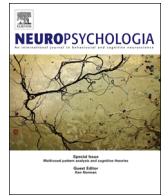




ELSEVIER

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Event-related potential responses to perceptual reversals are modulated by working memory load



Monika Intaitė^{a,*}, Mika Koivisto^{b,c}, Miguel Castelo-Branco^a

^a Visual Neuroscience Laboratory, IBILI, Faculty of Medicine, University of Coimbra, Azinhaga De Santa Comba, Celas, 3000-548 Coimbra, Portugal

^b Centre for Cognitive Neuroscience, University of Turku, 20014 Turku, Finland

^c Department of Psychology, University of Turku, 20014 Turku, Finland

ARTICLE INFO

Article history:

Received 19 July 2013

Received in revised form

14 January 2014

Accepted 15 February 2014

Available online 22 February 2014

Keywords:

Cognition

Normal volunteers

EEG/ERP

Ambiguous figure

Working memory load

ABSTRACT

While viewing ambiguous figures, such as the Necker cube, the available perceptual interpretations alternate with one another. The role of higher level mechanisms in such reversals remains unclear. We tested whether perceptual reversals of discontinuously presented Necker cube pairs depend on working memory resources by manipulating cognitive load while recording event-related potentials (ERPs). The ERPs showed early enhancements of negativity, which were obtained in response to the first cube approximately 500 ms before perceived reversals. We found that working memory load influenced reversal-related brain responses in response to the second cube over occipital areas at the 150–300 ms post-stimulus and over central areas at P3 time window (300–500 ms), suggesting that it modulates intermediate visual processes. Interestingly, reversal rates remained unchanged by the working memory load. We propose that perceptual reversals in discontinuous presentation of ambiguous stimuli are governed by an early (well preceding pending reversals) mechanism, while the effects of load on the reversal related ERPs may reflect general top-down influences on visual processing, possibly mediated by the prefrontal cortex.

© 2014 Elsevier Ltd. All rights reserved.

1. Introduction

Visual bistability is an important phenomenon because it can be used as a tool with the aim to understand the neural mechanisms underlying perceptual decision making (Kornmeier & Bach, 2012; Leopold & Logothetis, 1999). Ambiguous figures (e.g., the Necker cube) are bistable visual stimuli that can be perceived in two (or more) alternative ways. The visual system selects only one percept at a time as in general one cannot perceive a single physical stimulus in several ways simultaneously. If an ambiguous stimulus is viewed for an extended period of time, people perceive it as switching back and forth between the possible interpretations. Perceptual reversals occur without any physical change of the stimulus and hence provide a distinct possibility to study how perceptual interpretations are constructed irrespectively of low level stimulus properties.

There is a continuing debate concerning the role of low versus high level visual mechanisms in determining perceptual decisions. Two main types of theories explain the phenomenon of bistable perception. According to cognitive theories (e.g., Leopold & Logothetis, 1999),

higher order top-down perceptual processes in the brain determine the reversals of ambiguous stimuli. Satiation (sensory adaptation) theories (e.g., Toppino & Long, 1987) emphasize the operation of the bottom-up perceptual processes and hypothesize that the mechanism of the reversals of ambiguous figures is rather simple: satiation of the neural channels, responsible for one of the available percepts, causes the perceptual interpretation to change to the alternative one. An increasing number of studies indicate that both types of processes are important in the perception of ambiguous images (Hochberg & Peterson, 1987; Intaitė, Noreika, Šoliūnas, & Falter, 2013; Kornmeier & Bach, 2012; Kornmeier, Hein, & Bach, 2009; Long, Toppino, & Kostenbauder, 1983; Long & Toppino, 2004).

In studies on the contribution of high-level mechanisms in perceptual decision making, it is important to take into account the role of frontoparietal loops, in particular those that concern the involvement of attention and working memory mechanisms. These neural processes are closely linked at short time scales, because of the link between attentional stimulus selection and ensuing processing in working memory. Selective attention refers to the capacity of our brain to single out the relevant information for further processing while ignoring the irrelevant information. Working memory is the ability to actively maintain such information over short periods of time, but it has a limited capacity which may vary substantially between individuals (Cowan, 2001; Luck & Vogel, 1997; Vogel & Awh, 2008). There is

* Corresponding author. Tel.: +35 1239480200; fax: +35 1239480217.

E-mail address: mintait@fmed.uc.pt (M. Intaitė).

growing evidence regarding the interrelationship of working memory and selective attention in cognitive processes including perception, as they both require dedicated processing of the same information at short time scales prior to the decision (Awh, Jonides, & Reuter-Lorenz, 1998; Kumar, Soto, & Humphreys, 2009; Smyth & Scholey, 1994). Accordingly, their mechanisms are functionally overlapped (Awh et al., 1998; Awh & Jonides, 2001; Singhal & Fowler, 2004) especially during the short temporal windows requiring a perceptual decision response.

Several studies (Knapen, Brascamp, Adams, & Graf, 2009; Leopold, Wilke, Maier, & Logothetis, 2002; Maier, Wilke, Logothetis, & Leopold, 2003; Pearson & Brascamp, 2008) suggested that when the ambiguous images are presented intermittently, the transitions from one perceptual state to the next may be modulated by some form of perceptual memory. If stimulus and inter-stimulus intervals consist of several seconds, the participants tend to perceive an ambiguous stimulus in the same interpretation as they did before; here the brain uses the information obtained from previous computations for perceptual decision making. Brascamp et al. (2008) showed that perceptual alternations use some sort of memory, comparable to working memory. Sterzer & Rees (2008) reported percept-specific signals in the visual cortex during temporary delay periods following binocular rivalry. Those signals correlated with activity in prefrontal and parietal regions. Thus Sterzer & Rees (2008) hypothesized that bistable perception is influenced by higher-order mechanisms which share a common anatomical substrate with the mechanisms of working memory. In addition, Kornmeier & Bach (2012) suggested that a specific type of event-related brain potential (Frontopolar Positivity) reflects the involvement of working memory in the generation of reversals. Thus, if the working memory resources are actively involved in the construction of the alternative percept of the ambiguous stimulus, one could expect a concurrent working memory load (hereafter WML) to decrease the reversal rates and to reduce the efficiency of the neural processes involved in reversals.

According to the satiation theory, the perceptual reversals occur in early visual areas due to cycles between passive adaptation, recovery and mutual inhibition of competing neural channels. This theory assumes that perception of reversals is a rather automatic process, and secondary tasks should not interfere with it (Toppino & Long, 1987).

The aim of the present study is to gain more insight on the brain mechanisms involved in the phenomenon of perceptual bistability by exploring the effects of WML on perceptual reversals. More explicitly, the temporal locus of the possible effects of WML on perceptual reversals will be examined using event-related potentials (ERPs). ERPs are averages of electroencephalographic (EEG) responses usually calculated in response to the onset of the experimental event. ERPs, as temporally very precise measurements, help to elucidate the time-course of neural processing during perceptual and cognitive tasks. In earlier ERP studies on the perception of ambiguous stimuli, the backward-averaging technique was employed, that is, a reversal-indicating response was the reference point for averaging. The results showed that the amplitudes of the perceptual switching related potential (which occurred 500 ms prior to participants' response) were more positive than those elicited by a control task. This potential resembled the P3 wave as it had the same polarity and similar spatial distribution (Basar-Eroglu, Strüber, Stadler, & Kruse, 1993). Such late effects probably reflect the operation of post-perceptual processes (Donchin & Coles, 1988).

Intermittent Necker cube presentation mode with short (i.e., less than 1 s) stimulus and inter-stimulus intervals frequently provoke immediate reversal of the ambiguous figure at the onset of its second occurrence (Orbach, Zucker, & Olson, 1966) thus making it possible to average ERPs to the stimulus onset. Therefore, it has become conventional to use this presentation mode while recording ERPs to perceptual reversals. Three main reversal-related components have been obtained in the recent studies of visual bistability: Early

Positivity (EP) in P1 time window (Intaitė, Koivisto, & Revonsuo, 2013; Kornmeier & Bach, 2005; Kornmeier, Ehm, Bigalke, & Bach, 2007), Reversal Negativity (RN) around 150–250 ms (Intaitė, Koivisto, Rukšėnas, & Revonsuo, 2010; Kornmeier & Bach, 2004, 2005; Kornmeier et al., 2007; Pitts, Gavin, & Nerger, 2008; Pitts, Nerger, & Davis, 2007) and Late Positivity (LP) in P3 time window (Kornmeier & Bach, 2004, 2005; Kornmeier et al., 2007; Pitts et al., 2008), thus revealing different processing stages during perception of ambiguous images and enabling the investigation of potential WML effects on those stages. However, the relationship between these potentials to bottom-up and top-down processes remains unclear. Intaitė et al. (2010) measured the N2pc, an electrophysiological component reflecting the allocation of attention in visual tasks, in response to reversals of Necker lattices (both ambiguous and unambiguous) and found that both types of stimuli elicited RN, but only reversals of unambiguous stimuli elicited N2pc, suggesting that RN does not reflect the operation of the type of attention that is responsible for N2pc. Intaitė et al. (2013) manipulated perceptual load while the participants were required to detect perceptual reversals of unambiguous or ambiguous Necker cubes. The manipulation of load involved identification of letter strings presented at the onset of the second occurrence of the cube in intermittent presentation. Perceptual load did not have any behavioral effect on reversal rates. The RN was revealed only in response to reversals of unambiguous lattices and only over the right hemisphere, and its amplitude was not influenced by the magnitude of the perceptual load. However, Pitts et al. (2008) examined the effects of intention on perceived reversals of Necker stimuli and found that intention-to-reverse enhanced the amplitude of the RN. This suggests that intentional control influences relatively early processes occurring after the stimulus onset (i.e., around 150 ms). In addition, Pitts, Martínez, Brewer, and Hillyard (2011) revealed that ERPs in response to figure-ground discrimination of ambiguous vase-face figure are modulated by selective attention. Therefore, more experiments are needed in order to clarify the possible interrelationship between perceptual ambiguity, attention and higher order processes.

