded from the reported analyses.

6.2.1. Unilateral changes

The variability of the mean amplitudes was estimated by a 2 × 3 × 5 × 2 repeated measures ANOVA with the factors Condition (RC, NC), Response (left change, right change and no-change), Area (frontal, central, parietal, occipital and temporal electrodes) and Hemisphere (left and right). ERPs in the RC and NC conditions are represented in Figures 6.1 and 6.2, respectively.

P1 (100-150 ms).

Significant Response × Area ($F(8,72)=4.22$; $p<0.034$) interaction was found, therefore 2 × 3 × 2 repeated measures ANOVAs with the factors Condition (RC, NC), Response (left change, right change and no-change), and Hemisphere (left and right) were conducted separately for each area.

Significant effect for Response was found only at frontal electrodes ($F(2,20)=4,19$; $p<0.04$), when mean amplitudes in response to no-changes were significantly less negative than those in response to left changes ($p<0.02$).

N1 (150-200 ms).

No significant Response related effects, or interactions were observed in this time window.

P2 (200-250 ms).

Significant effect for Response ($F(2,18)=10.23$; $p<0.004$) was found: mean amplitudes in response to no-changes were significantly less negative than those in response to left changes ($p<0.008$), or right changes ($p<0.002$). Significant Condition × Response × Hemisphere ($F(2,18)=5.35$; $p<0.02$) and Condition × Response × Area × Hemisphere ($F(8,27)=2.99$; $p<0.05$) interactions were found. These interactions were further analysed by conducting separate 3 × 5 × 2 ANOVAs with the factors Response (left change, right change and no-change) and Hemisphere (left and right) for each condition individually.

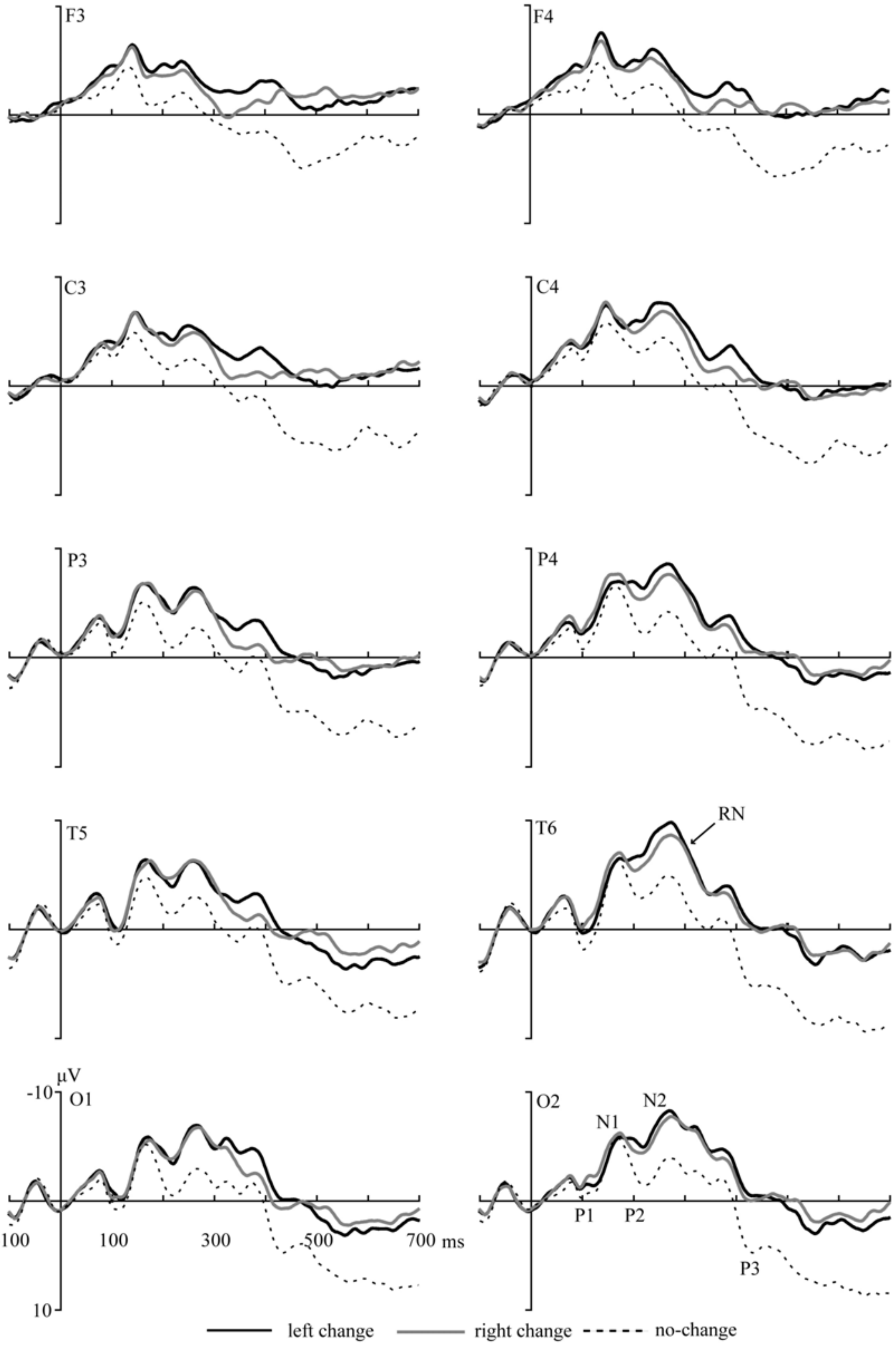


Figure 6.1 Grand-average ERPs in response to the second stimulus display on trials where participants reported seeing a real change of the left stimulus (black lines), right stimulus (grey lines) or no-change (small dashed lines) in the orientation of the stimuli. Significant negative differences (RN) between left/right changes and no-changes were observed in P2 and N2 time windows in all areas (N=12).

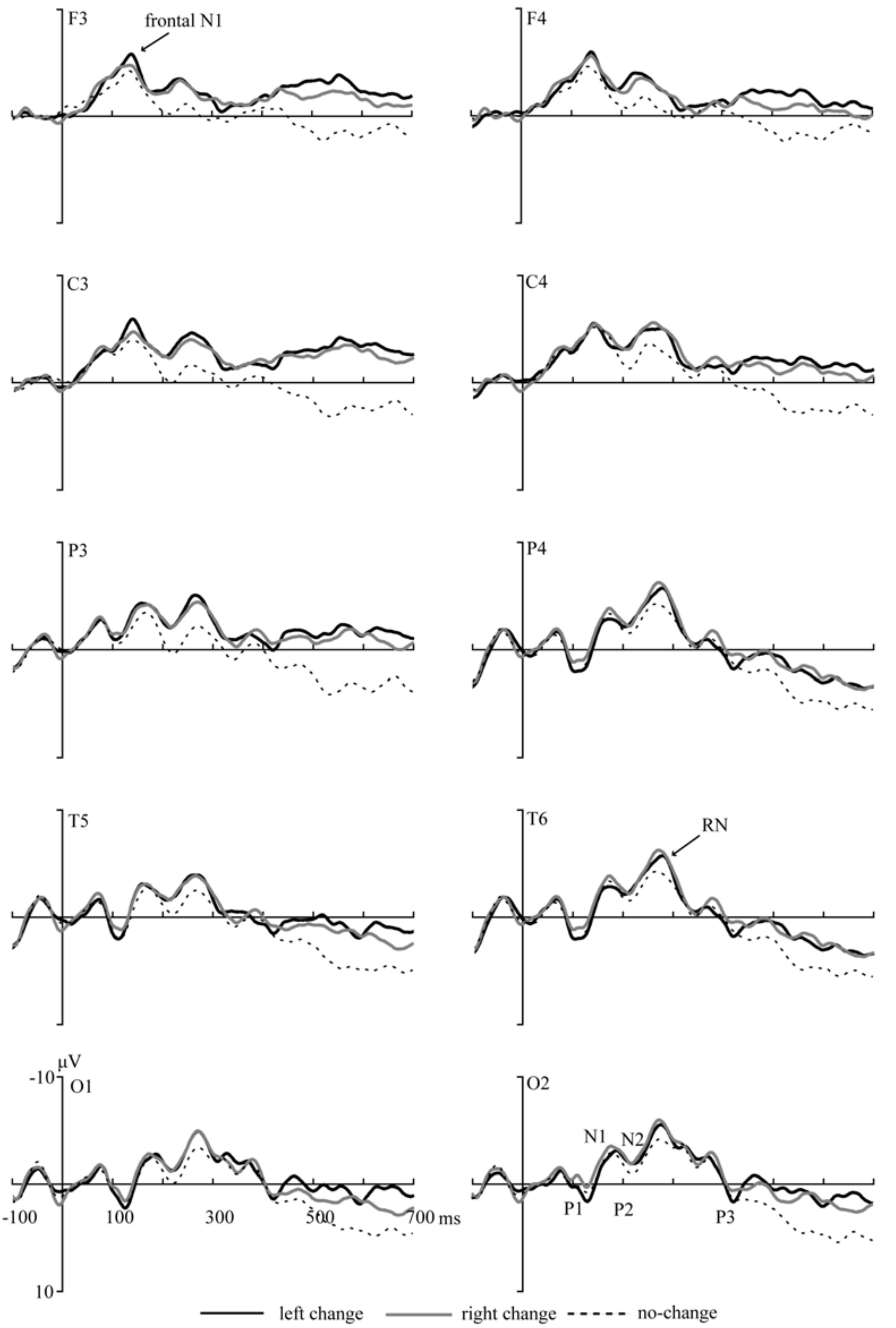


Figure 6.2 Grand-average ERPs in response to the second stimulus display on trials where participants reported seeing a perceptual change of the left stimulus (black lines), perceptual change of the right stimulus (grey lines) or no-change (small dashed lines) in the orientation of the stimuli. During P2 time window significant negative difference (RN) between left/right perceptual changes and no-changes was observed only in frontal areas. During N2 time window RNs were observed in all areas (N=12).

The RC condition. Significant main effects for Response were observed in all areas: frontal ($F(2,22)=10.40$; $p<0.004$), central ($F(2,20)=9.97$; $p<0.005$), parietal ($F(2,20)=12.99$; $p<0.003$), occipital ($F(2,24)=13.07$; $p<0.002$) and temporal ($F(2,24)=18.19$; $p<0.0001$). For all these sites, the mean amplitudes in response to no-changes were significantly less negative than those in response to left (all p-values < 0.008) or right changes (all p-values < 0.007).

Significant Response × Hemisphere interaction ($F(2,24)=5.55$; $p<0.02$) was found only for the temporal electrodes. Additional analyses, conducted on each temporal electrode site separately, showed that amplitudes in response to left (all p-values < 0.01) and right (all p-values < 0.002) changes were significantly more negative than those in responses to no-changes over both hemispheres.

The NC condition. Main effect for Response was obtained only at frontal electrodes ($F(2,20)=4.75$; $p<0.05$), showing that mean amplitudes in response to left ($p<0.03$) and right ($p<0.002$) changes were significantly more negative than those in response to no-changes.

Since significant differences between change and no-change in the NC condition were observed only in the frontal areas, it might indicate the delayed onset of RN in the NC condition, as RN in the RC condition was elicited over all observed electrodes.

N2 (250-300 ms).

A main effect for Response ($F(2,18)=12.79$; $p<0.02$) was found showing that amplitudes to no-change responses were significantly less negative than those to left ($p<0.005$) and right ($p<0.0001$) changes.

6.2.2. N2 posterior contralateral

The grand average difference waves (Left change: T6-T5 and O2-O1; Right change: T5-T6 and O1-O2) were used to concentrate the analyses specifically on the N2pc component which is usually observed in the N2 latency range at posterior electrodes contralateral to the side of a unilateral change in a display of bilateral stimuli (Eimer, 1996). The difference waves for the RC and NC conditions separately are depicted in Fig. 6.3. A 2 × 2 × 2 × 2 ANOVA with the factors Condition (RC, NC), Change location (left, right), Response (change, no-change) and Area (occipital, temporal) was performed on the mean amplitudes (270-320 ms). A significant effect for Change location (left, right) was obtained ($F(1,11)=6.12$; $p<0.04$). It revealed that the N2pc in response to the changes on the left side was significantly larger than that to the changes on the right side. Significant Condition × Response × Area ($F(1,11)=6.76$; $p<0.03$), Change location × Response × Area ($F(1,11)=8.23$; $p<0.02$) and Condition × Change location × Response ($F(1,11)=5.37$; $p<0.05$) interactions were also detected.

These interactions were further studied by conducting separate 2 × 2 × 2 ANOVAs with the factors Change location (left and right), Response (change, no change) and Area (occipital, temporal) separately for the RC and NC conditions in order to determine in which condition changes (vs. no-changes) elicited stronger contralateral response.

In the RC condition significant Change location × Response ($F(1,12)=7.64$; $p<0.02$) and Change location × Response × Area ($F(1,12)=9.37$; $p<0.02$) interactions were observed. Further analyses, conducted separately on each area, showed that Response (change, no-change) had a significant effect at temporal electrodes ($F(1,12)=6.71$; $p<0.03$). The significant Change location × Response interaction ($F(1,12)=12.91$; $p<0.005$) was obtained because of significantly larger N2pc in response to perceived changes in comparison to no-change trials for exogenous left changes in temporal electrodes ($F(1,12)=16.64$; $p<0.003$), whereas for exogenous right changes the amplitudes in response to changes were more positive than those to no-change trials over temporal lobe ($F(1,12)=5.84$; $p<0.04$).

The analyses conducted on the NC condition did not find any significant results, suggesting that perceptual reversals in response to ambiguous figures did not elicit any N2pc.

