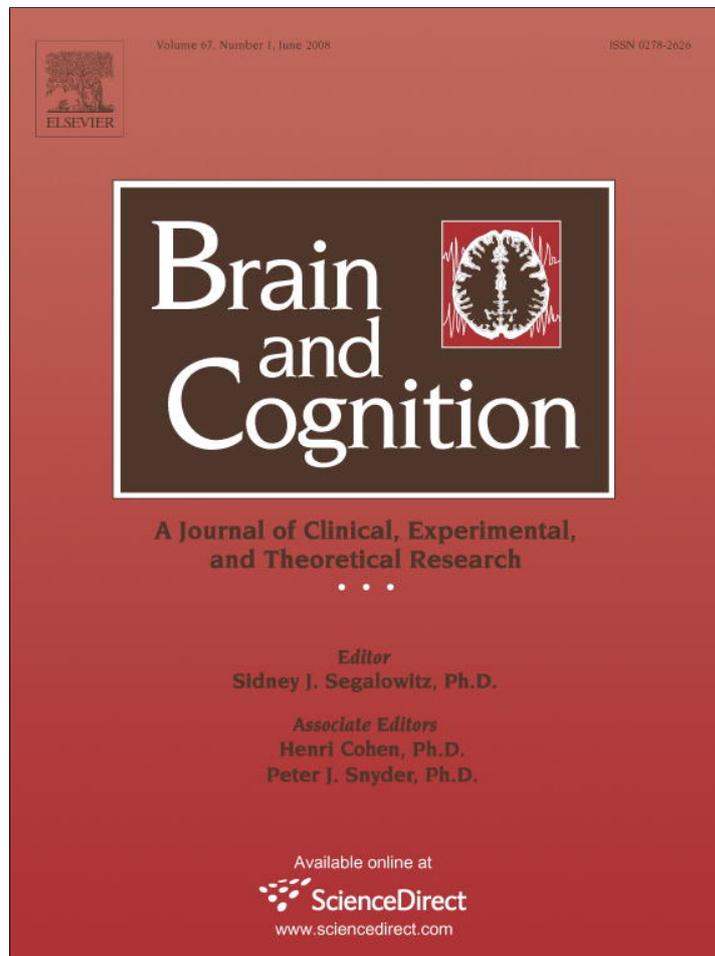


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Early top-down influences on bistable perception revealed by event-related potentials

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Abstract

A longstanding debate exists in the literature concerning bottom-up vs. top-down influences on bistable perception. Recently, a technique has been developed to measure early changes in brain activity (via ERPs) related to perceptual reversals (Kornmeier & Bach, 2004). An ERP component, the reversal negativity (RN) has been identified, and is characterized as an increase in negative potential over the posterior scalp from 150 to 350 ms for perceptual reversals compared to perceptual stability. This finding, although interesting, has not helped resolve issues related to the bottom-up vs. top-down debate because top-down influences have not been directly manipulated. The current study focused on resolving some of these issues by measuring the RN while observers maintained one of three ‘intentional approaches’, (1) try to reverse perception as often as possible, (2) try to stabilize perception for as long as possible, and (3) maintain a passive approach. Enhancements in RN amplitude were found for the intention-to-reverse condition compared to the passive condition. This finding suggests an early influence (150 ms) of top-down control on perceptual reversals of bistable figures. Results are discussed in terms of competing attention shifting vs. fatigue-based theories of bistable perception.

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Keywords: Bistable perception; Bistable figures; Reversal negativity; Perceptual reversals; Top-down; ERPs; Selective attention; Object perception

1. Introduction

Bistable figures are visual stimuli in which physical input to the retina remains constant, while distinct changes (“reversals”) in object perception occur (see Fig. 1). Use of such stimuli in the laboratory provides a unique advantage in that endogenous influences on object perception can be measured while exogenous factors remain unchanged. While it is clear that perceptual reversals of bistable figures are endogenous in nature, the roles of bottom-up (involuntary) vs. top-down (voluntary) processes in perceptual reversals are not well understood. Recently, event-related potentials (ERPs) have been employed to measure the

time-course of changes in brain activity correlated with perceptual reversals of bistable figures. Such temporally precise measurements may help answer some of the outstanding questions about bottom-up vs. top-down influences on bistable perception.