We studied the relationship between perceptual reversals, working memory and ERPs. The participants were required to detect perceptual reversals of ambiguous Necker cubes while performing a concurrent task with varying levels of WML. In order to manipulate the amount of available working memory resources, the WML stimuli (letter strings) consisted of either no letters (sham-load), four (easy-load) or six (hard-load) consonants. The concurrent task involved memorization of the letter strings which were followed by discontinuous presentations of the Necker cube. Therefore, if perceptual reversals depend on the available working memory resources, the WML should reduce the amount of perceived reversals and diminish the amplitudes of the electrophysiological correlates of reversals either in EP (around 100 ms), RN (around 250 ms), or LP (after 300 ms) time window, depending on how early or late mechanism is involved. On the other hand, the satiation theory predicts no WML effects on the perceived reversal rates and reversal-related ERPs as the task unrelated to perceptual reversal should have no influence on the automatic sensory processes.

2. Methods

2.1. Participants

Twenty-nine healthy participants (13 male; mean age=24.7 years, SD=3.3) took part in the study. They had normal or corrected-to-normal vision and were naive as to the specific experimental question. All individuals were right-handed, as confirmed by Edinburgh Handedness Inventory (Oldfield, 1971). A written informed consent (in accordance to the declaration of Helsinki) was obtained from all participants and the study was formally approved by the institutional ethics committee.

2.2. Stimuli

2.2.1. Memory stimuli

In order to manipulate WML, a memory set, consisting of the memory prime and the memory probe, was presented in each trial. The memory prime was either

four asterisks (*; sham-load condition, size $0.4^\circ \times 0.4^\circ$), or the letter strings (font: Courier New, letter size $0.5^\circ \times 0.2^\circ$) consisting of 4 (easy-load condition) or 6 (hard-load condition) capital consonants (except K, Q and H) and it was presented in the beginning of each trial (see Fig. 1B). The memory probe was presented in the end of each trial and consisted of two arrows (arrow size $0.4^\circ \times 0.4^\circ$) to the left (\ll) or the right (\gg) in the sham-load condition or one letter in both load conditions.

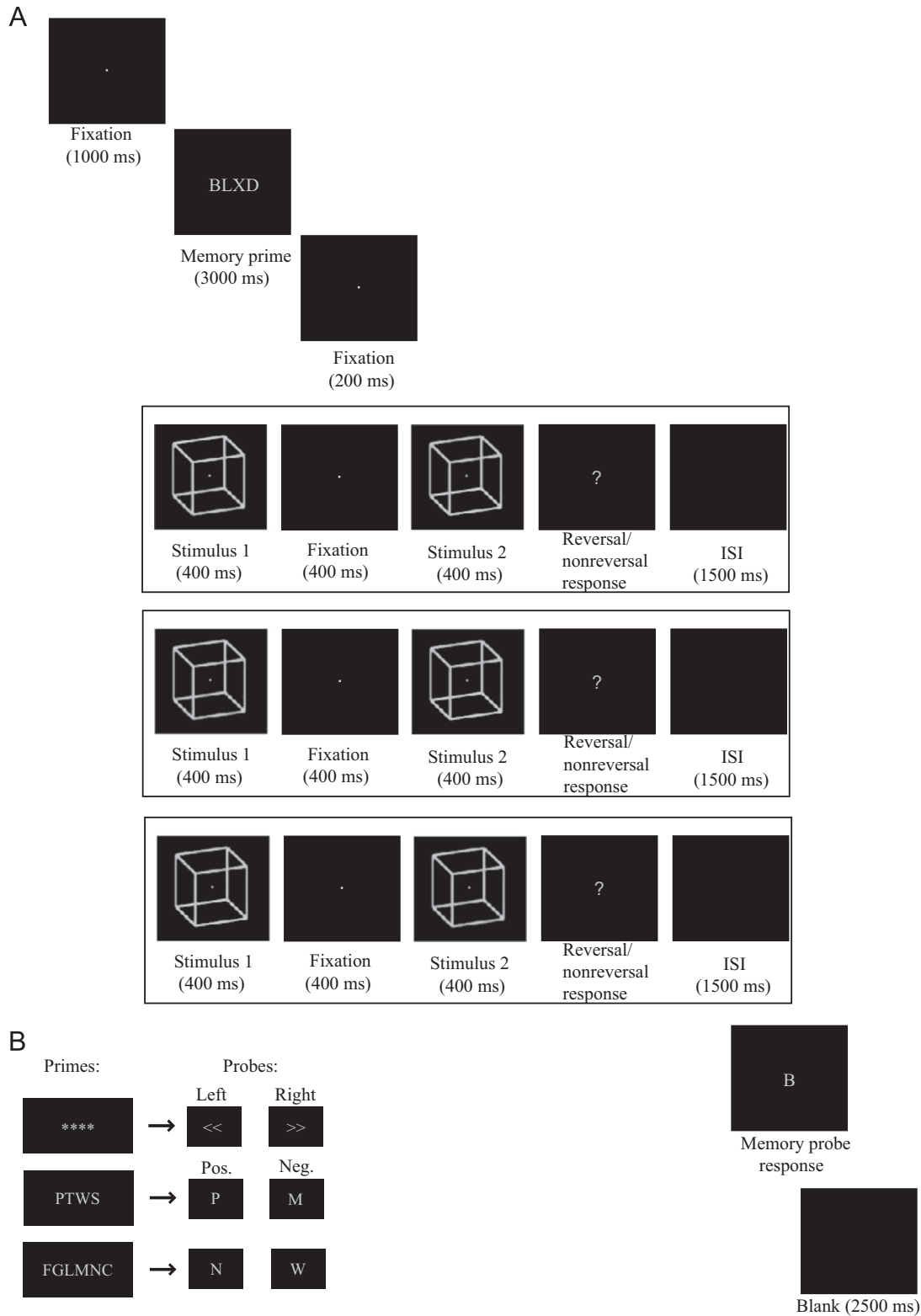


Fig. 1. (A) An illustration of a single experimental trial displaying an easy working memory load trial: a string consisting of four consonants is followed by three pairs of Necker cubes and a positive memory probe stimulus. Participants were instructed to memorize the letter stimuli and provide reversal/nonreversal response after each cube pair (question mark indicated the response time). Finally, participants had to decide if the memory probe was presented (or not) in the initial letter string, (B) Schematic representation of the memory primes and probes in the sham, easy (4 letters) and hard (6 letters) load conditions.

Memory primes and probes were presented in white (20 cd/m²) on a black background (0.1 cd/m²). Multiple randomized sequences of letters were created for the memory sets and the occurrence (as well as the position) of each letter in the memory set was equiprobable. Within each memory prime all the letters were different.

2.2.2. Reversal stimulus

The ambiguous Necker cube (Fig. 1A), of size 3° × 3°, was used as stimulus. It was presented on a 19 in. CRT monitor with a frame rate of 85 Hz from a viewing distance of 150 cm. It was presented in white (20 cd/m²) on a black background (0.1 cd/m²).

2.3. Procedure

In the beginning of the session, a static version of a Necker cube was shown for each observer. If an observer was initially unable to perceive the ambiguity of the figure, he was prompted by the experimenter until he was able to perceive the figure in both interpretations.

In the actual experiment, each trial began with the fixation dot appearing for 1000 ms. It was followed by the presentation of the memory prime (containing either asterisks or letters) for 3000 ms followed by the fixation dot for 200 ms. Participants were asked to memorize the letter stimuli and just to look at the asterisks. After the memory prime, three pairs of ambiguous Necker cubes were presented. In each pair the first cube was presented for 400 ms, followed by the fixation dot for 400 ms and by the second cube for 400 ms. Thus, the observers could perceive the second cube of each pair as subjectively changing or not changing its orientation in relation to the cube in the first display. A question mark followed each cube pair and the participant had to press one button when he/she perceived a perceptual reversal in the orientation of the second cube and another button when he/she perceived both cubes of the pair in the same orientation. The location of the cube between the first and second display in each Necker cube pair was randomly jittered by small changes (about ±0.3°) to avoid afterimages and trivial local cues. The blank intervals from one cube pair to the next were 1500 ms. The fixation dot, when presented, was always in the center of the screen. The participants were asked to keep fixating in the center of the screen and not to move their eyes during the presentations of the Necker cube pairs.