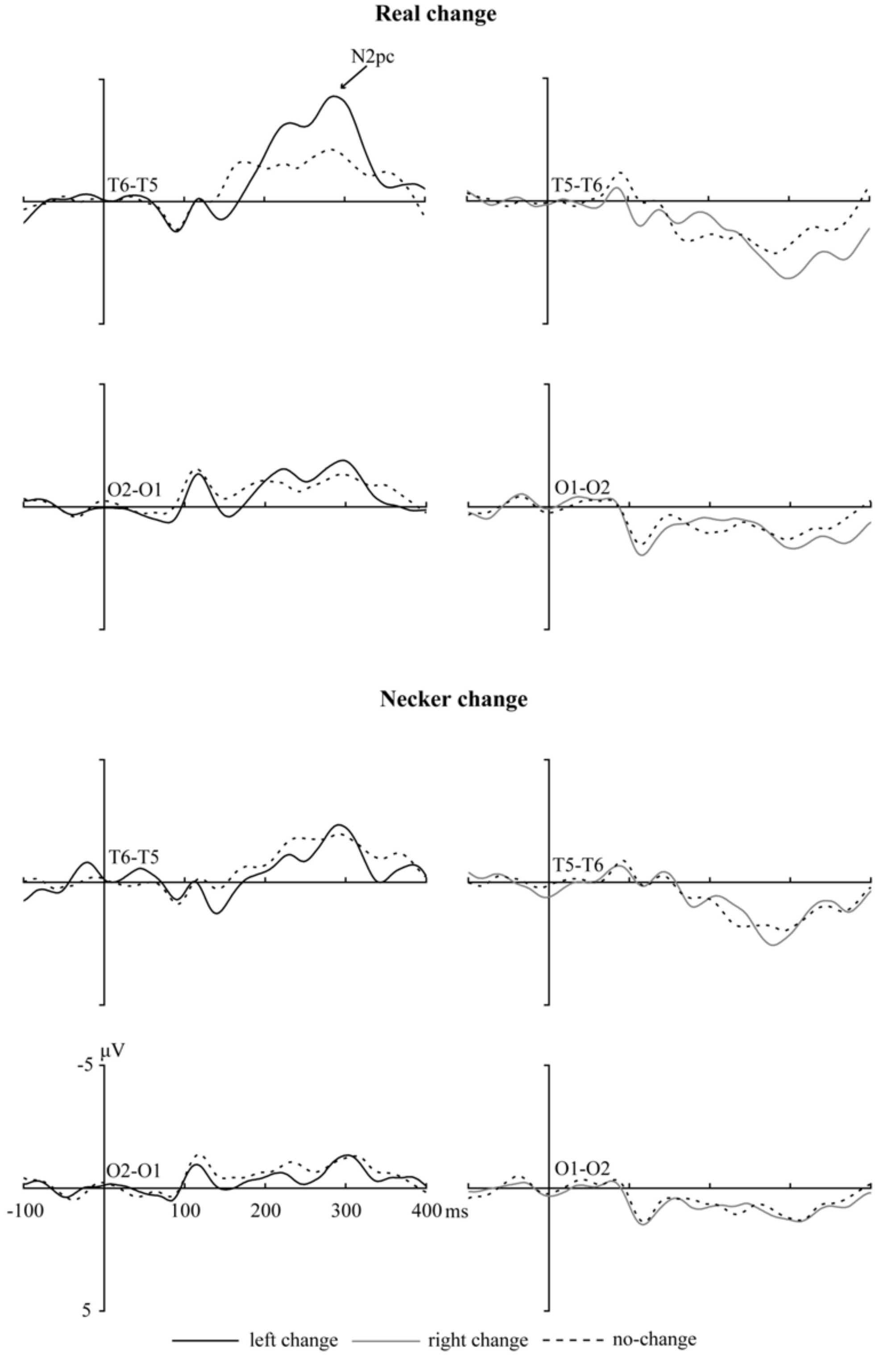


Figure 6.3 Difference waves (contralateral–ipsilateral) from the onset of the second display in the RC and NC conditions over posterior temporal (T) and occipital lobes (O). In the RC condition, larger N2pc was elicited by left changes in comparison to no-changes over temporal electrodes (N=12).

P3 (300-500 ms).

No significant Response related effects or interactions were observed in this time window.

6.2.3. Bilateral changes

The variability of the mean amplitudes was estimated by a 2 × 2 × 5 × 2 repeated measures ANOVA with the factors Condition (RC, NC), Response (bilateral change and no-change), Area (frontal, central, parietal, occipital and temporal electrodes) and Hemisphere (left and right). ERPs for the RC and NC conditions are presented in Figures 6.4 and 6.5, respectively.

P1 (100-150 ms).

No significant Response related effects or interactions were observed in this time window.

N1 (150-200 ms).

No significant Response related effects or interactions were observed in this time window.

P2 (200-250 ms).

Significant Condition × Response ($F(1,9)=7{,}49$; $p<0.03$) and Condition × Response × Area ($F(4,36)=6{,}70$; $p<0.02$) interactions were observed. These interactions were further studied by conducting separate repeated measures 2 × 5 × 2 ANOVAs with the factors Response (bilateral change and no-change), Area (frontal, central, parietal occipital and temporal electrodes) and Hemisphere (left and right) for each condition individually.

The RC condition. Significant Response × Area interaction ($F(4,36)=12{,}14$; $p<0.002$) was obtained, and it was further analysed by repeated measures 2 × 2 ANOVAs with the factors Response (bilateral change and no-change) and Hemisphere (left and right) on each area individually. No Response involving effects or interactions were found over any of the areas.

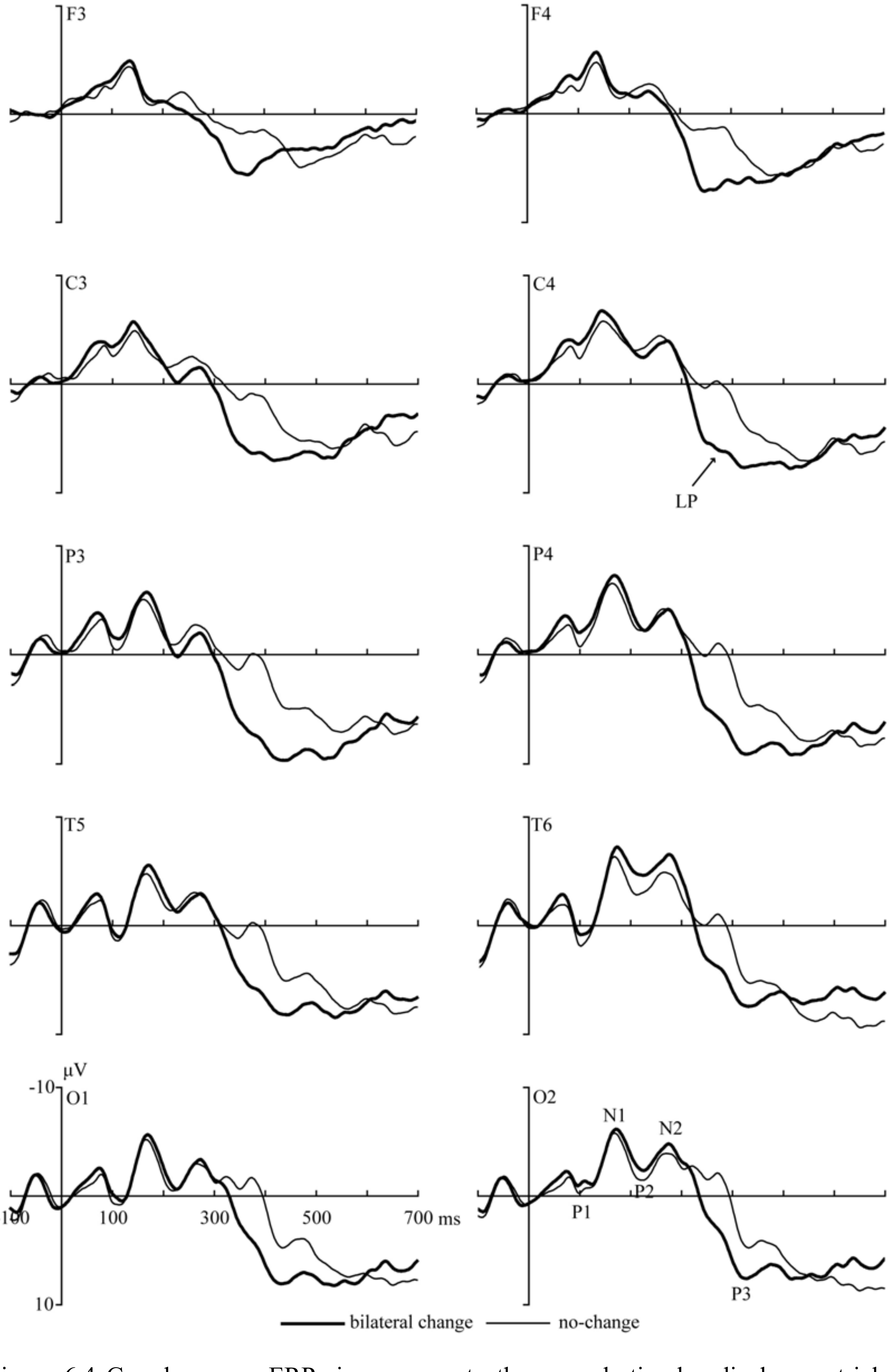


Figure 6.4 Grand-average ERPs in response to the second stimulus display on trials were participants reported seeing bilateral real changes (thick black lines) and no-changes (thin black lines). Significant differences between bilateral real changes and no-changes (late positivity – LP) were observed in all areas, except frontal, during P3 time window (N=11).

The NC condition. Significant effect for Response ($F(1,10)=6,90$; $p<0.03$) was observed, indicating that amplitudes to bilateral change trials were more negative than those to no-change trials.

N2 (250-300 ms).

Significant Condition × Response interaction ($F(1,9)=7,94$; $p<0.03$) was obtained, therefore separate 2 × 5 × 2 repeated measures ANOVAs with factors Response (bilateral change and no-change), Area (frontal, central, parietal, occipital and temporal electrodes) and Hemisphere (left and right) were conducted on each condition individually.

The RC condition. No significant Response related effects or interactions were observed in this condition.

The NC condition. Main effect for Response ($F(1,10)=5,92$; $p<0.04$) was found: mean amplitudes in response to bilateral changes were significantly more negative than those in response to no-changes ($p<0.04$).

P3 (300-500 ms).

Significant Condition × Response ($F(1,9)=10,33$; $p<0.02$) and Response × Area × Hemisphere ($F(4,36)=4,07$; $p<0.04$) interactions were observed, which were further analysed by subsequent 2 × 5 × 2 repeated measures ANOVAs with factors Response (bilateral change and no-change), Area (frontal, central, parietal, occipital and temporal electrodes) and Hemisphere (left and right) for each condition individually.

The RC condition. Main effect for Response ($F(1,9)=17,09$; $p<0.004$) was revealed: mean amplitudes in response to the bilateral changes were significantly more positive than those in response to no-changes ($p<0.004$). Significant Response × Area ($F(4,36)=4,78$; $p<0.03$) and Response × Area × Hemisphere ($F(4,36)=6,62$; $p<0.01$) interactions were also revealed, which were further analysed by separate 2 × 2 repeated measures ANOVAs with factors Response (bilateral change and no-change) and Hemisphere (left and right) for each area individually.

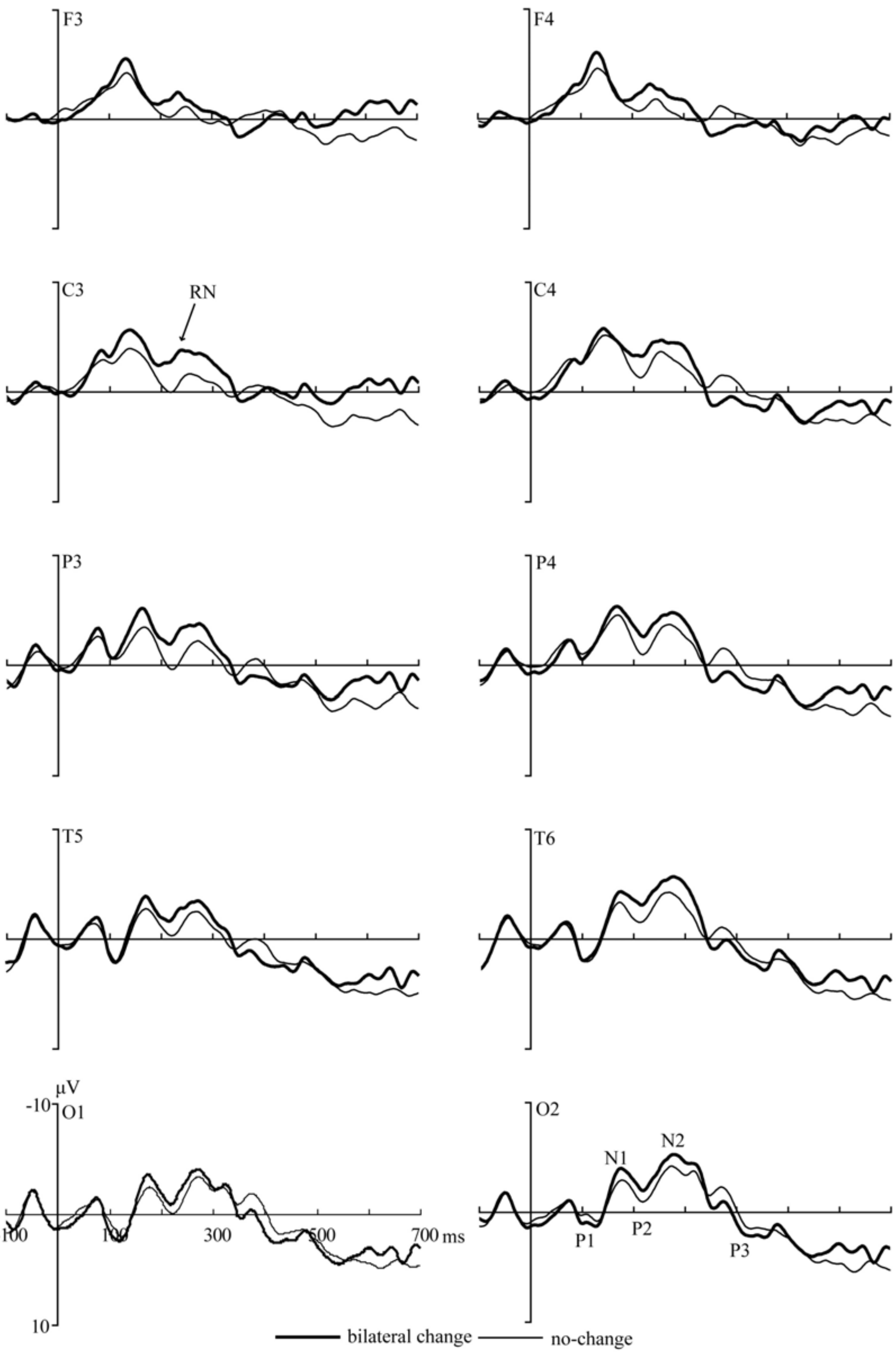


Figure 6.5 Grand-average ERPs in response to the second stimulus display on trials were participants reported seeing bilateral perceptual changes (thick black lines) and no-changes (thin black lines). Significant negative differences (RN) between bilateral perceptual changes and no-changes were observed in all areas during P2 time window (N=11).