Previous ERP studies of bistable perception (Basar-Eroglu, Struber, Stadler, & Kruse, 1993; Isoglu-Alkac et al, 1998; Kornmeier & Bach, 2004, 2005; O’Donnel, Hendler, & Squires, 1988; Pitts, Nerger, & Davis, 2007) identified a late positive component, or LPC (originally described as ‘P300-like’) with a central-posterior scalp distribution related to perceptual reversals. The LPC (or P300) is thought to represent ‘context updating’ processes in visual short-term memory (VSTM) (Donchin & Coles, 1988; Luck, 2005; Picton, 1992). Specifically, the amplitude of the LPC is enhanced when the current perceptual/motor context needs to be updated (Donchin & Coles, 1988). In bistable perception studies, it is likely that LPC amplitude

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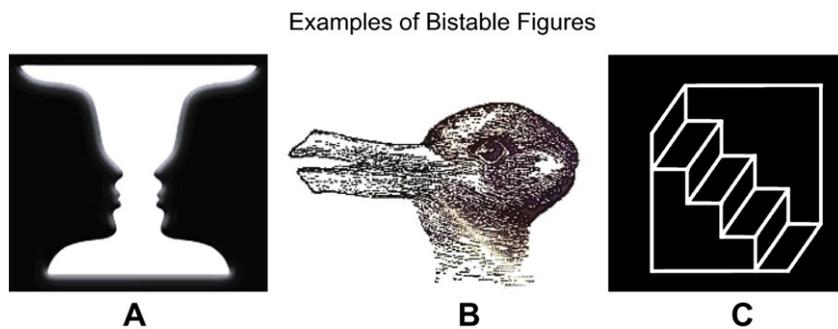


Fig. 1. Examples of bistable stimuli. Rubin's face/vase (A) can be seen as two face profiles or as one central vase. Jastrow's duck/rabbit (B) can be seen as a left facing duck or a right facing rabbit. Schroeder's staircase (C) can be seen as three up-right stairs or as four upside-down stairs.

enhancements for perceptual reversals represent the updating of VSTM because while the stimulus is physically the same, the current perception has changed. Due to the timing (350–650 ms) and functional interpretation (context updating in VSTM) of the LPC, this component most likely represents *post*-perceptual processing that occurs after figure disambiguation.

Recently, Kornmeier and Bach (2004) found that presenting temporally discontinuous stimuli (800 ms duration; 400 ms ISI) while time-locking recordings to stimulus onset, produced much sharper and more clearly defined ERP components that may represent perceptual or *pre*-perceptual processing. In their paradigm, perceptual reversals are entrained to stimulus onset, i.e. reversals occur across stimulus presentations, and only one of the two percepts is experienced during the 800 ms stimulus duration (see Pitts et al., 2007 for a movie demonstration of this stimulus presentation paradigm).

Using this new paradigm, Kornmeier and Bach (2004) identified an early ERP component related to endogenous reversals of a Necker lattice, a figure composed of nine Necker cubes in a 3×3 lattice (Fig. 2). They characterized this component by computing difference waves from stability and reversal trials. The largest difference between the two waveforms was recorded at occipital and parietal (posterior) electrode sites, and began at about 150 ms and peaked at 250 ms post-stimulus onset. The authors coined the term “reversal negativity” (RN) to describe the increase in negative ERP amplitude for reversals. In a second study, an earlier reversal component was identified, the “reversal positivity”, which began at about 100 ms, peaked at 120 ms post-stimulus onset, and was recorded at posterior electrode locations (Kornmeier & Bach, 2005). Attempts to replicate this early reversal positivity have produced mixed results however, possibly due to the large number of trials necessary to identify differences in such early components (Pitts et al., 2007). Kornmeier and Bach (2004, 2005) interpreted these ERP differences as evidence for ‘early disambiguation’ of the bistable figure.