At the end of each trial, the memory probe was presented and the participant had to indicate whether the letter presented in the memory probe matched (positive probe) or did not match (negative probe) any of the letters presented in the prime. Participants were asked to discriminate positive and negative probes (or left-oriented versus right-oriented arrows in the sham-load trials) by pressing designated buttons with their index and middle fingers. The inter-trial interval between the observer's response to the memory probe and the beginning of the next trial was 1000 ms.

The response hand was counterbalanced: half of the participants performed the first half of the experiment (i.e., two experimental blocks) by providing the responses with the right hand, and the second part with the left hand. For the other half of the participants, this order was reversed. It was emphasized that they should press the 'reversal' button only when they actually saw a perceptual reversal, and guessing was not permitted. In response to the memory set, if the participant could not remember whether the letter was a part of the memory prime presented in the beginning of the trial, or not, he/she was asked to guess. In both tasks, response speed and accuracy were both emphasized.

The experiment included 56 sham-load, 56 easy-load and 56 hard-load trials (thus including 168 Necker cube pairs in each load condition) presented in random order and divided in four stimulus blocks. Short breaks (about 2–3 min) were provided between the stimulus blocks and a long break (approx. 10 min) in the middle of the experiment. In the beginning of the session, each participant performed a short practice block of 20 trials in order to get used to the task requirements.

2.4. Electrophysiological recordings and analysis

EEG was recorded using Ag/AgCl electrodes from extended 10/20 system sites Fp1, Fp2, F3, F4, F7, F8, Fz, FC3, FC4, F17, F18, FCz, C3, C4, T7, T8, Cz, CP3, CP4, TP7, TP8, CPz, P3, P4, P7, P8, Pz, O1, O2, Oz. The nose was used as reference location and an electrode above Fz was used as ground. An electrode placed 1.5 cm to the right of the right eye was used for monitoring horizontal eye movements, and an electrode below the right eye was used for monitoring blinks and vertical eye movements. EEG was amplified by using a band pass of 0.15 to 200 Hz, with the sampling rate of 1000 Hz. The impedance of electrodes was kept below 10 kΩ. The parts of trials in response to Necker cube pairs that showed evidence of artefacts (> 70 μV) in any of the electrodes were rejected off-line. Based on EOG data, the parts of trials in response to Necker cube pairs that had eye movements, or blink artefacts (> 70 μV) were discarded from analyses. To reliably examine the effect of WML on the perceptual decision making, only the Necker cube pairs within correct WML trials were included in the analyses. After the exclusion of the trials with memory errors, the ERPs were averaged separately for perceptual reversals and nonreversals in sham, easy and hard WML conditions. For a participant's data to be included in ERP analyses, at least 25 artifact-free Necker cube pairs per cell were

required. In the statistical analyses, we reported the original degrees of freedom, but corrected the *p*-values according to Huynh–Feldt correction whenever the degrees of freedom were greater than 1. The degrees of freedom are reported together with effect sizes (partial eta squared: η^2).

2.4.1. ERP analyses of the first cube

The baseline correction was performed to the activity in the –100–0 ms preceding the first cube. After artefact rejection, the individual ERPs for perceptual reversals were calculated on the basis of on average 51 (SD=12.40), 51 (SD=11.93) and 43 (SD=14.97) Necker cube pairs in the sham, easy and hard loads, respectively. The corresponding values for perceptual nonreversals were 83 (SD=21.94), 75 (SD=21.63) and 70 (SD=27.72), respectively. Three participants had a strong effect of WML on the perception of Necker cube reversals (i.e., < 25 reversal-related ERPs followed by correct probe responses in hard-load WML trials). Therefore, to be able to use the data from these participants, we included all reported reversals from the hard-load condition in their behavioral and ERP analyses.

2.4.2. ERP analyses of the second cube

We commenced the analyses of the ERPs to the second cube after confirming the validity of the baseline –100–0 ms preceding the second cube. Thus we took the 700–800 ms time window from the ERPs of the first cube (which corresponds to –100–0 ms baseline for the second cube) and ran the repeated measures ANOVA to check whether there is an ERP overlap from the first to the second cube and/or anticipation artifacts near the onset of the second cube. The analysis did not reveal significant effects or interactions involving WML and/or perceptual reversals. Therefore, the baseline correction was performed to the activity in the –100–0 ms preceding the second cube. After artefact rejection, the individual ERPs for perceptual reversals were calculated on the basis of on average 56 (SD=13.26), 55 (SD=14.17) and 48 (SD=17.20) Necker cube pairs in the sham, easy and hard loads, respectively. The corresponding values for perceptual nonreversals were 93 (SD=19.30), 84 (SD=21.39) and 78 (SD=27.67), respectively. Three participants had a strong effect of WML on the perception of Necker cube reversals (i.e., < 25 reversal-related ERPs followed by correct probe responses in hard-load WML trials). Therefore, to be able to use the data from these participants, we included all reported reversals from the hard-load condition in their behavioral and ERP analyses.

3. Results

3.1. Behavioral performance

Accuracy (Fig. 2A) and response times (Fig. 2B) to the memory probe and the frequency of perceived reversals of the Necker cube (Fig. 2C) were analyzed with one-way ANOVAs including the Load (3 levels: sham, easy and hard) as a within-subject factor.

3.1.1. Accuracy

A significant effect for Load ($F(2,56)=36.96$; $p < 0.0001$, $\eta^2=0.57$) was found: responses to the probe were more accurate under sham-load than under easy ($p < 0.0001$) and hard loads ($p < 0.0001$). Moreover, responses to the probe under easy-load were more accurate than under hard-load ($p < 0.0001$).

After exclusion of erroneous WML trials, on average (SD) 56 (0) trials in the sham-load condition, 51.7 (5.18) in the easy-load condition, and 47.3 (6.46) in the hard-load condition remained for the analyses of response times and reversal rates.

3.1.2. Response times

A significant effect for Load ($F(2,56)=57.85$; $p < 0.0001$, $\eta^2=0.67$) was found. Response times increased with load: RTs were longer from sham to easy ($p < 0.0001$), from sham to hard ($p < 0.0001$) and from easy to hard load ($p < 0.0001$).

3.1.3. Reversals

For each load condition, we divided the number of reversal responses given in correct WML trials by the amount of Necker cube pairs presented in the correct WML trials for the data of each participant. When these reversal rate proportions were analyzed (one-way ANOVA with Load as a factor), no significant differences were observed in the number of perceived reversals as a function of working memory load ($F=1.40$). Additional ANOVA including

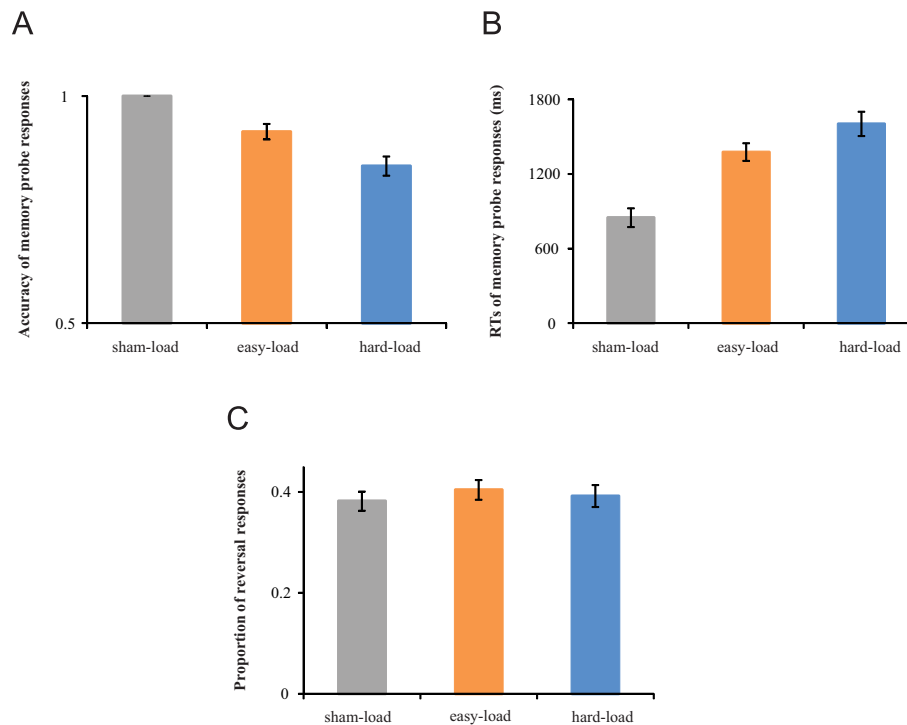


Fig. 2. (A) The accuracy of memory probe responses under sham, easy or hard working memory load for all participants ($N=29$). (B) The reaction times in response to memory probes under sham, easy or hard working memory load for all participants. (C) The proportion of reported Necker cube reversals under sham, easy or hard working memory load for all participants. Error bars represent ± 1 standard error above and below the mean.