Significant effect for Response was found for central (F(1,10)=7,97; p<0.02), parietal (F(1,10)=11,08; p<0.009), occipital (F(1,11)=6,39; p<0.03) and temporal (F(1,11)=6,43; p<0.03) electrodes: mean amplitudes in response to the bilateral changes were significantly more positive than those in response to no-changes (all p-values < 0.03). Significant Response × Hemisphere interactions were observed for frontal (F(1,10)=8,26; p<0.02) and temporal (F(1,11)=5,28; p<0.05) areas, which were further analysed for each electrode site individually. Significant effects for Response were observed over frontal right hemisphere electrode (F(1,10)=8,67; p<0.02) and temporal left hemisphere electrode (F(1,11)=12,20; p<0.006): mean amplitudes in response to bilateral changes were significantly more positive than those in response to no-changes (all p-values < 0.02).

The NC condition. No significant Response related effects or interactions were observed in this condition.

6.2.4. Comparison of unilateral and bilateral changes

The comparison analyses were conducted with an aim to evaluate whether the amount of the change is reflected in the contents of the visual awareness. A 2 × 4 × 5 × 2 repeated measures ANOVA with the factors Condition (RC, NC), Response (left change, right change, bilateral change and no-change), Area (frontal, central, parietal, occipital and temporal electrodes) and Hemisphere (left and right) was performed.

In P2 and N2 time windows Condition × Response interactions (F(3, 24) = 7.67 and 5.13, ps < 0.03) were observed, which were analyzed additionally. In the RC condition, left and right unilateral changes elicited RN in both of these time windows, but in condition of bilateral changes RN was not obtained. In the NC condition, both unilateral and bilateral perceptual changes elicited RN, but these changes did not differ significantly.

EXPERIMENT II

7. METHODS

7.1. Participants

This section, except for the part described below, is identical to the 'Participants' section of Experiment I (p. 30).

The experiment was conducted with eighteen healthy students (nine female), (mean age=22.5 years, SD=2.3) which were all confirmed to be right-handed (mean handedness values =0.92, SD=0.01).

7.2. Stimuli

The subjects completed the real change (hereafter RC) and Necker change (hereafter NC) conditions. RC stimuli included only unambiguous lattices (Fig. 7.1A) constructed from nine unambiguous cubes, as stimuli, whereas NC stimuli included both unambiguous lattices and Necker lattices constructed of nine ambiguous Necker cubes (Fig. 7.1B). Each stimulus was of size 3.6° × 3.6° and was presented at a viewing distance of 150 cm on a 21 in. computer screen with a frame rate of 60 Hz. They were presented in white (20 cd/m²), on a black background (0.1 cd/m²).

Half of the presented displays were blended with letters (font: Myriad, size: 26). A letter string was superimposed on the centre of ambiguous or unambiguous lattice. Letter strings consisted of five capital letters presented in red colour, and included either target letters 'N' or 'X' only (low load letter strings) (see Fig. 7.1A), or one of the target letters together with non-target letters 'H', 'K', 'M' and 'Z' (high load letter strings) (see Fig. 7.1B). Displays containing either high or low load letter strings were presented equally frequently and in random order. In half of the displays target letter was 'N', and in the other half ‘X’, respectively. In the high perceptual load displays each target letter was presented as first, second, third, and so on. Multiple randomized sequences for the positions of non-target letters were created, so subjects were not able to identify the target letter (or the position of it) based on the positions of the non-target letters.

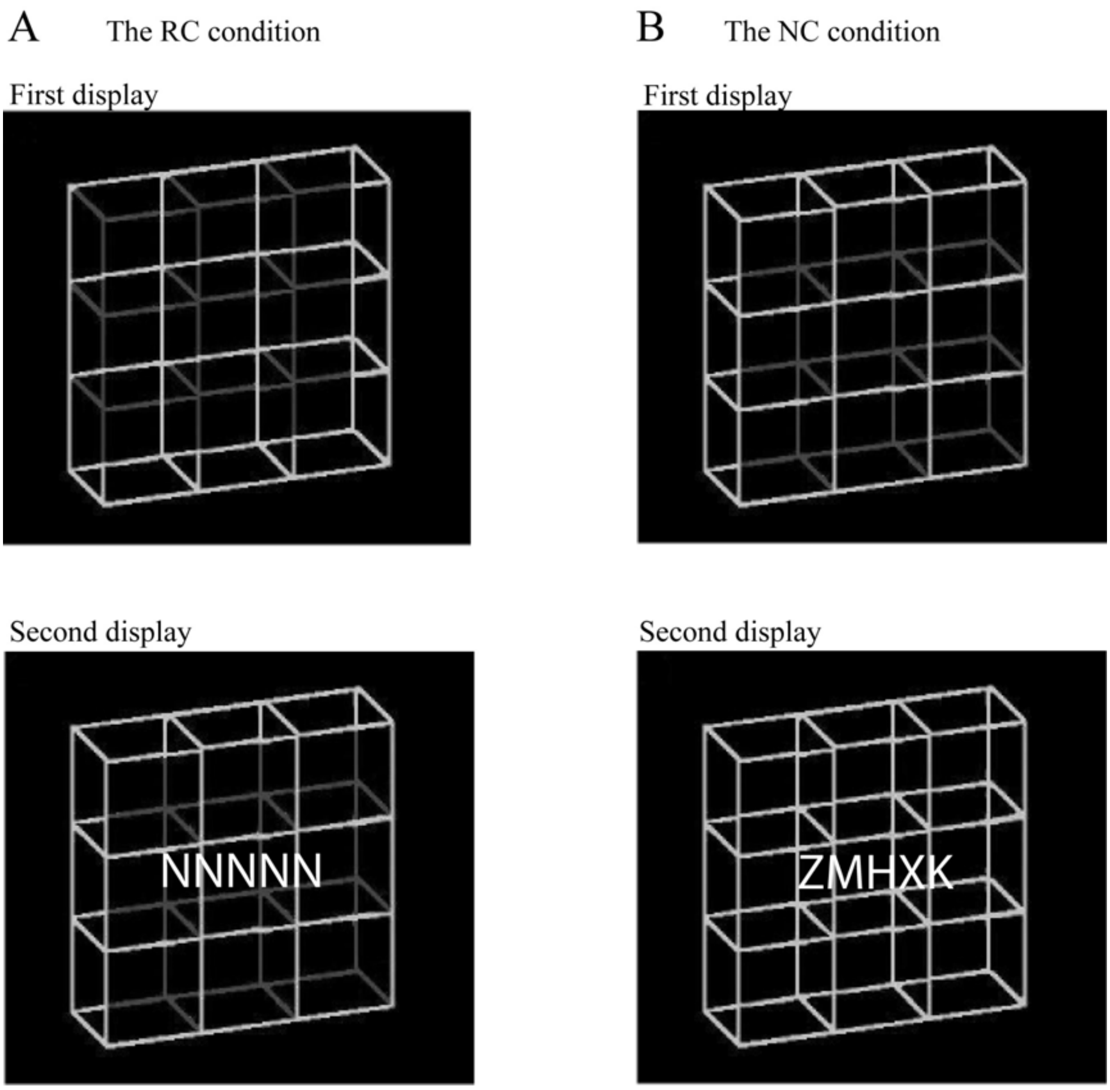


Figure 7.1 Examples of stimulus displays. A: the real change condition (presented change) and perceptual load is low (target letter – N). B: the Necker change condition (possible perceptual change) and perceptual load is high (target letter – X). Note that letter strings were actually presented in red colour.

In order to avoid afterimages and trivial local cues, the position of the lattice between the first and second display in each trial was randomly jittered by small changes (about ± 0.3°).

7.3. Procedure

Before the experiment, a Necker lattice stimulus was shown to each of the participants. If an observer was initially unable to perceive either one of the two possible orientations of the figure, the experimenter helped him, until the participant could easily perceive the ambiguity of the stimulus.

At first, every person performed a small practice block of 20 trials (with only 4 letters in the string) in order to get familiar with the task. Afterwards, each participant performed a separate practice block for the NC and separate block for the RC conditions (each consisting of 60 trials). The practice trials helped the observers to get used to the general requirements of the task: timing of stimulus presentations, the importance of fixating, and the performance of the task (i.e., detection of the change/no-change and estimation of the target letter). The participants were asked to fixate their gaze on the central fixation cross (when available), or letter strings, and not to move their eyes within trials. Eye movements and blinks were monitored with the help of continuous EOG recording.

The beginning of each trial was indicated by the fixation cross appearing for 1000 ms. After it, the first display (containing an unambiguous lattice) was presented for 200 ms, followed by a fixation cross for 200 ms, and subsequently by the second display (ambiguous or unambiguous depending on the block) for 400 ms (Fig 7.2). Based on the data of pilot experimentations it was decided to keep the display durations quite short in comparison to other studies (e.g., Kornmeier and Bach, 2004; Pitts et al. 2007; Qiu et al. 2009), as prolonged presentation of the second display would simplify the task of high perceptual load.

The unambiguous lattice was presented in the first display of both the RC and the NC conditions. This design was chosen with an aim to facilitate the initiation of the perceptual reversals, as it was a hard task for observers to perceive reversals under the influence of presented perceptual loads. Another reason for this methodological arrangement was an aim to keep identical stimulus displays between both conditions. There were two stimulus configuration possibilities for the first display as an unambiguous lattice in ‘up’ or ‘down’ orientation was presented.

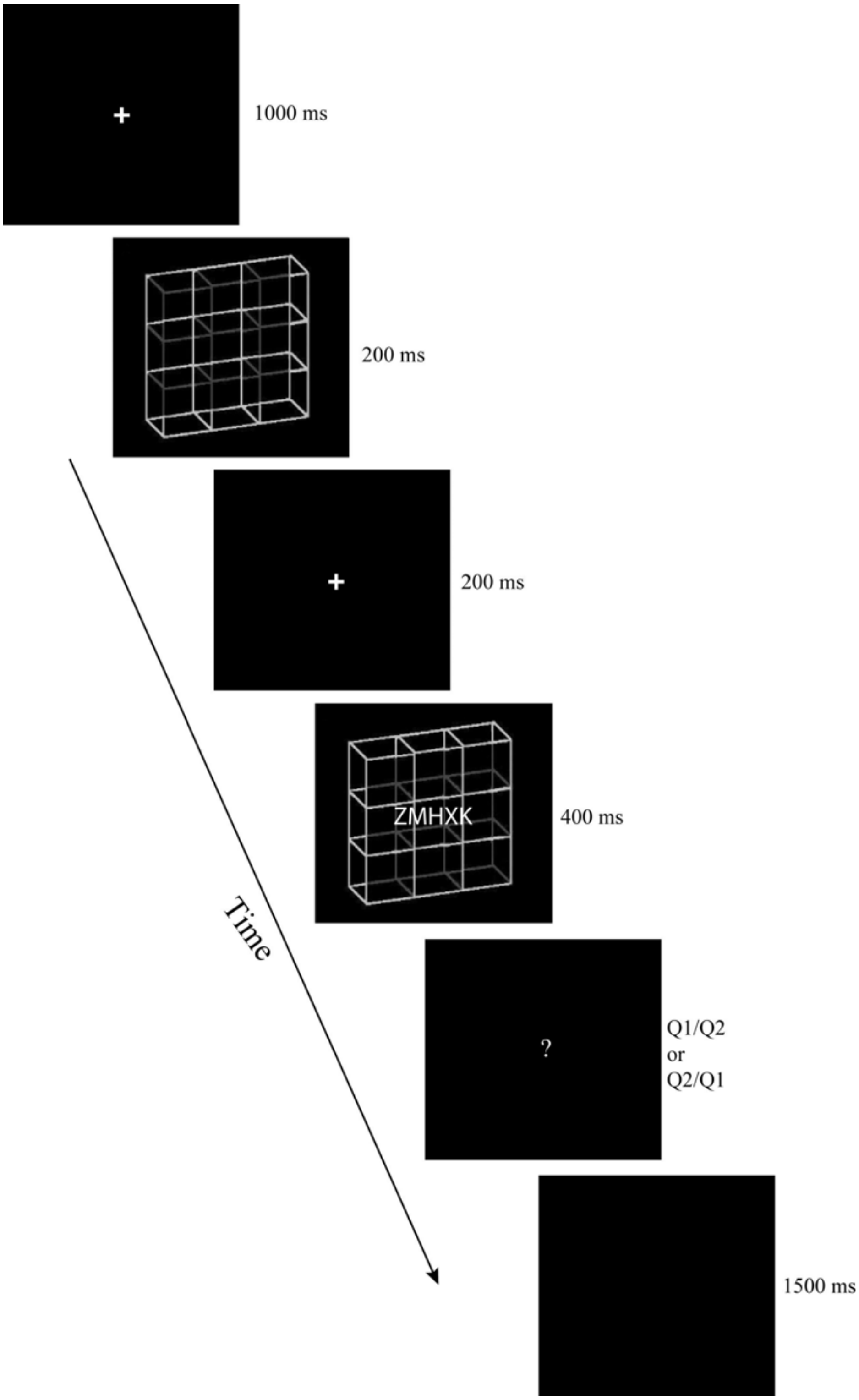


Figure 7.2 An illustration of a single experimental trial in the RC condition.

In the second display of RC condition an unambiguous lattice (with five centrally located identical or different letters) was presented. The observers could see whether the lattice changed or didn't change its' orientation.

In the second display of the NC condition a Necker lattice (with five centrally located identical or different letters) was presented. The observers could perceive Necker lattice in the same or different orientation as compared to unambiguous lattice from the first display.

After the second display, a blank screen was presented, and the participant had to provide their answers. The participants were encouraged to be as fast and accurate as possible. The inter-trial interval, which started directly after the observer's second response, and lasted till beginning of the next trial, was 1500 ms (Fig 7.2).

The participants compared the orientations of the stimulus in the second display with that of the first one. They were instructed to press 'change' button when they saw a change of orientation in the lattice, or 'no-change' button if they didn't see a change of orientation in the stimulus. They also had to press appropriate buttons depending if they saw 'N' in the letter string, and another button if they saw 'X'. Half of the subjects performed the first part of the experiment (i.e., one RC and one NC block) first responding about the 'change/no-change' and after that identified target letter, and in the second part they first provided answer for the target letter ('X or N'), and then replied about perceived changes/no-changes. For the other half of the participants, this order was reversed. The participants were asked not to respond, when they did not perceive any change and let perceptual reversals to occur naturally. It was stressed that they should press a button only when they actually saw a change, and guessing was not allowed. As to response to another question, if the participant missed the target letter, he/she had to guess.

RC condition consisted of 240 trials and NC condition consisted of 320 trials in total. Each of the two conditions was divided into two blocks of trials and this resulted in the four stimulus blocks presented to each participant. In the middle of experiment a longer break (approx. 10 min) was provided, and shorter breaks (about 2-3 min) were provided between the stimulus blocks. A complete experiment with one subject lasted approximately two hours.

7.4. Electrophysiological recordings and analysis

This section, except for the part described below, is identical to the 'Electrophysiological recordings and analysis' section of Experiment I (p. 36).

ERPs were averaged separately for different types of change (change, no-change) and load (high, low) in the RC and NC conditions. Mean amplitudes were analysed in the P1 (110–140 ms), N1 (140–180 ms), P2 (200–240 ms), N2 (240–280 ms), and P3 (400–700 ms) time windows, beginning from the onset of the second stimulus display.

Reversal Positivity (early positive ERP enhancement related to perceptual reversals) (Kornmeier and Bach, 2005) is usually observed as enhanced positivity in response to perceptual reversals about 100-160 ms after the onset of the second display, so that it might overlap with P1 and N1 waveforms. Reversal Negativity (early negative ERP enhancement related to perceptual reversals) (Kornmeier and Bach, 2004) is ordinarily observed as enhanced negativity in response to perceptual reversals about 200-300 ms after the onset of the second display, so that it might overlap with P2 and N2 waveforms.

8. RESULTS AND DISCUSSION

8.1. Behavioural performance

2 × 2 ANOVA with the factors Response succession (first task, second task) and Load (high, low) was performed on the responses of the change detection and perceptual load tasks for the RC and the NC conditions separately.

8.1.1. Change detection

In the RC condition, under low perceptual load, changes were detected more accurately in comparison to change detection under high perceptual load ($F(1,17)=40.18$; $p<0.0001$). Significant Load × Response succession ($F(1,17)=6.06$; $p<0.03$) interaction was also found. Subsequent analyses revealed that under high perceptual load, when change detection response was assigned first, the number of correct responses was significantly higher, in comparison to the condition when this response was assigned second ($F(1,17)=5.47$; $p<0.04$).

No significant main effects for changes detected under high or low perceptual load, succession of responses, or interactions of these values were observed in the NC condition.

8.1.2. Letter detection

In both the RC ($F(1,17)=54.57$; $p<0.0001$) and the NC ($F(1,17)=44.42$; $p<0.0001$) conditions, the numbers of correct letter responses were significantly higher under low perceptual load in comparison to that of under high perceptual load.

In the RC condition, main effect of Response succession was also revealed, as participants tend to provide more correct answers in response to load task when it was assigned as first, than it was assigned as second ($F(1,17)=14.46$; $p<0.002$). Significant Load × Response succession

($F(1,17)=9.64$; $p<0.007$) interaction was also found. Subsequent analyses revealed that under high perceptual load the number of correct responses was significantly higher when response to load task was assigned as first, than it was assigned as second ($F(1,17)=15.26$; $p<0.002$).

8.2. Electrophysiological data

In the analyses of ERPs only significant effects or interactions involving Response (change, no-change), or Load (high, low) factors, were reported. At least 25 artefact-free trials per configuration of Response and Load were required for a participant's data to be included in the analyses.

The variability of the mean amplitudes was estimated by a 2 × 4 × 2 × 2 × 2 repeated measures ANOVA with the factors Condition (RC, NC), Area (central, parietal, occipital and temporal electrodes), Hemisphere (left, right), Response (change, no-change) and Load (high, low). ERPs in the RC condition are represented in Figures 8.1 and 8.2 and ERPs in the NC condition are depicted in Figures 8.3 and 8.4.

P1 (110-140 ms).

In this time window significant main effect for Response ($F(1,17)=5.35$; $p<0.04$) was revealed, indicating that ERPs on change trials were less negative than on no-change trials. Main effect for Load ($F(1,17)=5.14$; $p<0.04$) was obtained, showing that P1 amplitudes in response to high load trials were significantly more negative in comparison to those in response to low load trials. Significant Area × Response ($F(3,51)=8.11$; $p<0.006$), Area × Load ($F(3,51)=3.99$; $p<0.05$) and Condition × Hemisphere × Load ($F(1,17)=5.60$; $p<0.04$) interactions were found and were further analysed by separate Condition (RC, NC) × Hemisphere (left, right) × Response (change, no-change) × Load (high, low) ANOVAs on each area individually.

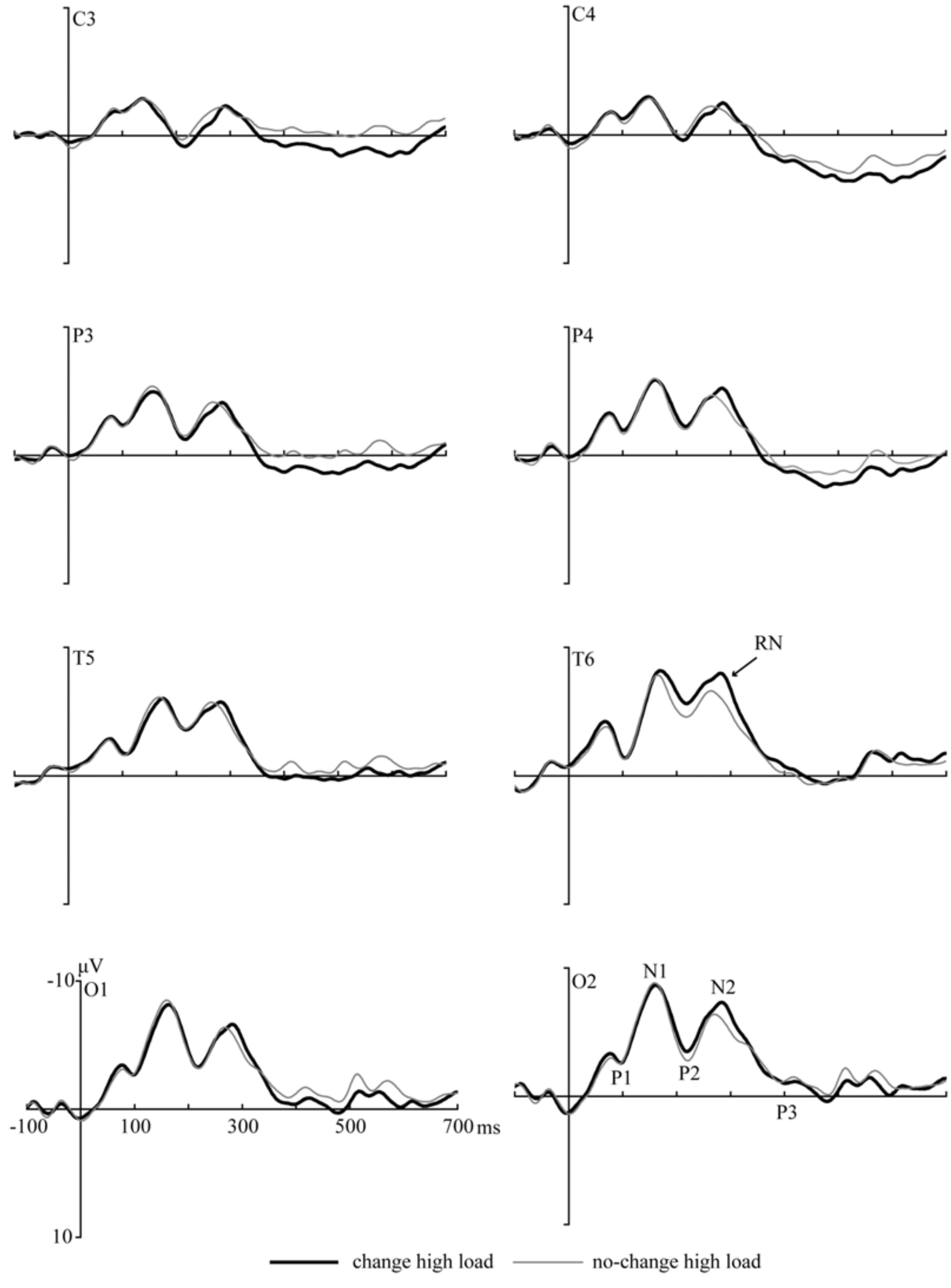


Figure 8.1 Grand-average ERPs in response to the second stimulus display on trials where participants reported seeing a real change (black lines), or seeing no-change (grey lines) while simultaneously performing the task of high perceptual load. During P2 time window a significant difference between change and no-change (RN) was observed only in temporal right hemisphere electrode site, and during N2 time window it was also observed in right hemisphere occipital electrode site (N=18).

Significant effects for Response were found only for occipital ($F(1,17)=8.71$; $p<0.01$) and temporal ($F(1,17)=6.88$; $p<0.02$) electrode sites: indicating that P1 amplitudes in response to changes were significantly less negative than those in response to no-changes.

Significant main effects for Load were found only for central ($F(1,17)=11.36$; $p<0.005$) and parietal ($F(1,17)=5.71$; $p<0.03$) areas: mean amplitudes in response to high perceptual load task were significantly more negative than those in response to low load.

Significant Condition × Hemisphere × Load interactions were obtained only for parietal ($F(1,17)=8.36$; $p<0.02$) and temporal ($F(1,17)=5.15$; $p<0.04$) areas, which were further analysed, but no more significant Response or Load effects were obtained.

N1 (140-180 ms).

Significant Condition × Area × Hemisphere × Response ($F(3,51)=4.55$; $p<0.03$) and Condition × Hemisphere × Response ($F(1,17)=6.04$; $p<0.03$) interactions were found, but further analyses did not reveal any significant Response or Load effects.

P2 (200-240 ms).

Significant Area × Response ($F(3,51)=5.07$; $p<0.03$), Condition × Area × Response ($F(3,51)=6.15$; $p<0.02$), Hemisphere × Response ($F(1,17)=5.47$; $p<0.04$), Condition × Hemisphere × Response ($F(1,17)=5.00$; $p<0.04$), Area × Hemisphere × Response ($F(3,51)= 7.86$; $p<0.002$) and Condition × Area × Hemisphere × Response ($F(3,51)=7.99$; $p<0.002$) interactions were observed. For further analyses of these interactions, separate Area (central, parietal, occipital and temporal) × Hemisphere (left, right) × Response (change, no-change) × Load (high, low) ANOVAs were performed on each of the conditions individually.

The RC condition. Significant Area × Response ($F(3,51)=11.30$; $p<0.02$), Hemisphere × Response ($F(1,17)=11.65$; $p<0.004$) and Area × Hemisphere × Response ($F(3,51)= 12.99$; $p<0.0001$) interactions were observed. These interactions were further analysed by separate Hemisphere (left, right) × Response (change, no-change) × Load (high, low) ANOVAs on each area individually.