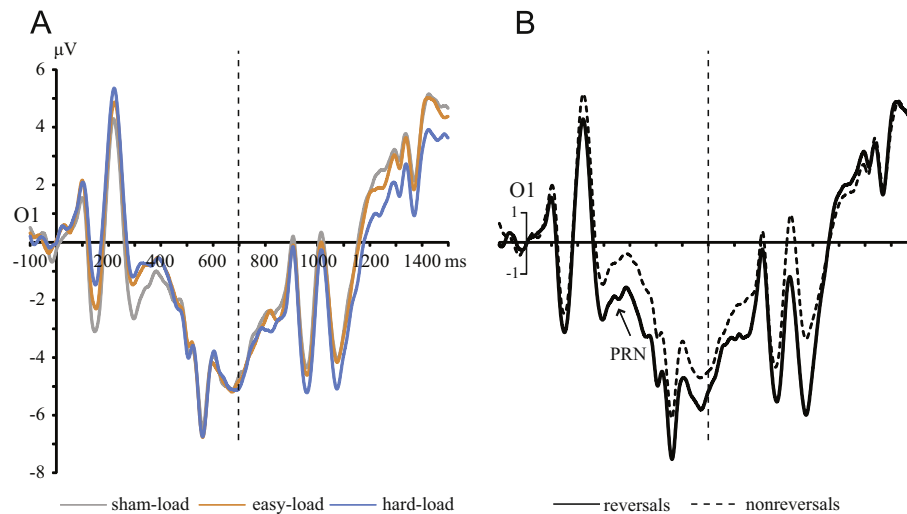


Fig. 3. (A) Grand-average ERP waveforms in response to the first stimulus display in trials where participants completed sham (light gray lines), easy (dark gray (orange in the web version) lines) or hard (black (blue in the web version) lines) working memory load task collapsed across reversal/nonreversal trials. Mean amplitudes in response to sham-load were significantly more negative/less positive than those in response to easy and hard loads between 100 and 200 ms (P1 and N1 time windows) in central, parietal, occipital and temporal electrodes and between 200 and 300 ms (P2 and N2 time windows) in occipital and temporal electrodes. The dashed vertical line marks the onset of the second stimulus display. (B) Grand-average ERP waveforms in response to the first stimulus display in trials where participants reported reversals (black lines) or nonreversals (dashed black lines) collapsed across load conditions. Pre-Reversal Negativity (PRN; enhanced negativity in response to reversals) was observed between 200 and 300 ms (P2 and N2 time windows) in central, parietal, occipital and temporal electrodes. The dashed vertical line marks the onset of the second stimulus display.

the data from all the trials (correct and incorrect responses to the probes) was also conducted, but the effect of Load was not statistically significant ($F=1.26$).

3.2. Electrophysiology

3.2.1. First cube analyses: mean ERP amplitudes

The data from 27 participants were included in the analyses of the first cube ERPs. We performed 3 (Load: sham, easy and hard) \times 4

(Area: C3C4, P3P4, P7P8 and O1O2) \times 2 (Hemisphere: left and right) \times 2 (Type: reversal and nonreversal) repeated measures ANOVAs on the mean amplitudes in the P1 (100–150 ms), N1 (150–200 ms), P2 (200–250 ms) and N2 (250–300 ms) time windows. The time windows were selected by visual inspection of the grand average potentials. We found that Load had an effect on ERPs ($F(2,52) \geq 3.58$; $p < 0.04$, $\eta p^2 \geq 0.12$), in the P1, N1, P2 and N2 time windows (Fig. 3A). In these time windows, mean amplitudes in response to sham-load were significantly more negative/less positive

than those in response to easy (all p -values < 0.05) and hard (all p -values < 0.02) loads. Our results are worth comparing with previous studies on visual working memory (Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005) which typically found sustained negative ERPs in response to items in the memory set especially during harder WML tasks. In our study the ERPs were measured in response to ambiguous stimuli that were presented during the maintenance interval and were not a part of the memory set. Thus our results are consistent with the results of the dual-task studies that used a WML task (Jongen & Jonkman, 2011; Singhal & Fowler, 2004) and showed that ERPs to a particular task under WML were more positive/less negative in amplitude than the ERPs to the same task without WML. Furthermore, regardless of working

memory load, ERPs elicited by the first cube were more negative in the P2 and N2 time windows when a reversal was about to occur upon presentation of the next cube 500–600 ms later. We found pre-reversal activity on ERPs ($F(1,26) \geq 6.84$; $p < 0.02$, $\eta^2 \geq 0.21$), in the P2 and N2 time windows (Fig. 3B): the event-related potentials preceding perceptual reversals were more negative than those preceding nonreversals. This represents a new effect, pre-reversal negativity (PRN), which suggests that processing during the first cube may determine whether a reversal will occur or not (see also Intaité et al., 2013). Load \times Type interactions were not significant in any of the time windows (all F -values < 0.53). It is important to note that there were no ERP differences between the conditions during 700–800 ms period (Load: $F=0.10$; Type: $F=1.16$), that is,

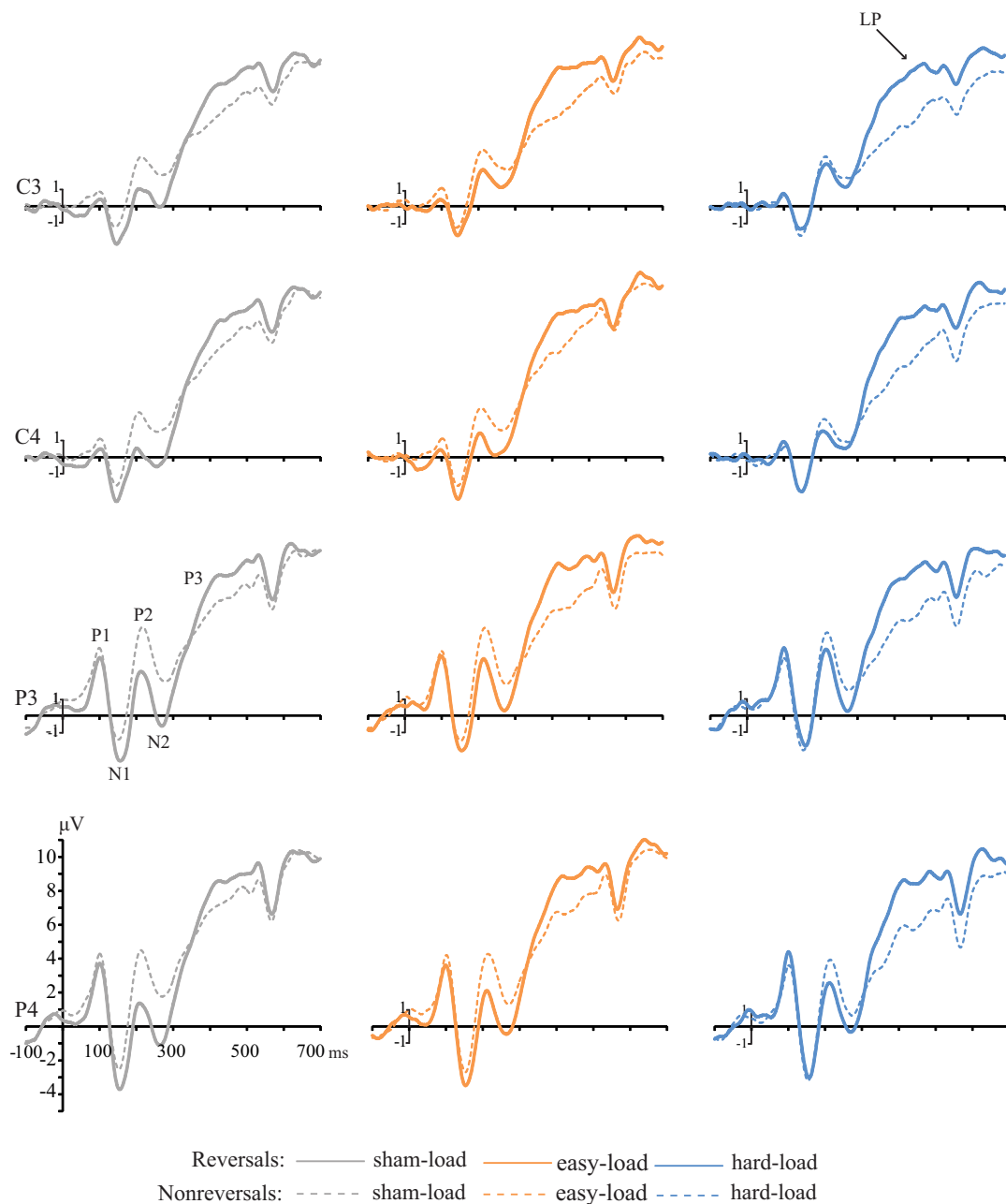


Fig. 4. Grand-average ERP waveforms in response to the second stimulus display in trials where participants reported reversals under sham (light gray lines), easy (dark gray (orange in the web version) lines) and hard (black (blue in the web version) lines) working memory load and when they did not report reversals under sham (dashed light gray lines), easy (dashed dark gray (orange in the web version) lines) or hard (dashed black (blue in the web version) lines) working memory load over central and parietal areas. Reversal Negativity (RN; enhanced negativity in response to reversals) was observed between 140 and 280 ms (N1, P2, N2 time windows). Late Positivity (LP; enhanced positivity in response to reversals) was observed between 300 and 500 ms (P3 time window).

–100–0 ms prior to the onset of the second cube. Therefore this time window can be used as an unbiased baseline in the analyses of the ERPs to the second cube.