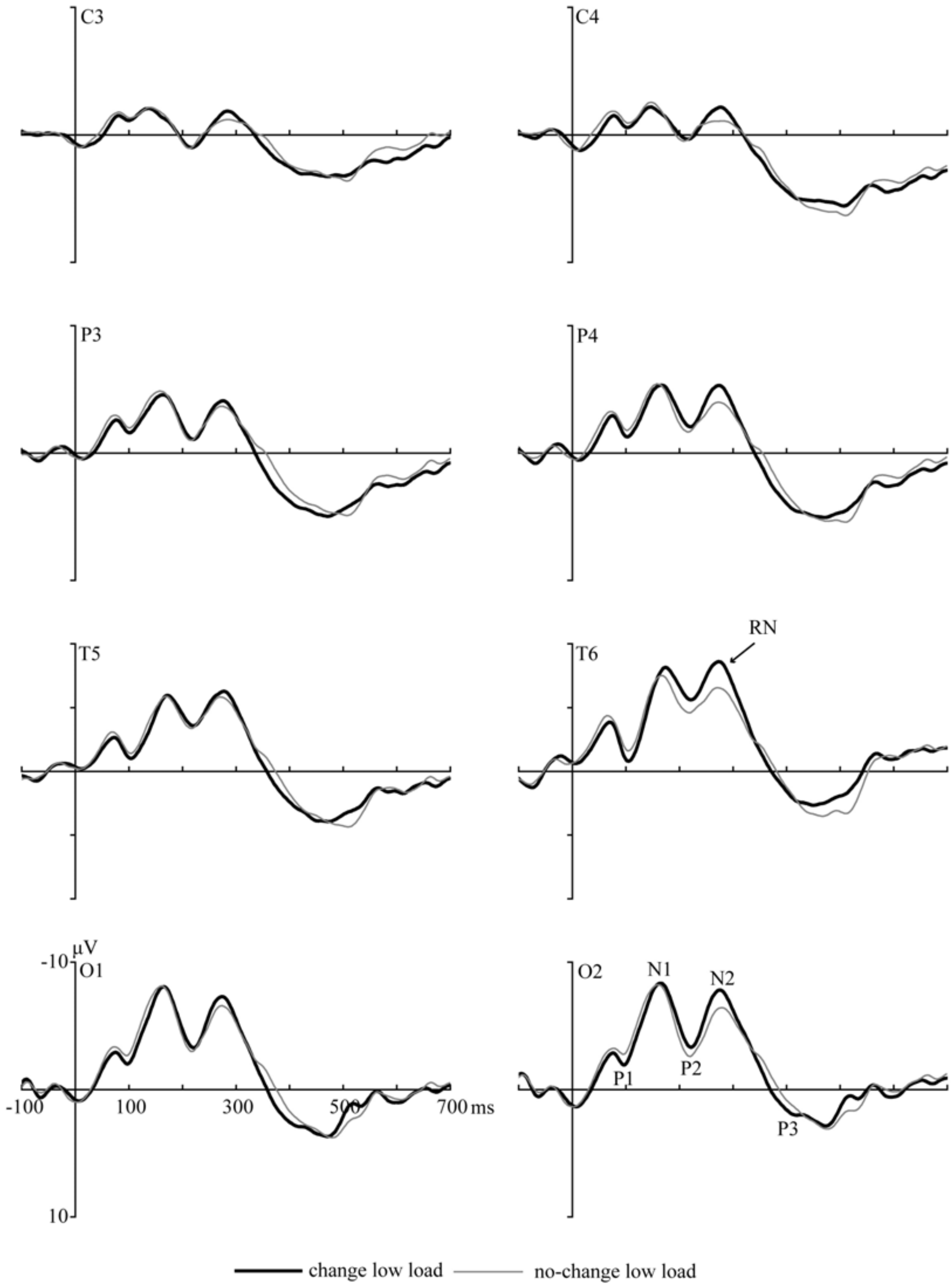


Figure 8.2 Grand-average ERPs in response to the second stimulus display on trials where participants reported seeing a real change (black lines), or seeing no-change (grey lines) while simultaneously performing the task of low perceptual load. During N2 time window a significant difference between change and no-change (RN) was observed only in temporal and occipital right hemisphere electrode sites (N=18).

Separate analyses of the areas showed significant Hemisphere × Response interactions over parietal ($F(1,17)=7.97$; $p<0.02$), occipital ($F(1,17)=13.69$; $p<0.003$) and temporal ($F(1,17)=21.01$; $p<0.0001$) electrode sites. These interactions were subsequently analysed by separate Response (change, no-change) × Load (high, low) ANOVAs on each electrode site individually.

Significant effect for Response was found only for right hemisphere temporal electrode ($F(1,17)=6.02$; $p<0.03$). Mean amplitudes were significantly more negative in response to change compared to those in response to no-change.

The NC condition. In this condition no significant Response, or Load related effects, or interactions were found.

N2 (240-280 ms).

In this time window, significant Condition × Area × Response ($F(3,51)=7.49$; $p<0.007$), Hemisphere × Response ($F(1,17)=12.23$; $p<0.004$), Condition × Hemisphere × Response ($F(1,17)=6.74$; $p<0.02$), Area × Hemisphere × Response ($F(3,51)=9.29$; $p<0.002$), Condition × Area × Hemisphere × Response ($F(3,51)=6.63$; $p<0.004$), Area × Load ($F(3,51)=13.04$; $p<0.002$) and Condition × Area × Response × Load ($F(3,51)=4.54$; $p<0.03$) interactions were found. These interactions were further analysed by separate Area (central, parietal, occipital and temporal) × Hemisphere (left, right) × Response (change, no change) × Load (high, low) ANOVAs on each of the two conditions individually.

The RC condition. In this condition, significant Area × Response ($F(3,51)=5.40$; $p<0.03$), Hemisphere × Response ($F(1,17)=19.01$; $p<0.0001$), Area × Hemisphere × Response ($F(3,51)=12.19$; $p<0.0001$) and Area × Load ($F(3,51)=5.73$; $p<0.03$) interactions were obtained. These interactions were further analysed by separate Hemisphere (left, right) × Response (change, no-change) × Load (high, low) ANOVAs on each area individually.

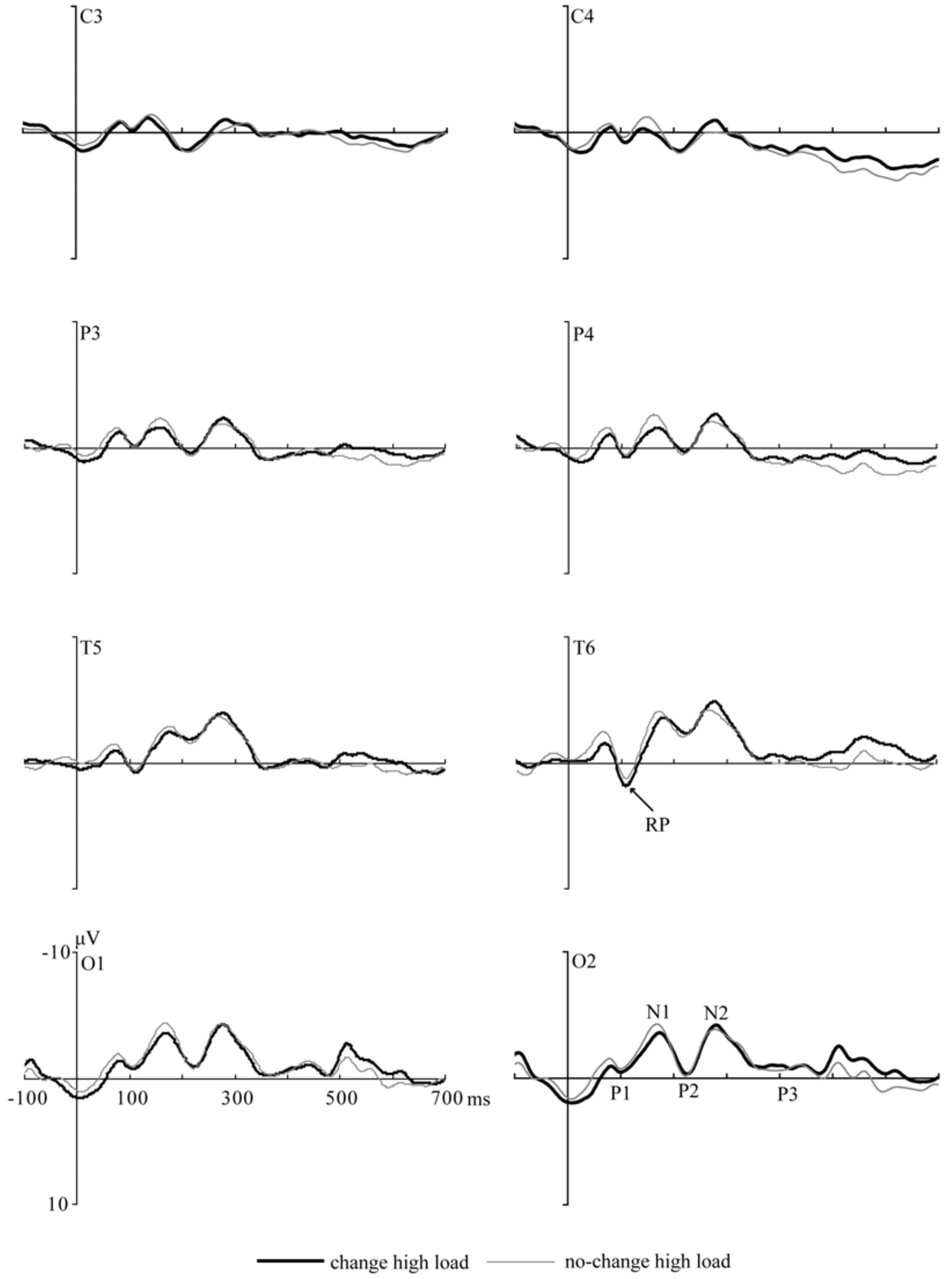


Figure 8.3 Grand-average ERPs in response to the second stimulus display on trials where participants reported seeing a perceptual change (black lines), or seeing no-change (grey lines) while simultaneously performing the task of high perceptual load. In the P1 time window, Reversal Positivity (RP) was obtained (N=18).

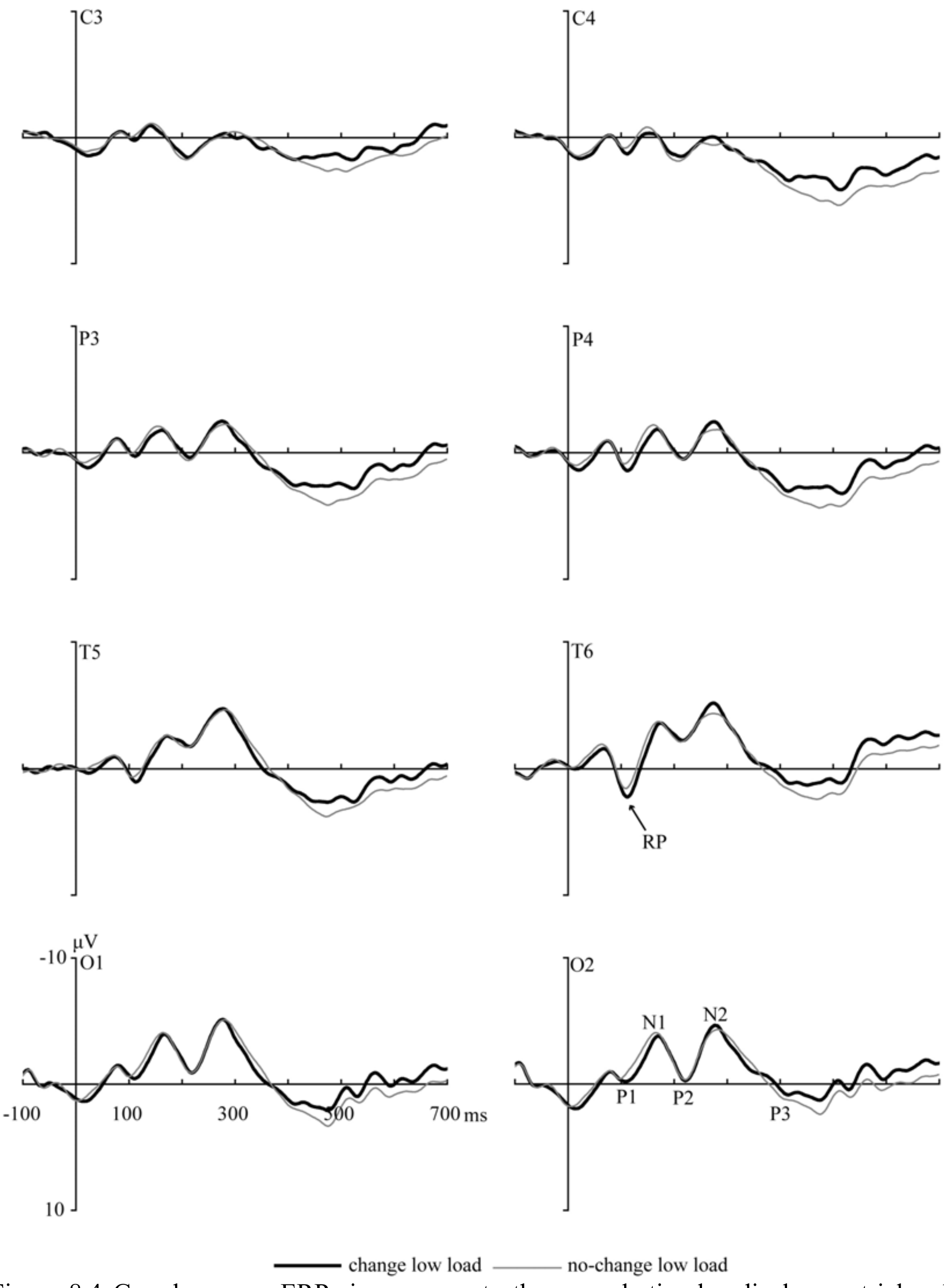


Figure 8.4 Grand-average ERPs in response to the second stimulus display on trials where participants reported seeing a perceptual change (black lines), or seeing no-change (grey lines) while simultaneously performing the task of low perceptual load. In the P1 time window, Reversal Positivity (RP) was obtained (N=18).

Significant effect for Response ($F(1,17)=4.72$; $p<0.04$) was detected over temporal areas, showing that ERPs in response to change trials were more negative than in response to no-change trials. Significant Hemisphere × Response interactions were obtained over parietal ($F(1,17)=16.95$; $p<0.002$), occipital ($F(1,17)=13.02$; $p<0.003$) and temporal ($F(1,17)=28.84$; $p<0.0001$) areas. These interactions were subsequently analysed by separate Response (change, no-change) × Load (high, low) ANOVAs on each electrode site individually.

Subsequent analyses showed main effects for Response only for right hemisphere occipital ($F(1,17)=4.75$; $p<0.05$) and temporal ($F(1,17)=13.10$; $p<0.003$) electrode sites, indicating that ERPs to changes were significantly more negative than those to no-changes.

The NC condition. In this condition no significant Response, or Load related effects, or interactions were found.

P3 (400-700 ms).

In this time window, significant effect for Load ($F(1,17)=15.63$; $p<0.002$) was detected, when ERPs in response to low load task were significantly more positive than those in response to high load task. Significant Condition × Area × Response ($F(3,51)=6.47$; $p<0.01$), Hemisphere × Response ($F(1,17)=6.80$; $p<0.02$), Area × Hemisphere × Response ($F(3,51)=3.59$; $p<0.04$), Hemisphere × Response × Load ($F(1,17)=9.88$; $p<0.007$), Area × Hemisphere × Response × Load ($F(3,51)=9.98$; $p<0.04$), Condition × Load ($F(1,17)=4.80$; $p<0.05$), Hemisphere × Load ($F(1,17)=28.10$; $p<0.0001$) and Area × Hemisphere × Load ($F(3,51)=37.65$; $p<0.0001$) interactions were observed. These interactions were subsequently analysed by separate Area (central, parietal, occipital and temporal) × Hemisphere (left, right) × Response (change, no-change) × Load (high, low) ANOVAs on each condition individually.

The RC condition. Significant effect for Load ($F(1,17)=22.57$; $p<0.0001$) was revealed: mean ERPs to low load task were significantly more positive than those to high load task. Significant Area × Response ($F(3,51)=5.97$; $p<0.02$), Hemisphere × Response ($F(1,17)=5.17$; $p<0.04$), Hemisphere × Load ($F(1,17)=21.93$; $p<0.0001$) and Area × Hemisphere ×

Load ($F(3,51)=27.92$; $p<0.04$) interactions were also obtained which were further analysed by Hemisphere (left, right) × Response (change, no-change) × Load (high, low) ANOVAs separately on each area.

Significant effects for Load were observed over all areas: central ($F(1,17)=21.93$; $p<0.0001$), parietal ($F(1,17)=26.16$; $p<0.0001$), occipital ($F(1,17)=15.31$; $p<0.002$) and temporal ($F(1,17)=19.26$; $p<0.0001$): mean amplitudes in response to low load task were significantly more positive in comparison to those elicited in response to high load task. Significant interactions were observed over all reported areas. Over central ($F(1,17)=5.94$; $p<0.03$) and temporal ($F(1,17)=5.96$; $p<0.03$) areas significant Hemisphere × Response interactions were obtained. Over parietal ($F(1,17)=11.08$; $p<0.005$) occipital ($F(1,17)=17.96$; $p<0.002$) and temporal ($F(1,17)=52.03$; $p<0.0001$) areas Hemisphere × Load interactions were observed. Over occipital ($F(1,17)=4.87$; $p<0.05$) and temporal ($F(1,17)=4.55$; $p<0.05$) areas significant Hemisphere × Response × Load interactions were also revealed. All these interactions were subsequently analysed by Response (change, no-change) × Load (high, low) ANOVAs on each electrode site separately.

Significant effect for Response ($F(1,17)=6.10$; $p<0.03$) was obtained only over left hemisphere central electrode site: mean amplitudes in response to change were significantly more positive than those in response to no-change. Significant effects for Load were observed over all observed electrode sites (all p-values < 0.04): mean amplitudes in response to low load task were significantly more positive in comparison to those elicited in response to high load task.

The NC condition. Significant Hemisphere × Load ($F(1,17)=25.36$; $p<0.0001$) and Area × Hemisphere × Load ($F(3,51)=29.25$; $p<0.0001$) interactions were obtained which were further analysed by separate Hemisphere (left, right) × Response (change, no-change) × Load (high, low) ANOVAs on each area individually.

Significant effect for Load was observed over parietal areas only ($F(1,17)=6.19$; $p<0.03$), mean amplitudes in response to low perceptual load task were significantly more positive than those is response to high perceptual load task. Significant Hemisphere × Load interactions were found over parietal ($F(1,17)=20.87$; $p<0.0001$), occipital ($F(1,17)=34.38$; $p<0.0001$) and temporal ($F(1,17)=51.06$; $p<0.0001$) areas. Area × Hemisphere × Load interactions were obtained only for parietal ($F(3,51)=5.02$; $p<0.04$) and occipital ($F(3,51)=12.03$; $p<0.004$) areas. These interactions were further analysed by separate Response (change, no-change) × Load (high, low) ANOVAs for each electrode site individually. Significant effects for Load were obtained only over central electrode site of the right hemisphere and over parietal, occipital and temporal electrode sites of the left hemisphere (all p-values <0.04), mean amplitudes in response to low load task were significantly more positive than amplitudes in response to high load task.

8.3. Comparison of data distributed according to task sequence

Additional repeated measures 2 × 4 × 2 × 2 × 2 ANOVAs with factors Response succession (change as first task, change as second task) × Area (central, parietal, occipital and temporal electrodes) × Hemisphere (left and right) × Response (change, no-change) × Load (high, low) were conducted on the NC and RC conditions separately. Participant's data were included in ERP analyses, if at least 20 artefact-free single trials per change/response succession configuration were collected. Due to insufficient amount of correct trials, data of only 12 subjects (from 18) were analysed in the RC condition and data of only 9 subjects (from 18) were analysed in the NC condition.

The RC condition. Significant effect for Response ($F(1,11)=5.25$; $p<0.05$) was shown for activity of right hemisphere, during the P2 time window, when response to change task was assigned as second. Additional analyses showed significant effects for Response at occipital ($F(1,11)=6.95$; $p<0.03$) and temporal ($F(1,11)=7.31$; $p<0.03$) electrodes: mean amplitudes of change were significantly more negative than those of no-change.

Significant effect for Response ($F(1,11)=5.12$; $p<0.05$) was obtained over temporal areas in the N2 time window, when response to change task was assigned as second, showing that mean amplitudes of change were significantly more negative than those of no-change.

Analyses of the P3 time window revealed significant effect for Response ($F(1,11)=5.05$; $p<0.05$) over parietal areas: when response to change task was assigned as first, ERPs on change trials were more positive than those on no-change trials.

The NC condition. Significant Response related activity was revealed only in the P1 time window, that is, main effect for Response ($F(1,8)=9.41$; $p<0.02$) was found, indicating that ERPs on change trials were less negative than on no-change trials.

9. GENERAL DISCUSSION

Two studies were conducted in order to determine the possible relationship between Reversal Negativity (RN) and selective attention. One study was designed to test the hypotheses that RN might be an equivalent of N2 posterior contralateral (N2pc), or a subtype of Visual Awareness Negativity (VAN). In a second one, the hypothesis that RN might be susceptible to the amount of presented perceptual load was put into question.

In the first study, which examined the possible laterality of the RN, the RN was obtained, thus confirming the results of almost all previous ERP experiments related to perception of ambiguous stimuli (Kornmeier and Bach, 2004, 2005, Kornmeier et al., 2007; Pitts et al., 2007; Pitts et al., 2008; Britz et al., 2009, Qiu et al., 2009), except Kornmeier and Bach (2009). RN was obtained for both real and perceptual unilateral changes of the lattices, and the onset of RN elicited by the real change was approximately 50 ms earlier than that of Necker change elicited RN. This finding replicated the data obtained by other researchers (Kornmeier and Bach 2004; Kornmeier and Bach 2006) and it suggests longer processing of apparent Necker lattice reversals in comparison to perception of real changes. Interestingly, the data of bilateral changes for NC and RC conditions diverged in P2 and P3 time windows, as there was no RN obtained for RC and no Late Positivity obtained for NC. There is no explanation why RN of bilateral perceptual change is observed in P2 time window, but there is no difference between change and no-change conditions in the RC paradigm, as real change is subjectively more intense in comparison to perceptual change. Another difference from earlier studies is that usually RN is visible over occipital and parietal areas (Kornmeier and Bach, 2004; Kornmeier and Bach, 2005; Pitts et al. 2007; Pitts et al. 2008; Britz et al. 2009). Only when effects of different inter-stimulus intervals on the amplitude of RN were examined (Kornmeier et al., 2007) RN was additionally observed over central and even frontal electrodes. In the first experiment of this study RN was obtained not only over occipital and parietal but it extended to central and even frontal areas. There are no considerable explanations why the distribution of RN over the scalp is so large, but there are several possible factors that might influence this finding:

(a) extended distribution over the scalp could be related to processing of two simultaneously presented lattices, as there are no previous ERP (or other brain imaging) studies involving the common change of two lattices;

(b) it might be related to the selection of electrodes of other researchers, because in some studies the data only from occipital and parietal electrodes were analysed (Kornmeier and Bach 2004; Pitts et al., 2007);

(c) the use of unambiguous – ambiguous lattice presentation mode in a single experimental trial;

(d) relatively short stimuli presentation durations, that is, 200 and 400 ms in comparison to 800 ms (or longer) presentation durations of other studies (Kornmeier and Bach 2004; Kornmeier and Bach 2005; Pitts et al., 2007; Pitts et al., 2008; Britz et al., 2009; Qiu et al., 2009).

Otherwise, having in mind the polarity, time window and distribution of ERPs according to the provided response (change vs. no-change) there is no reason to consider that the obtained negative difference is not RN.

However, in the second experiment, examining the effect of perceptual load on the perception of ambiguous figures, the RN was completely suppressed. In the time windows from N1 to N2, (approx. 140-320 ms post-stimulus) where RN might possibly be obtained (Kornmeier and Bach, 2004, 2005, Kornmeier et al., 2007; Pitts et al., 2007; Pitts et al., 2008; Britz et al., 2009, Qiu et al., 2009) no significant differences between perceptual change and no-change were observed. This effect was detected independently of the magnitude of a presented perceptual load. In the RC condition, RN was restricted to right hemisphere temporal electrode site in the P2 time window (200-240 ms) and extended to right hemisphere occipital electrode site in the N2 time window (240-280 ms). But no significant differences between RNs, with respect to high or low perceptual load tasks, were obtained. However, the obtained laterality of the real change elicited RN might be related to data obtained by Britz et al. (2009). They used high-density EEG and found activity in a region of right inferior parietal cortex approximately 50 ms before perceived reversal of ambiguous Necker lattice. Similar unilateral distribution of RN was obtained by Pitts et al. (2008), when observers were asked to voluntarily modulate the perception of ambiguous figures (sustained attention task). Their data revealed lateralization of RN to the right posterior scalp locations. Comparable activities, contralateral to attended spatial locations, occurring within the superior parietal lobule and intraparietal sulcus were observed with the help of fMRI when participants voluntarily changed the orientations of the Necker cube (Slotnick and Yantis, 2005).

Reversal Positivity (RP), that is, an enhanced positive potential in response to perceived change in comparison to no-change, observed in some of the previous studies (Kornmeier and Bach, 2005; Kornmeier et al., 2007, Britz et al, 2009; Pitts et al., 2007; Qiu et al., 2009), was not obtained in the first experiment. But mean amplitudes over the frontal areas in response to no-changes were significantly less negative than those in response to left changes in the time window from 100-150 ms post-stimulus. This result might be related to the frontal N1 enhancements obtained by Pitts et al. (2007) around 175 ms post-stimulus and Qiu et al. (2009) around 80-120 ms post-stimulus. Researchers suggested that this component might signify the operation of early spatial selection processes in visual attention. Nevertheless, RP was found in the second experiment. However, this effect was present independently of the magnitude of the presented perceptual load. This finding may provide support for the theory of Pitts et al. (2008) claiming that selective attention has an impact on the perception of ambiguous stimuli. But no significant differences between RPs, with respect to high or low perceptual load tasks, were obtained.

In the P1 (110-140 ms) and P3 (400-700 ms) time windows, significant effects for Load were also revealed: mean amplitudes in response to low perceptual load task were significantly less negative/more positive in comparison to the amplitudes elicited in response to high perceptual load task.

This finding replicated the data obtained by other researchers (Handy et al., 2001) and shows that there was an impact of perceptual load on the obtained ERPs. This result shows that manipulation of selective attention via perceptual load was successful; therefore, it is not reasonable to claim that low perceptual load task was also too difficult for observers (or, alternatively, that high load task was too easy) and use it as an explanation why RN in all perceptual change conditions was completely suppressed.

As to the data related to Late Positivity (LP), there is a discrepancy with most of the previous research that found late positive correlate of perceptual reversals (Basar-Eroglu et al., 1993; O'Donnell et al., 1988; Strüber et al., 2001; Kornmeier and Bach, 2004, 2005; Kornmeier et al. 2007; Pitts et al., 2007; Pitts et al., 2008; Britz et al., 2009; Qiu et al. 2009). In both experiments, the LP component was observed only for the reversal of unambiguous lattices (real change paradigm): in the first study, LP was observed over all analysed areas except frontal (i.e., central, parietal, occipital and temporal) and in the second study it was visible only over parietal areas independently of the magnitude of the presented load, and only when response to change task was assigned as first. Moreover, Kornmeier and Bach (2009) also found LP in response only to reversals of unambiguous lattice. It is possible that the LP is not a necessary correlate of perceptual reversal, as it might be related to the specific processes involved in updating of visual information in the short term memory that are occurring after the perceptual change (Pitts et al., 2008).