3.2.2. Second cube analyses: mean ERP amplitudes. Second cube analyses: mean ERP amplitudes

We performed 3 (Load: sham, easy and hard) \times 4 (Area: C3C4, P3P4, P7P8 and O1O2) \times 2 (Hemisphere: left and right) \times 2 (Type: reversal and nonreversal) repeated measures ANOVAs on the mean amplitudes in the P1 (90–130 ms), N1 (140–180 ms), P2 (200–240 ms), N2 (240–280 ms) and P3 (300–500 ms) time windows. The time windows were selected by visual inspection of the grand average potentials. We found that Type had a main effect in the N1, P2 and N2 time windows ($F(1,28) \geq 5.98$; $p < 0.03$, $\eta^2 \geq 0.18$). In these time windows, reversals were associated with larger negativity than nonreversals, showing that RN occurred (Fig. 4). No main effects for Load were observed in any of the areas (all F -values < 1). Significant Load \times Area ($F(6,168) \geq 4.69$; $p < 0.002$, $\eta^2 \geq 0.14$) and Area \times Type ($F(3,84) \geq 5.87$; $p < 0.004$, $\eta^2 \geq 0.17$) interactions were observed in the P2 and N2 time windows. Further analyses in both time windows revealed significant effects for Type over all areas: central ($F(1,28) \geq 13.86$; $p < 0.0001$, $\eta^2 \geq 0.33$), parietal ($F(1,28) \geq 26.96$; $p < 0.0001$, $\eta^2 = 0.49$), temporal ($F(1,28) \geq 24.94$; $p < 0.0001$, $\eta^2 \geq 0.47$) and occipital ($F(1,28) \geq 27.82$; $p < 0.0001$, $\eta^2 \geq 0.50$). Variations in the spatial distribution as well as in the temporal extent of RNs have been reported in earlier studies (Intaité et al., 2010; Kornmeier et al., 2007; Pitts et al., 2008; Qiu et al., 2009); in the present study the RN had a wide scalp distribution extending from posterior (Fig. 5) to central sites. Significant Hemisphere \times Type interaction ($F(1,28) = 9.83$; $p < 0.005$, $\eta^2 = 0.26$) was obtained only in the P2 time window, which occurred due to stronger effect of Type ($F(1,28) = 28.29$; $p < 0.0001$, $\eta^2 = 0.50$) over the right hemisphere. Most importantly, significant Load \times Type interactions were observed in the P2 ($F(2,56) = 3.65$; $p < 0.05$, $\eta^2 = 0.12$) and N2 ($F(2,56) = 4.07$; $p < 0.04$, $\eta^2 = 0.13$) time windows. These interactions indicate that load decreased the magnitude of the reversal related ERPs (i.e., RN) and that this effect started around 200 ms post-stimulus.

In the P3 time window significant Load \times Area ($F(6,168) = 4.78$; $p < 0.002$, $\eta^2 = 0.15$) and Area \times Type ($F(3,84) = 22.73$; $p < 0.0001$, $\eta^2 = 0.45$) interactions were observed and mean amplitudes in response to reversals were significantly more positive than those in response to nonreversals ($F(1,28) = 5.22$; $p < 0.04$, $\eta^2 = 0.16$), indicating that LP occurred. Subsequent analyses revealed that ERPs elicited by reversals were significantly more positive than those elicited by nonreversals over central ($F(1,28) \geq 5.94$; $p \leq 0.03$, $\eta^2 \geq 0.18$) and parietal ($F(1,28) \geq 4.94$; $p \leq 0.04$, $\eta^2 \geq 0.15$) areas. Significant effects for Load were observed over the temporal ($F(2,56) = 3.46$; $p < 0.04$, $\eta^2 = 0.11$) and occipital ($F(2,56) = 3.29$; $p < 0.05$, $\eta^2 = 0.11$) areas. Over temporal areas mean amplitudes in response to sham and easy loads were significantly more positive than those in response to hard-load (all p -values < 0.05). Over occipital areas mean amplitudes in response to sham-load were significantly more positive than those in response to hard-load ($p < 0.03$).

Furthermore, to isolate the effects of reversals and load in more detail, the reversal – nonreversal difference waves were analyzed as a function of load in the time windows (N1–P3) that showed significant effects (RN, LP) for reversals.

3.2.3. Second cube analyses: difference waves

We computed reversal response minus nonreversal response difference traces in each of the three load conditions for the central, temporal and occipital areas (Fig. 6). The time windows for the prominent components in the difference traces, that is, reversal negativity (RN) (150–300 ms) and late positivity (LP) (300–500 ms)

were determined by visual inspection. Consequently, the amplitude minimum (or maximum, for positive peaks) was defined from the averages of each participant and in each single average the ± 10 ms window of the largest excursion was selected and their amplitudes were analyzed by repeated-measures ANOVAs.

A 2 (Area: P7P8 and O1O2) \times 2 (Hemisphere: left and right) \times 3 (Load: sham, easy and hard) ANOVA was conducted on the peak amplitudes of the RN. A 2 (Hemisphere: left and right) \times 3 (Load: sham, easy and hard) ANOVAs was conducted on the peak amplitudes of the LP over the central areas.

RN (150–300 ms). Significant Area \times Load ($F(2,56) = 5.05$; $p < 0.02$, $\eta^2 = 0.15$) interaction was obtained. Further analyses revealed significant effect for Load only over occipital areas ($F(2,56) = 4.25$; $p < 0.04$, $\eta^2 = 0.13$): mean peak amplitudes under sham-load were significantly more negative than those in response to both easy ($p < 0.02$) and hard ($p < 0.009$) loads. The decrease in the amplitudes of RN with increasing WML was confirmed by significant linear ($F(1,28) = 8.20$, $p < 0.009$, $\eta^2 = 0.23$) contrast. The reversal related peaks (i.e., RN) differed significantly from the intercept in each load condition: sham ($F(1,28) = 105.33$; $p < 0.0001$, $\eta^2 = 0.79$), easy ($F(1,28) = 53.51$; $p < 0.0001$, $\eta^2 = 0.66$) and hard load ($F(1,28) = 32.24$; $p < 0.0001$, $\eta^2 = 0.54$).

LP (300–500 ms). Significant effect for Load ($F(2,56) = 3.50$; $p < 0.04$, $\eta^2 = 0.11$) was revealed: mean peak amplitudes under sham-load were significantly less positive than those under hard load ($p < 0.04$). The reversal related peaks differed significantly from the intercept in each load condition: sham ($F(1,28) = 20.37$; $p < 0.0001$, $\eta^2 = 0.42$), easy ($F(1,28) = 28.48$; $p < 0.0001$, $\eta^2 = 0.50$) and hard ($F(1,28) = 66.16$; $p < 0.0001$, $\eta^2 = 0.70$).

In summary, the results showed that peak amplitudes of RN (150–300 ms) under sham WML were more negative than those in response to both easy and hard loads. Peak amplitudes of LP under sham-load were less positive than those under hard load.

4. Discussion

We studied the effects of working memory load (WML) on reversals of ambiguous figures in discontinuous stimulus presentation (Kornmeier & Bach, 2004; Leopold et al., 2002; Orbach et al., 1966) while measuring ERPs. The results revealed that the WML manipulation was successful as accuracy in response to the memory probes decreased and response times increased when working memory was loaded. These findings confirm that the WML levels were appropriately selected.

Nevertheless, WML did not alter the frequency of perceptual reversals in discontinuous presentation of the Necker cube. However, when WML was manipulated in an otherwise similar behavioral experiment, but the Necker cube was *constantly* presented for 10 s, WML decreased the frequency of perceptual reversals (Intaité, Koivisto, & Castelo-Branco, *in press*). This pattern suggests that the mechanism(s) responsible for perceptual reversals in discontinuous and continuous presentation paradigms could be operating in a different manner (Noest, Van Ee, Nijs, & van Wezel, 2007; Pastukhov & Braun, 2013). However, it is important to note that the reversal rates obtained with the discontinuous presentation may be influenced by the type and duration of the stimuli, the ISI between the first and second stimuli in the pairs, and the gap duration after the response (Kornmeier et al., 2007; Leopold et al., 2002; Maier et al., 2003; Noest et al., 2007; Orbach, Ehrlich, & Heath, 1963; Orbach et al., 1966; Pastukhov & Braun, 2013). Our stimulation parameters are very similar to those in most of the ERP studies on perception of ambiguous stimuli (Kornmeier & Bach, 2004, 2005; Kornmeier et al., 2007; Kornmeier, Pfäffle, & Bach, 2011; Qiu et al., 2009),