As the first experiment was designed specifically to measure the N2pc, it included unilateral reversals visible when two stimuli are presented on the screen. N2pc component was obtained only in one condition, that is, for real changes observed on the left side (activation of the right hemisphere). Similar result was observed by Eimer (1996) with word targets varying in their semantic content. Eimer (1996) suggested that top-down mechanisms susceptible to task-related characteristics might have caused such a unilateral feature of N2pc. N2pc was not obtained for the reversals of Necker lattices, but observers perceived changes of the ambiguous stimuli as proved by RN which was elicited in response to the reversals of the lattices. Furthermore, N2pc and RN revealed different scalp distributions, as RN was elicited over occipital, temporal, parietal, central and frontal electrodes, while N2pc was restricted to occipital and temporal electrodes. Overall, the obtained results imply that RN and N2pc do not reveal the activity of the same mechanism. As to behavioural data, no difference was observed between left and right changes of the RC condition, although there was an N2pc visible for left changes, suggesting that attention was allocated especially to stimuli on the left. Therefore, the difference indicated by N2pc did not have behaviourally obtainable effects on the data of the real changes.

In addition, Brisson and Jolicoeur (2007) and Brisson et al. (2007) tried to answer the question whether N2pc reflects the impact of the top-down processes on the activity of bottom-up processes. In their first study, Brisson and Jolicoeur (2007) presented the stimuli for three different durations (i.e., 50, 200 or 350 ms) and hypothesized that if N2pc reflects relationship between top-down and bottom-up perceptual processes, the amplitude of N2pc should be largest for the longest stimulus duration, as this duration would provide a longer interval of time during which sensory areas could be modulated by attentional mechanisms in comparison to shorter stimulus intervals. On the contrary, their results revealed that N2pc obtained for the longest stimulus duration had the smallest amplitude in comparison to both shorter durations. In the follow-up study, Brisson et al. (2007) modified the intensity of the stimulus and hypothesized that if N2pc indicates the interaction of bottom-up and top-down processes, its amplitude will increase with larger stimulus intensity. Nevertheless their data revealed that amplitude of N2pc and stimulus intensity bears no relationship. This result could not be determined by an insufficient bottom-up modulation, as larger amplitudes in response to more intensive stimulus around the P1 time window (110-130 ms post-stimulus) were obtained. The results of these experiments might be in some way related to the research findings of bistable perception exploring studies, as there is increasing evidence on the joint activity of both bottom-up and top-down perceptual processes in the perception of ambiguous figures (Long and Toppino, 2004; Long and Moran, 2007; Mitroff et al., 2006), so this might be related to the fact that perceptual reversals do not elicit N2pc.

Since the first experiment included not only unilateral, but also bilateral changes of the presented stimuli, it was possible to compare the RNs elicited by unilateral and bilateral change conditions. If RN was an electrophysiological correlate of changes in subjective visual awareness, than RN induced by bilateral reversals would differ from RN induced by unilateral changes, as perceptual experience of bilateral reversals is experienced as subjectively more intense (Long et al., 1983). However, the results did not support this prediction, as the difference between bilateral and unilateral reversals of Necker lattices was negligible, and RN was not elicited by exogenous bilateral reversals. Since real changes are subjectively stronger than perceptual changes of the Necker lattices, there are no reasons to presume that perceptual changes would be more pronounced than real changes. So no direct relationship was found between the magnitude of perceptual change and the obtained RN. Also the fact, that observers saw bilateral real reversals of unambiguous stimuli (as only data with correct answers were included in the analyses), but this finding is not reflected in their ERPs, suggests that changes in the contents of visual awareness do not correlate with RN. The results suggest that RN is not a subtype of VAN.

The main aim of the current studies was to investigate the cognitive interpretation of RN through estimation of the possible role of selective attention in the perception of ambiguous stimuli. However, the data of both experiments suggest that RN is more likely a response specific to perceptual reversals of ambiguous figures, as it was not affected by different selective attention related tasks. In addition, the data also revealed that RN is not a subtype of VAN. It is highly likely that RN is neither directly related to selective attention, nor to visual awareness. Nevertheless, both attention and awareness are complex phenomena that are in some ways related to each other and current experiments cover only small aspects of them. Therefore, it is too early to claim that selective (or other subtypes of) attention is not operating in the perception of ambiguous figures, as N2pc and perceptual load are particular effects representing some part of the operation of the mechanisms related to selective attention. It is highly likely that experiments including different kind of attentional manipulations (i.e., attended vs. unattended displays; spatial-selective attention related tasks, etc.) might demonstrate effects of selective attention on perceptual reversals.

10. CONCLUSIONS

1. Perception of ambiguous figures is not directly modulated by selective attention, as Reversal Negativity, event-related potentials component reflecting the changes in the perceptual interpretation of the observed object, is not affected by selective attention related tasks.
2. Reversal Negativity and N2 posterior contralateral are not elicited by the same mechanism.
3. Reversal Negativity did not correlate in any direct manner with the number of changes in the content of visual awareness during perceptual reversals (Reversal Negativity is not a subtype of Visual Awareness Negativity).
4. A task of either high or low perceptual load, conducted simultaneously with task of the perceptual reversals, completely eliminates Reversal Negativity.
5. Reversal Positivity is an event-related potentials response dependent on attention, as it was not suppressed by perceptual load, but it does not necessarily depend on selective attention.
6. Late Positivity is not a direct correlate of perceptual reversal of ambiguous picture, as it is obtained only in the case of real change.
7. Reversal Negativity is neither directly related to mechanisms of selective attention, nor to those of visual awareness. Presumably it is a brain response typical for reversals of ambiguous figures.

11. REFERENCES

1. Adams P. A. & Haire M. (1958). Structural and Conceptual Factors in the Perception of Double-Cube Figures. *The American Journal of Psychology*. 71, 548–556.
2. Anllo-Vento L. & Hillyard S. A. (1996). Selective attention to the color and direction of moving stimuli: Electrophysiological correlates of hierarchical feature selection. *Perception & Psychophysics*. 58, 191–206.
3. Babich S. & Standing L. (1981) Satiation effects with reversible figures. Percept Mot Skills 52:2, 210.
4. Basar-Eroglu C., Strüber D., Stadler M. & Kruse E. (1993). Multistable visual perception induces a slow positive EEG wave. *International Journal of Neuroscience*. 73, 139–151.
5. Bisiach E., Ricci R., Lai E., De Tanti A. & Inzaghi M. G. (1999). Unilateral neglect and disambiguation of the Necker cube. *Brain*. 122, 131–140.
6. Brisson B. & Jolicoeur P. (2007). The N2pc component and stimulus duration. *Neuroreport*. 18, 1163–1166.
7. Brisson B., Robitaille N. & Jolicoeur P. (2007). Stimulus intensity affects the latency but not the amplitude of the N2pc. *Neuroreport*. 18, 1627–1630.
8. Britz J., Landis T. & Michel C. M. (2009). Right parietal brain activity precedes perceptual alternation of bistable stimuli. *Cerebral Cortex*. 19, 55–65.
9. Burton G. (2002). Successor states in a four-state ambiguous figure. *Psychonomic Bulletin & Review*. 9, 292–297.
10. Cohen L. (1959). Rate of apparent change of a Necker cube as a function of prior stimulation. *American Journal of Psychology*. 72, 327–344.

11. Corrozi C. B., Long G. M. & Toppino T. C. (1993) Fatigue-like effects in the cooperative mechanism revealed with side-by-side reversible figures. Bulletin of the Psychonomic Society 31:518–520.
12. Duncan J. (1980). The locus of interference in the perception of simultaneous stimuli. *Psychological Review*, *87*, 272–300
13. Eimer M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalography and clinical Neurophysiology* 99, 225–34.
14. Eimer M. & Mazza V. (2005). Electrophysiological correlates of change detection. *Psychophysiology,* 42, 328–342.
15. Flügel J. C. (1913) The influence of attention in illusions of reversible perspective. Br J Psychol 5, 357–397.
16. Girelli M. & Luck S. J. (1997). Are the same attentional mechanisms used to detect visual search targets defined by color, orientation and motion? *Journal of Cognitive Neuroscience.* 9, 238–253.
17. Girgus J. J., Rock I. & Egatz R. (1977). The effect of knowledge of reversibility on the reversibility of ambiguous figures. *Perception & Psychophysics*, 22, 550–556.
18. Gopnik A. & Rosati A. (2001). Duck or rabbit? Reversing ambiguous figures and understanding ambiguous interpretations. *Developmental Science.* 4, 175–183.
19. Handy T.C., Soltani M. & Mangun G. R. (2001). Perceptual load and visuocortical processing: event-related potentials reveal sensory-level selection. *Psychological Science.* 12, 213–218.
20. Heath H. A. & Orbach J. (1963). Reversibility of the Necker cube: IV. Responses of elderly people. *Perceptual and Motor Skills.* 17, 625–626.
21. Hillyard S. A. & Anllo-Vento L. (1998). Event-related brain potentials in the study of visual selective attention. *Proceedings of the National Academy of Sciences of the United States of America.* 95, 781–787.

22. Holt G. L. & Matson J. L. (1976). The effects of age on perceptual changes using two new perspectives of the Necker cube. *Bulletin of the Psychonomic Society.* 8, 4–6.
23. Hunt J. M. & Guilford J. P. (1933). Fluctuation of an ambiguous figure in dementia praecox and in manic-depressive patients. *Journal of Abnormal and Social Psychology.* 27, 443– 452.
24. Klemm W.R., Li T. H. & Hernandez J. L. (2000). Coherent EEG indicators of cognitive binding during ambiguous figure tasks. *Consciousness and Cognition.* 9, 66–85.
25. Koivisto M. & Revonsuo A. (2003). An ERP study of change detection, change blindness, and visual awareness. *Psychophysiology*, 40, 423–429.
26. Koivisto M. & Revonsuo A. (2007). Electrophysiological correlates of visual consciousness and selective attention. *Neuroreport*, 18, 753–756.
27. Koivisto M. & Revonsuo A. (2008). Comparison of event-related potentials in attentional blink and repetition blindness. *Brain Research*, 1189, 115–126.
28. Koivisto M., Revonsuo A. & Lehtonen M. (2006). Independence of visual awareness from the scope of attention: an electrophysiological study. *Cerebral Cortex* 16. 415–424.
29. Koivisto M., Revonsuo A. & Salminen N. (2005). Independence of visual awareness from attention at early processing stages. *Neuroreport*. 16, 817–821.
30. Koivisto M., Lähteenmäki M., Soerensen T.A., Vangkilde S., Overgaard M. & Revonsuo A. (2008). The earliest electrophysiological correlate of visual consciousness? *Brain and Cognition*. 66, 91–103.
31. Kornmeier J. & Bach M. (2004). Early neural activity in Necker-cube reversal: Evidence for low-level processing of a gestalt phenomenon. *Psychophysiology,* 41, 1–8.

32. Kornmeier J. & Bach M. (2005). The Necker cube – an ambiguous figure disambiguated in early visual processing. *Vision Research,* 45, 955–960.
33. Kornmeier J. & Bach M. (2006). Bistable perception – along the processing chain from ambiguous visual input to a stable perception. *International Journal of Psychophysiology*, 62, 345–349.
34. Kornmeier J. & Bach M. (2009). Object perception: when our brain is impressed but we do not notice it. *Journal of Vision, 9*, 1–10.
35. Kornmeier J., Ehm W., Bigalke H., & Bach M. (2007). Discontinuous presentation of ambiguous figures: How interstimulus-interval durations affect reversal dynamics and ERPs. *Psychophysiology,* 44, 552–560.
36. Lavie N. & Tsal Y. (1994). Perceptual load as a major determinant of the locus of selection in visual attention. *Perception & Psychophysics.* 56, 183–197.
37. Lavie N. (1995). Perceptual load as a necessary condition for selective attention. *Journal of Experimental Psychology: Human Perception and Performance.* 21, 451–468.
38. Lavie N. (2006). The role of perceptual load in visual awareness. *Brain Research,* 1080, 91–100.
39. Leopold D. A., Wilke M., Maier A. & Logothetis N. K. (2002). Stable perception of visually ambiguous patterns. *Nature Neuroscience.* 6, 605–609.
40. Leopold D. A. & Logothetis N. K. (1999) Multistable phenomena: changing views in perception. *Trends in Cognitive Sciences.* 3, 254–264.
41. Long G. M. & Moran C. (2007) How to keep a reversible figure from reversing: Teasing out top-down and bottom-up processes. *Perception,* 35, 431–45.
42. Long G. M. & Olszweski A. D. (1999) To reverse or not to reverse: When is an ambiguous figure not ambiguous? Am J Psychol, 112, 41–71.