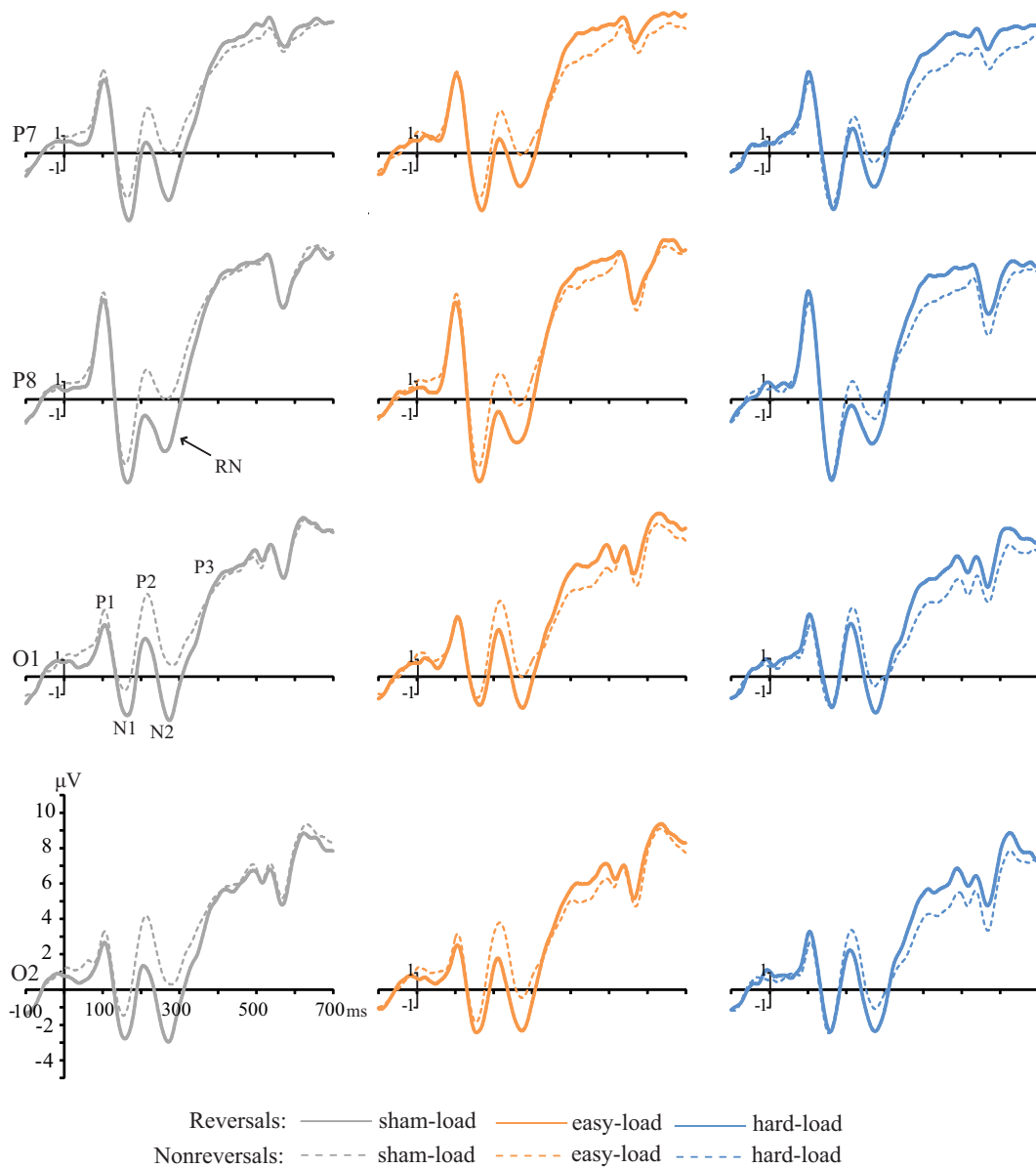


Fig. 5. Grand-average ERP waveforms in response to the second stimulus display in trials where participants reported reversals under sham (light gray lines), easy (dark gray (orange in the web version) lines) and hard (black (blue in the web version) lines) working memory load and when they did not report reversals under sham (dashed light gray lines), easy (dashed dark gray (orange in the web version) lines) or hard (dashed black (blue in the web version) lines) working memory load over temporal and occipital areas. Reversal Negativity (RN; enhanced negativity in response to reversals) was observed between 140 and 280 ms (N1, P2, N2 time windows).

but less similar in comparison with the paradigms used by Britz, Landis, & Michel (2009), Pitts et al. (2007),(2008); Pitts, Martínez, Stalmaster, Nerger, & Hillyard (2009).

Satiation (i.e., neural adaptation) theory (Toppino & Long, 1987) would predict no effects of WML on the frequency of perceived reversals, or on reversal-related ERPs. Thus, the behavioral data of our study supports this theory. However, WML induced a graded amplitude decrease on the amplitudes of RN (i.e., enhanced negativity in response to reversals about 150–300 ms post-stimulus), suggesting that concurrent top-down effects are present. This shift from negativity toward positivity as a function of WML continued in P3 time window (i.e., LP), a later component frequently reported in ERP studies of visual bistability (Britz et al., 2009; Kornmeier & Bach, 2004,2005; Kornmeier et al., 2007; Pitts et al., 2008; Qiu et al., 2009). This component has been suggested to be related to post-perceptual processes taking place after figure disambiguation (Pitts et al., 2008; Qiu et al., 2009). More specifically, its amplitude was higher, more positive, in the hard-load condition than in the sham-load condition

at central electrode sites. The enhanced LP supports the view that enhanced amplitudes of P3-related ERPs indicate the larger amount of mental capacity invested in the task (Kok, 2001; Sirevaag, Kramer, Coles, & Donchin, 1989). Enhanced P3-type potentials in response to task-relevant stimuli under harder WML have previously been reported in studies using other types of visual stimulation (Jongen & Jonkman, 2011; Jonkman et al. 2000). In addition, the data is consistent with the dual-task ERP literature, which shows that modulation of the difficulty of one task leads to reduced processing in response to another task (Jongen & Jonkman, 2011; Jonkman et al., 2000; Singhal & Fowler, 2004). Given that reversal rates were not influenced by the working memory load, the shift toward positivity in the reversal-related ERP components (RN, LP) may reflect influences of load on 'late' processing phases of ambiguous stimuli.

We found reversal-related electrophysiological differences already during the presentation of the first cube. The trials associated with perceptual reversals elicited an intriguing pre-reversal negativity (PRN) roughly 600 ms before the appearance of

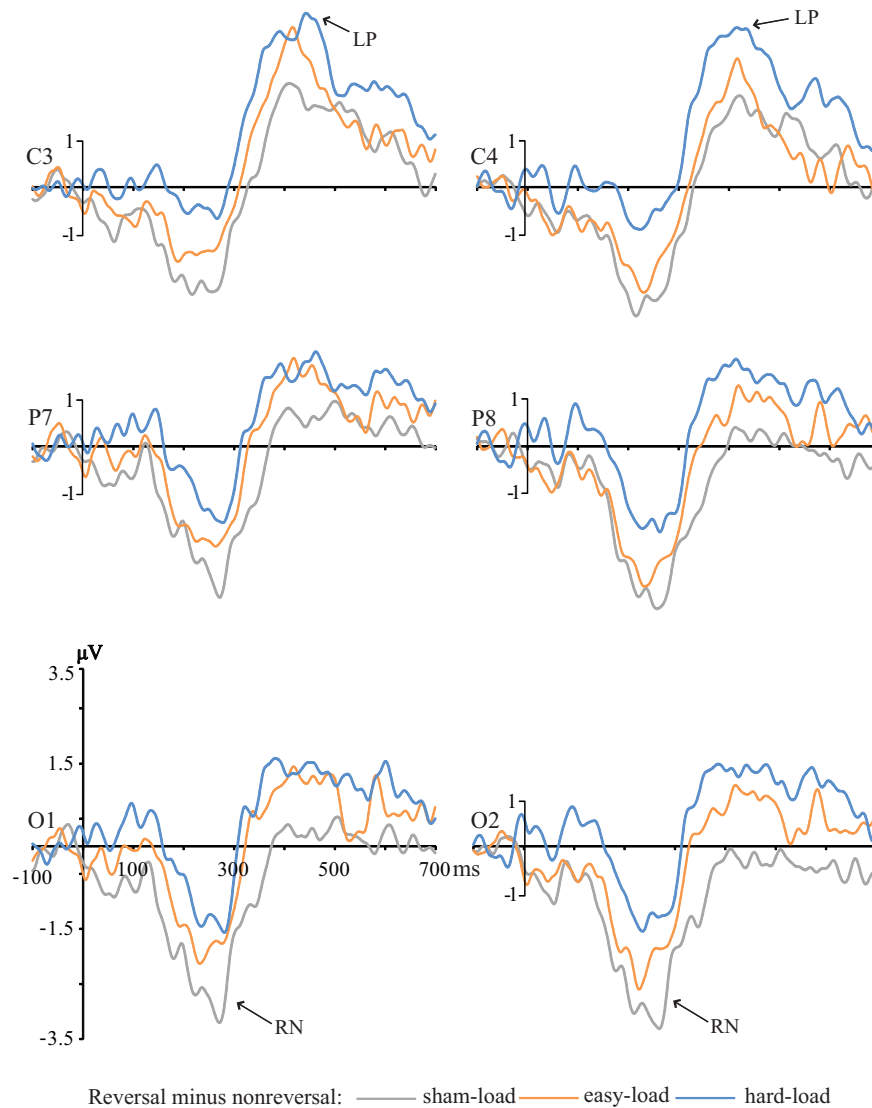


Fig. 6. The difference waves (reversal – nonreversal) from the central, temporal and occipital areas illustrate the reversal-related effects in ERPs. Reversal negativity (RN) was significant over occipital areas 150–300 ms post stimulus and Late Positivity (LP) was observed over central areas 300–500 ms post stimulus in response to perceptual reversals.

the second cube which was not influenced by WML. This implies that the neural processes which determine the possible occurrence of reversals start when the participants are viewing the first cube. These observations are in line with the findings of reversal related brain activity just before the onset of the to-be-reversed stimulus (or right at it) (Britz et al., 2009; Britz, Pitts, & Michel, 2011; Intaitė et al., 2013), suggesting that the processes during the first cube in discontinuous presentation may be as important or even more important in determining the occurrence of reversals than the ones which are occurring during the second cube and which are reflected in RN and LP. Furthermore, we obtained more positive ERPs over the first cube in response to WML. However, WML did not influence the PRN which occurred in the same time windows. Thus, we conclude that perceptual reversals in the discontinuous (under the conditions of this experiment) presentation mode are likely based on a rather early (anticipatory) mechanism and occur with minimal attentional resources. Moreover, the results of the current experiment converge with the results of the study in which the participants were asked to detect perceptual reversals of discontinuously presented Necker lattices

and concurrently performed a perceptual load task (Intaitė et al., 2013). Intaitė et al. (2013) concluded that during the discontinuous presentation the reversals occur almost without attention. However, because the perceptual load task was presented simultaneously with the onset of the second stimulus, their manipulation of load could influence only the processing of the second stimulus. Our data extend and strengthen the conclusion of Intaitė et al. (2013) as here the WML encompassed the processing of both first stimulus and the second (reversed) stimulus.