43. Long G. M. & Toppino, T. C. (2004). Enduring Interest in Perceptual Ambiguity: Alternating Views of Reversible Figures. *Psychological Bulletin*, 130, 748–768.
44. Long G. M. & Toppino T. C. (1981). Multiple representations of the same reversible figure: Implications for cognitive decisional interpretations. *Perception*, 10, 231–234.
45. Long G. M., Toppino T. C. & Kostenbauder J. F. (1983). As the cube turns: Evidence for two processes in the perception of a dynamic reversible figure. *Perception & Psychophysics, 34,* 29–38.
46. Long G. M., Toppino T. C. & Mondin G. W. (1992) Prime time: Fatigue and set effects in the perception of reversible figures. *Perception and Psychophysics,* 52, 609–616.
47. Luck S. J. (2005). An introduction to the event-related potential technique. Cambridge, MA: MIT Press.
48. Maier A., Wilke M., Logothetis N. K. & Leopold D. A. (2003). Perception of temporally interleaved ambiguous patterns. *Current Biology.* 13, 1076–1085.
49. Meenan J. P. & Miller L. A. (1994). Perceptual flexibility after frontal or temporal lobectomy. *Neuropsychologia,* 32, 1145–1149.
50. Miller S. M., Liu G. B., Ngo T. T., Hooper G., Riek S., Carson R. G. & Pettigrew J. D. (2000). Interhemispheric switching mediates perceptual rivalry. *Current Biology.* 10, 383–392.
51. Mitroff S. R., Sobel D. M. & Gopnik A. (2006) Reversing how to think about ambiguous figure reversals: Spontaneous alternating by uninformed observers. *Perception,* 35, 709–715.
52. Mohamed T. N., Neumann M. F. & Schweinberger S. R. (2009). Perceptual load manipulation reveals sensitivity of the face-selective N170 to attention. *Neuroreport.* 20, 782–787.
53. O'Donnell B. F., Hendler T. & Squires N. K. (1988). Visual evoked potentials to illusory reversals of the Necker cube. *Psychophysiology*, 25, 137–143.

54. Oldfield R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia,* 9, 97–113.
55. Orbach J., Ehrlich D. & Heath H. (1963). Reversibility of the Necker cube: I. An examination of the concept of "satiation of orientation." *Perceptual and Motor Skills*, 17, 439–458.
56. Orbach J., Zucker E. & Olson R. (1966). Reversibility of the Necker cube: VII. Reversal rate as a function of figure-on and figure-off durations. *Perceptual and Motor Skills,* 22, 615–618.
57. Pelton L. H. & Solley C. M. (1968). Acceleration of Reversals of a Necker Cube. *The American Journal of Psychology.* 81, 585–588.
58. Picton T. W., Bentin S., Berg P., Donchin E., Hillyard S. A., Johson R. jr., Miller G. A., Ritter W., Ruchkin D. S., Rugg M. D. & Taylor M. J. (2000). Guidelines for using human event-related potentials to study cognition: Recording standards and publication criteria. *Psychophysiology, committee report,* 37, 127–152.
59. Pitts M. A., Nerger J. L. & Davis T. J. R. (2007). Electrophysiological correlates of perceptual reversals for three different types of multistable images. *Journal of Vision,* 7, 1–14.
60. Pitts M. A., Gavin W. J. & Nerger J. L. (2008). Early top-down influences on bistable perception revealed by event-related potentials. *Brain and Cognition,* 67, 11–24.
61. Qiu J., Wei D., Li H., Yu C., Wang T. & Zhang Q. (2009). The vase–face illusion seen by the brain: An event-related brain potentials study. *International Journal of Psychophysiology.* 74, 69–73.
62. Rees G., Frith C. D. & Lavie N. (1997). Modulating Irrelevant Motion Perception by Varying Attentional Load in an Unrelated Task. *Science.* 278, 1616–1619.
63. Reisberg D. & O'Shaughnessy M. (1984). Diverting subjects' concentration slows figural reversals. *Perception.* 13, 461–468.
64. Ricci C. & Blundo C. (1990). Perception of ambiguous figures after focal brain lesions. *Neuropsychologia,* 28, 1163–1173.

65. Rock I., Gopnik A. & Hall S. (1994). Do young children reverse ambiguous figures? *Perception.* 23, 635–644.
66. Schoth F., Waberski T. D., Krings T., Gobbele R. & Buchner H. (2007). Cerebral processing of spontaneous reversals of the rotating Necker cube. *Neuroreport.* 18, 1335–1338.
67. Shimada Y., Meguro K., Kasai M., Shimada M., Ishii H., Yamaguchi S. & Yamadori A. (2006). Necker cube copying ability in normal elderly and Alzheimer's disease. A community-based study: The Tajiri project. *Psychogeriatrics,* 6, 4–9.
68. Slotnick S. D. &Yantis S. (2005). Common neural substrates for the control and effects of visual attention and perceptual bistability. *Cognitive Brain Research.* 24, 97–108.
69. Strüber D., Basar-Eroglu C., Miener M. & Stadler M. (2001). EEG gamma-band response during the perception of Necker cube reversals. *Visual Cognition.* 8, 609–621.
70. Toppino T. C. (2003) Reversible-figure perception: Mechanisms of intentional-control. *Perception and Psychophysics,* 65, 1285–1295.
71. Toppino T. C. & Long G. M. (1987) Selective adaptation with reversible figures: Don't change that channel. *Perception and Psychophysics,* 42, 37–48.
72. Treisman A. M. (1969). Strategies and models of selective attention. *Psychological Review*, *76*, 282–299.
73. von Grünau M. W., Wiggin S. & Reed M. (1984) The local character of perspective organization. *Perception and Psychophysics,* 35, 319–324.
74. Wallace B. & Priebe F. A. (1985). Hypnotic susceptibility, interference and alternation frequency to the Necker cube illusion. *The Journal of General Psychology.* 112, 271–277.
75. Weckowicz T. E., Tam C. N. I., Mason J. & Bay K. S. (1987). Speed in test performance in depressed patients. *Journal of Abnormal Psychology.* 87, 578–582.

76. Windmann S., Wehrmann M., Calabrese P. & Güntürkün O. (2006). Role of the Prefrontal Cortex in Attentional Control over Bistable Vision. *Journal of Cognitive Neuroscience,* 18, 456–471.

12. PUBLICATIONS

1. Monika Intaitė, Mika Koivisto, Osvaldas Rukšėnas, Antti Revonsuo. Reversal negativity and bistable stimuli – Attention, awareness or something else? *Brain and Cognition*, 74 (1), 24–34 (ISSN 1612-4782).
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Papers in preparation

Monika Intaitė, Mika Koivisto, Osvaldas Rukšėnas and Antti Revonsuo. Impact of the presented perceptual load on event-related potentials elicited by reversals of ambiguous figures.

Conference proceedings

1) Monika Intaitė, Ona Gurčinienė and Alvydas Šoliūnas. 'Biasing effect on perception of two simultaneously presented reversible figures'. *Proceedings of the Fourth Scientific Conference of Faculty of Natural Sciences*, Vilnius, Lithuania, November 23rd–24th, 2006, p. 256-257 [in Lithuanian]

2) Monika Intaitė, Alvydas Šoliūnas, Ona Gurčinienė and Osvaldas Rukšėnas. 'Perception of two simultaneously presented Necker cubes'. *Proceedings of National scientific-practical conference 'Virtual Instruments in Biomedicine*, Klaipėda, Lithuania, May 18th, 2007, p. 85-90

3) Monika Intaitė, Alvydas Šoliūnas, Ona Gurčinienė and Osvaldas Rukšėnas. 'Impact of instruction and observation periods on perception of two simultaneously presented ambiguous figures'. *IV International scientific conference "Psychophysiologycal and visceral functions in norm and*

pathology" dedicated to P. G. Bogach 90-years anniversary, Kiev, Ukraine, October 8th–10th, 2008, p. 30-31

4) Monika Intaitė, Alvydas Šoliūnas, Ona Gurčinienė and Osvaldas Rukšėnas. 'Two simultaneously presented ambiguous figures: Influence of figure type, two-choice vs. three choice response instructions and prolonged viewing on image perception'. *Proceedings of 12th International conference on Biomedical Engineering*, Kaunas, Lithuania, October 23rd–24th, 2008, p. 301-304

5) Monika Intaitė, Mika Koivisto, Osvaldas Rukšėnas and Antti Revonsuo. ‚EEG study on the perception of bistable Necker cube gratings'. *Perception supplement issue of 32nd European Conference on Visual Perception*, 38, Regensburg, Germany, August 24th–28th, 2009, p. 148

Conference presentations

Oral:

1) "The impact of adaptation on perception of two ambiguous figures presented simultaneously". The International Natural Sciences Students Conference. March, 2006

2) 'Biasing effect on perception of two simultaneously presented reversible figures'. The XLIII Students Conference of Faculty of Natural Sciences. May, 2006 [in Lithuanian]

Poster:

3) "Effect of bias on perception of two simultaneously presented ambiguous figures". The Fourth Scientific Conference of Faculty of Natural Sciences November, 2006 [in Lithuanian]

4) “Impact of instruction and observation periods on perception of two simultaneously presented ambiguous figures”. The IV International scientific conference “Psychophysiological and visceral functions in norm and pathology” dedicated to P. G. Bogach 90-years anniversary, October, 2008

5) “EEG study on the perception of bistable Necker cube gratings”. 32nd European Conference on Visual Perception, August, 2009

6) “Impact of the presented perceptual load on event-related potentials elicited by reversals of ambiguous figures”. 2nd CINN summer school in Cognitive Neurodynamics, July, 2010

Publications not included in dissertation

1) Monika Intaitė, Ona Gurčinienė, Alvydas Šoliūnas (2006). Perception of reversible figures presented alone or in pairs. *Laboratorine Medicina*, 2 (30), 23-26 [in Lithuanian]

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14. CURRICULUM VITAE

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Education

2006- Present: pursuing **Ph.D.** in Biophysics, Vilnius University, Vilnius, Lithuania, Dissertations advisor: Osvaldas Ruksenas (Habil. Dr. Biomed. Sci., Professor)
2004-2006: **M.Sc.** in Neurobiology, Vilnius University, Vilnius, Lithuania.
2000-2004: **B.A.** in Philosophy, Vilnius University, Vilnius, Lithuania.
1988-2000: Vilnius Mindaugas Secondary School, Vilnius, Lithuania

Academic awards

1) 2007-2010 Research scholarships for doctoral students from Lithuanian Science and Study Foundation
2) 2008 Erasmus Lifelong Learning Programme scholarship for research work at University of Turku
3) 2008-2009 Centre for International mobility (CIMO) fellowship for research work at University of Turku
4) 2009-2010 Erasmus scholarship for research work at University of Turku

Scientific Interests

- Visual perception: ambiguous figures, binocular rivalry, change blindness, visual awareness
- Brain imaging: EEG, ERP
- Computational neuroscience

Positions held

2007.09-Present: Junior research fellow, Vilnius University, Vilnius, Lithuania
2006.09-2007.09 Senior assistant, Vilnius University, Vilnius, Lithuania

Teaching experience

2006-2008: conduction of laboratory exercises for the course "Neurobiology of Sensation and Perception"
2007-2009: supervision of term papers and theses (undergraduate students)

Research experience

2004- Present: *Doctoral and Masters Research:* Department of Biochemistry and Biophysics, Vilnius University, (research advisors: dr. Alvydas Šoliūnas, dr. Ona Gurčinienė and prof. Osvaldas Rukšėnas):

- analysis of literature;
- design and conduct of experiments on human perception of ambiguous figures;
- statistical data analysis;
- preparation of papers, oral and poster presentations at conferences etc.;

2008-2010 Research visits to Centre for Cognitive Neuroscience, University of Turku, Finland

- to get work experience with electroencephalographic equipment;
- creation of experimental stimuli with specialised programs;
- mastering skills for data registration;
- data analysis;
- preparation of manuscripts.

Scientific visits

1) Traineeship at 'Centre for Cognitive Neurosciences', Department of Psychology, Faculty of Social Sciences, University of Turku. Supported by Erasmus Lifelong Learning Programme. Period of visit: March 3rd – June 3rd, 2008.
2) Fellowship at 'Centre for Cognitive Neurosciences', Department of Psychology, Faculty of Social Sciences, University of Turku. Supported by Centre for International Mobility. Period of visit: October 1st, 2008 – March 1st, 2009.
3) Traineeship at 'Centre for Cognitive Neurosciences', Department of Psychology, Faculty of Social Sciences, University of Turku. Supported by Erasmus scholarship. Period of visit: September 1st – May 31st, 2010.

Related experience

Leonardo da Vinci pilot projects: "Computerised laboratory in science and technology teaching – part 2". Project period: 1st October 2005 to 31st December 2007. Project N°: SI-05-B-F-PP-176008.

The main outcomes of the project are the courses involving computer supported science and technology laboratory exercises. Duties: development and testing of new psychophysical laboratory exercises.

Summer schools and workshops

1. European Spring Event on Neuroethics, Ludwigshafen, Germany, 2007;
2. MEDILS summer school Symposium on Imaging and Simulation of Human Brain Activity, Croatia, Split, Croatia, 2007;
3. International school Advanced Methods in Biophysics, Trakai, Lithuania, 2007
4. Supervision of scientific papers, Vilnius University, Lithuania, 2007

5. 37th annual meeting of the Society for Neuroscience, San Diego, California, 2007
6. Ethical aspects of scientific research with humans, Vilnius University, Lithuania, 2007
7. IBRO International Workshop on Complex Neural Networks From synaptic transmission to seeing the brain in action, Debrecen, Hungary, 2008
8. Psychology of communication, Vilnius University, Lithuania, 2008
9. DISCOS summer school about Self and self-disorders, Centre for Subjectivity Research, University of Copenhagen, Denmark, 2008
10. 3rd International Summer School in Biomedical Engineering, University of Weimar, Germany, 2008
11. 10th Workshop on Optimization and Inverse Problems in Electromagnetism, University of Ilmenau, Germany, 2008.
12. Brain Products workshop on EEG & TMS and EEG & fMRI, Reading, United Kingdom, 2010.
13. 2nd CINN summer school in Cognitive Neurodynamics, Reading, United Kingdom, 2010.

Skills and Qualifications

a. Microsoft Office, STATISTICA for Windows 7.1, SPSS, Adobe Illustrator
b. NeuroScan Presentation, NeuroScan Acquire, BrainVision Analyzer, E-Prime
c. Fluent English and Russian, moderate comprehension of Finnish, basic knowledge of French and German