Kornmeier & Bach (2012) proposed an integrative theory which states that two perceptual processes are operating during an observation of the ambiguous figure: destabilization and restabilization (disambiguation). First, the “currently seen” percept gets destabilized in a rather slow manner and then it is followed by a fast restabilisation of the “not seen percept”, resulting in a perceptual reversal. The integrative theory suggests separate ERP correlates of restabilization and destabilization. Destabilization related ERPs should be obtained before the stimulus is perceived as reversed, that is, before the second stimulus in a pair of ambiguous stimuli is presented. In this view, the PRN we observed

during the first cube can be considered as an ERP correlate of destabilization. However, we did not find the Reversal Positivity – restabilization correlate of perceptual reversals.

Although our results suggest that reversals are based on an early mechanism, this does not exclude the option that observers can intentionally manipulate their perception when the ambiguous images are presented continuously (Hochberg & Peterson, 1987; Kornmeier et al., 2009; Liebert & Burk, 1985; Pelton & Soley, 1968; Peterson & Hochberg, 1983; Strüber & Stadler, 1999; Toppino, 2003; Van Ee, Van Dam, & Brouwer, 2005) or even intermittently (Kornmeier et al., 2009; Pitts et al., 2008). However, sheer volitional effort is not sufficient to prevent involuntary reversals from occurring (Kornmeier et al., 2009; Toppino, 2003); thus intentional processing or attention does not fully explain the reversals – they may have only a modulatory influence. There is also evidence that the prefrontal cortex plays a modulatory role in of perceptual ambiguity, but its exact function is not clarified yet (Kleinschmidt, Büchel, Zeki, & Frackowiak, 1998; Lumer & Rees, 1999; Ricci & Blundo, 1990; Sterzer, Kleinschmidt, & Rees, 2009; Sterzer & Rees, 2008; Windmann, Wehrmann, Calabrese, & Güntürkün, 2006). However, according to our knowledge, all the studies suggesting involvement of the prefrontal cortex in the perception of ambiguous stimuli (Kleinschmidt et al., 1998; Lumer & Rees, 1999; Ricci & Blundo, 1990; Sterzer & Rees, 2008; Windmann et al., 2006) used continuous presentation mode. As the reversals of constantly presented ambiguous stimuli might be influenced by higher level mechanisms more than the reversals of discontinuously presented stimuli (Noest et al., 2007; Pastukhov & Braun, 2013), the top-down manipulations could have an effect on reversal rates during continuous presentation, whereas during discontinuous presentation, the top-down manipulations would have little influence on reversal rates although they could modulate the amplitudes of RN and LP, components that occur after the earlier mechanisms have been engaged (i.e., during the first cube or early after the onset of the second cube), without having a causal influence on reversal rates. Thus, we conclude that perceptual reversals occur with minimal attentional resources and are governed by an early (preceding pending reversals) mechanism under the discontinuous presentation mode which was used here and which is similar to the presentation mode in frequent previous ERP studies (Kornmeier & Bach, 2004, 2005; Kornmeier et al., 2007, 2011; Qiu et al., 2009) on perceptual bistability.

Acknowledgments

This study was supported by the fellowship (SFRH/BPD/77563/2011) to M.I. and PEst-C/SAU/UI3282/2013, CENTRO-07-ST24-FEDER-00205 Grants to M.C.B. from Portuguese Foundation of Science and Technology. M.K. was supported by the Academy of Finland (Projects 125175 and 218272). The authors would like to thank Dr. Gabriel N. Costa for helpful comments and suggestions on the earlier versions of the manuscript. We would like to thank two anonymous reviewers for their helpful comments and suggestions.

References

- Awh, E., & Jonides, J. (2001). Overlapping mechanisms of attention and spatial working memory. *Trends in Cognitive Sciences*, 5, 119–126, [http://dx.doi.org/10.1016/S1364-6613\(00\)01593-X](http://dx.doi.org/10.1016/S1364-6613(00)01593-X).
- Awh, E., Jonides, J., & Reuter-Lorenz, P. A. (1998). Rehearsal in spatial working memory. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 780–790, <http://dx.doi.org/10.1037/0096-1523.24.3.780>.
- Basar-Eroglu, C., Strüber, D., Stadler, M., & Kruse, P. (1993). Multistable visual perception induces a slow positive EEG wave. *International Journal of Neuroscience*, 73, 139–151, <http://dx.doi.org/10.3109/00207459308987220>.
- Brascamp, J. W., Knapen, T. H. J., Kanai, R., Noest, A. J., van Ee, R., & van den Berg, A. V. (2008). Multi-timescale perceptual history resolves visual ambiguity. *PLoS One*, 3, e1497, <http://dx.doi.org/10.1371/journal.pone.0001497>.
- Britz, J., Landis, T., & Michel, C. M. (2009). Right parietal brain activity precedes perceptual alternation of bistable stimuli. *Cerebral Cortex*, 19, 55–65, <http://dx.doi.org/10.1093/cercor/bhn056>.
- Britz, J., Pitts, M. A., & Michel, C. M. (2011). Right parietal brain activity precedes perceptual alternation during binocular rivalry. *Human Brain Mapping*, 32, 1432–1442, <http://dx.doi.org/10.1002/hbm.21117>.
- Cowan, N. (2001). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences*, 24, 87–185, <http://dx.doi.org/10.1017/S0140525x01003922>.
- Donchin, E., & Coles, M. G. (1988). Is the P300 component a manifestation of context updating? *Behavioral and Brain Sciences*, 11, 357–427, <http://dx.doi.org/10.1017/S0140525x00058027>.
- Hochberg, J., & Peterson, M. A. (1987). Piecemeal organization and cognitive components in object perception: Perceptually coupled responses to moving objects. *Journal of Experimental Psychology: General*, 116, 370–380, <http://dx.doi.org/10.1037/0096-3445.116.4.370>.
- Intaite, M., Koivisto, M., & Castelo-Branco, M. (2014). The linear impact of concurrent working memory load on dynamics of Necker cube perceptual reversals. *Journal of Vision*, 14, 1–9, <http://dx.doi.org/10.1167/14.1.13>.
- Intaite, M., Koivisto, M., & Revonsuo, A. (2013). Perceptual reversals of Necker stimuli during intermittent presentation with limited attentional resources. *Psychophysiology*, 50, 82–96, <http://dx.doi.org/10.1111/j.1469-8986.2012.01486.x>.
- Intaite, M., Koivisto, M., Rukšenas, O., & Revonsuo, A. (2010). Reversal negativity and bistable stimuli: Attention, awareness, or something else? *Brain and Cognition*, 74, 24–34, <http://dx.doi.org/10.1016/j.bandc.2010.06.002>.
- Intaite, M., Noreika, V., Šoliūnas, A., & Falter, C. M. (2013). Interaction of bottom-up and top-down processes in the perception of ambiguous figures. *Vision Research*, 89, 24–31, <http://dx.doi.org/10.1016/j.visres.2013.06.011>.
- Jongen, E. M. M., & Jonkman, L. M. (2011). Effects of concurrent working memory load on distractor and conflict processing in a name-face Stroop task. *Psychophysiology*, 48, 31–43, <http://dx.doi.org/10.1111/j.1469-8986.2010.01037.x>.
- Jonkman, L. M., Kemner, C., Verbaten, M. N., Van Engeland, H., Camfferman, G., Buitelaar, J. K., et al. (2000). Attentional capacity, a probe ERP study: Differences between children with attention-deficit hyperactivity disorder and normal control children and effects of methylphenidate. *Psychophysiology*, 37, 334–346, <http://dx.doi.org/10.1111/1469-8986.3730334>.
- Kleinschmidt, A., Büchel, C., Zeki, S., & Frackowiak, R. S. J. (1998). Human brain activity during spontaneously reversing perception of ambiguous figures. *Proceedings of the Royal Society B: Biological Sciences*, 265, 2427–2433, <http://dx.doi.org/10.1098/rspb.1998.0594>.
- Knapen, T., Brascamp, J., Adams, W. J., & Graf, E. W. (2009). The spatial scale of perceptual memory in ambiguous figure perception. *Journal of Vision*, 9, 1–12, <http://dx.doi.org/10.1167/9.13.16>.
- Kok, A. (2001). On the utility of P3 amplitude as a measure of processing capacity. *Psychophysiology*, 38, 557–577, <http://dx.doi.org/10.1017/S0048577201990559>.
- 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, <http://dx.doi.org/10.1046/j.1469-8986.2003.00126.x>.
- Kornmeier, J., & Bach, M. (2005). The Necker cube – An ambiguous figure disambiguated in early visual processing. *Vision Research*, 45, 955–960, <http://dx.doi.org/10.1016/j.visres.2004.10.006>.
- Kornmeier, J., & Bach, M. (2012). Ambiguous figures – what happens in the brain when perception changes but not the stimulus. *Frontiers in Human Neuroscience*, 6, 1–23, <http://dx.doi.org/10.3389/fnhum.2012.00051>.
- 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, <http://dx.doi.org/10.1111/j.1469-8986.2007.00525.x>.
- Kornmeier, J., Hein, C. M., & Bach, M. (2009). Multistable perception: When bottom-up and top-down coincide. *Brain and Cognition*, 69, 138–147, <http://dx.doi.org/10.1016/j.bandc.2008.06.005>.
- Kornmeier, J., Pfäffle, M., & Bach, M. (2011). Necker cube: Stimulus-related (low-level) and percept-related (high-level) EEG signatures early in occipital cortex. *Journal of Vision*, 11, 1–11, <http://dx.doi.org/10.1167/11.9.12>.
- Kumar, S., Soto, D., & Humphreys, G. W. (2009). Electrophysiological evidence for attentional guidance by the contents of working memory. *The European Journal of Neuroscience*, 30, 307–317, <http://dx.doi.org/10.1111/j.1460-9568.2009.06805.x>.
- Leopold, D. A., & Logothetis, N. K. (1999). Multistable phenomena: Changing views in perception. *Trends in Cognitive Sciences*, 3, 254–264, [http://dx.doi.org/10.1016/S1364-6613\(99\)01332-7](http://dx.doi.org/10.1016/S1364-6613(99)01332-7).
- Leopold, D. A., Wilke, M., Maier, A., & Logothetis, N. K. (2002). Stable perception of visually ambiguous patterns. *Nature Neuroscience*, 5, 605–609, <http://dx.doi.org/10.1038/nn851>.
- Liebert, R., & Burk, B. (1985). Voluntary control of reversible figures. *Perceptual and Motor Skills*, 61, 1307–1310, <http://dx.doi.org/10.2466/pms.1985.61.3f.1307>.
- Long, G. M., & Toppino, T. C. (2004). Enduring interest in perceptual ambiguity: Alternating views of reversible figures. *Psychological Bulletin*, 130, 748–768, <http://dx.doi.org/10.1037/0033-2909.130.5.748>.
- 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, <http://dx.doi.org/10.3758/BF03205893>.
- Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature*, 390, 279–281, <http://dx.doi.org/10.1038/36846>.

- Lumer, E. D., & Rees, G. (1999). Covariation of activity in visual and prefrontal cortex associated with subjective visual perception. *Proceedings of the National Academy of Sciences of the United States of America*, 96, 1669–1673, <http://dx.doi.org/10.1073/pnas.96.4.1669>.
- Maier, A., Wilke, M., Logothetis, N. K., & Leopold, D. A. (2003). Perception of temporally interleaved ambiguous patterns. *Current Biology*, 13, 1076–1085, [http://dx.doi.org/10.1016/S0960-9822\(03\)00414-7](http://dx.doi.org/10.1016/S0960-9822(03)00414-7).
- Noest, A. J., Van Ee, R., Nijs, M. M., & van Wezel, R. J. A. (2007). Percept-choice sequences driven by interrupted ambiguous stimuli: A low-level neural model. *Journal of Vision*, 7, 1–14, <http://dx.doi.org/10.1167/7.8.10>.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, 9, 97–113, [http://dx.doi.org/10.1016/0028-3932\(71\)90067-4](http://dx.doi.org/10.1016/0028-3932(71)90067-4).
- 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, <http://dx.doi.org/10.2466/pms.1963.17.2.439>.
- 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, <http://dx.doi.org/10.2466/pms.1966.22.2.615>.
- Pastukhov, A., & Braun, J. (2013). Structure-from-motion: Dissociating perception, neural persistence, and sensory memory of illusory depth and illusory rotation. *Attention, Perception & Psychophysics*, 75, 322–340, <http://dx.doi.org/10.3758/s13414-012-0390-0>.
- Pearson, J., & Brascamp, J. (2008). Sensory memory for ambiguous vision. *Trends in Cognitive Sciences*, 12, 334–341, <http://dx.doi.org/10.1016/j.tics.2008.05.006>.
- Pelton, L., & Soley, C. (1968). Acceleration of reversals of a Necker cube. *The American Journal of Psychology*, 81, 585–588, <http://dx.doi.org/10.2307/1421064>.
- Peterson, M., & Hochberg, J. (1983). Opposed-set measurement procedure: A quantitative analysis of the role of local cues and intention in form perception. *Journal of Experimental Psychology: Human Perception and Performance*, 9, 183–193, <http://dx.doi.org/10.1037/0096-1523.9.2.183>.
- 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, <http://dx.doi.org/10.1016/j.bandc.2007.10.004>.
- Pitts, M. A., Martínez, A., Brewer, J. B., & Hillyard, S. A. (2011). Early stages of figure-ground segregation during perception of a face-vase. *Journal of Cognitive Neuroscience*, 23, 880–895, <http://dx.doi.org/10.1162/jocn.2010.21438.Early>.
- Pitts, M. A., Martínez, A., Stalmaster, C., Nerger, J. L., & Hillyard, S. A. (2009). Neural generators of ERPs linked with Necker cube reversals. *Psychophysiology*, 46, 694–702, <http://dx.doi.org/10.1111/j.1469-8986.2009.00822.x>.
- 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, <http://dx.doi.org/10.1167/7.1.6>.
- 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, <http://dx.doi.org/10.1016/j.ijpsycho.2009.07.006>.
- Ricci, C., & Blundo, C. (1990). Perception of ambiguous figures after focal brain lesions. *Neuropsychologia*, 28, 1163–1173, [http://dx.doi.org/10.1016/0028-3932\(90\)90052-P](http://dx.doi.org/10.1016/0028-3932(90)90052-P).
- Singhal, A., & Fowler, B. (2004). The differential effects of Sternberg short- and long-term memory scanning on the late Nd and P300 in a dual-task paradigm. *Cognitive Brain Research*, 21, 124–132, <http://dx.doi.org/10.1016/j.cogbrainres.2004.06.003>.
- Sirevaag, E., Kramer, A., Coles, M., & Donchin, E. (1989). Resource reciprocity: An event-related brain potentials analysis. *Acta Psychologica (Amst)*, 70, 77–97, [http://dx.doi.org/10.1016/0001-6918\(89\)90061-9](http://dx.doi.org/10.1016/0001-6918(89)90061-9).
- Smyth, M. M., & Scholey, K. A. (1994). Interference in immediate spatial memory. *Memory & Cognition*, 22, 1–13, <http://dx.doi.org/10.3758/BF03202756>.
- Sterzer, P., Kleinschmidt, A., & Rees, G. (2009). The neural bases of multistable perception. *Trends in Cognitive Sciences*, 13, 310–318, <http://dx.doi.org/10.1016/j.tics.2009.04.006>.
- Sterzer, P., & Rees, G. (2008). A neural basis for percept stabilization in binocular rivalry. *Journal of Cognitive Neuroscience*, 20, 389–399, <http://dx.doi.org/10.1162/jocn.2008.20039>.
- Strüber, D., & Stadler, M. (1999). Differences in top-down influences on the reversal rate of different categories of reversible figures. *Perception*, 28, 1185–1196, <http://dx.doi.org/10.1068/p2973>.
- Toppino, T. C. (2003). Reversible-figure perception: Mechanisms of intentional control. *Perception & Psychophysics*, 65, 1285–1295, <http://dx.doi.org/10.3758/BF03194852>.
- Toppino, T. C., & Long, G. M. (1987). Selective adaptation with reversible figures: Don't change that channel. *Perception & Psychophysics*, 42, 37–48, <http://dx.doi.org/10.3758/BF03211512>.
- Van Ee, R., Van Dam, L. C. J., & Brouwer, G. J. (2005). Voluntary control and the dynamics of perceptual bi-stability. *Vision Research*, 45, 41–55, <http://dx.doi.org/10.1016/j.visres.2004.07.030>.
- Vogel, E. K., & Awh, E. (2008). How to exploit diversity for scientific gain: Using individual differences to constrain cognitive theory. *Current Directions in Psychological Science*, 17, 171–176, <http://dx.doi.org/10.1111/j.1467-8721.2008.00569.x>.
- Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature*, 428, 748–751, <http://dx.doi.org/10.1038/nature02447>.
- Vogel, E. K., McCollough, A. W., & Machizawa, M. G. (2005). Neural measures reveal individual differences in controlling access to working memory. *Nature*, 438, 500–503, <http://dx.doi.org/10.1038/nature04171>.
- 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, <http://dx.doi.org/10.1162/089892906775990570>.