A recent study in our laboratory (Pitts et al., 2007), aimed at determining the generalizability of these ERP differences to other types of bistable stimuli, found P1 (≈ 120 ms), N1 (≈ 175 ms), and RN (170–370 ms) effects related to perceptual reversals. Based on previous electro-

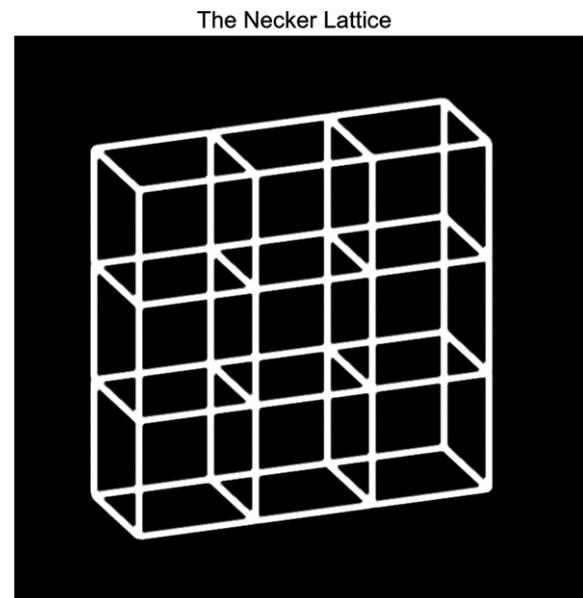


Fig. 2. The Necker lattice is composed of nine Necker cubes stacked on top of each other in a 3×3 array (Kornmeier & Bach, 2004). To reverse this image, view the lattice as ‘one big cube’. The ‘near-face’ can be perceived as popping-out toward the top-left or the bottom-right.

physiological, brain imaging, and neuropsychological research, we interpreted these ERP effects as evidence for a role of selective attention in bistable perception. Rather than assuming that the figure must have been disambiguated by the time the first ERP differences emerged, we hypothesize that these early ERP effects represent shifts in selective attention that precede figure disambiguation. For example, in other studies, P1 and N1 amplitude enhancements have been shown to represent spatial selection processes (Clark & Hillyard, 1996; Hillyard & Anllo-Vento, 1998; Hillyard, Vogel, & Luck, 1998; Luck et al, 1994; Mangun, 1995). We suggest that covert attention must be directed toward locations within bistable figures in order for features in those locations to be perceived as ‘nearest’ (e.g. either the bottom-right or top-left corners in Fig. 2). Also, the selection negativity (SeN) component (recorded at 150–350 ms post-stimulus) is known to be associated with selective attention to visual features such as color, motion, and orientation (Anllo-Vento & Hillyard, 1996; Hillyard & Anllo-Vento, 1998; Martin-Loeches,

Hinojosa, & Rubia, 1999; Michie et al, 1999; Smid, Jakob, & Heinze, 1997; Smid, Jakob, & Heinze, 1999; Valdes-Sosa, Bobes, Rodriguez, & Pinilla, 1998). Interestingly, the timing, polarity, and scalp topography of the SeN and the RN are very similar. If these two components are in fact identical, the RN might represent pre-disambiguation processes, i.e. selective attention.

One way to investigate the attention hypothesis of bistable perception is to introduce conditions involving voluntary control. If the RN is functionally equivalent to the SeN, we would expect the RN to be influenced by top-down attentional control. In all three experiments that have employed the new stimulus presentation paradigm (Kornmeier & Bach, 2004, 2005; Pitts et al., 2007), observers were instructed to 'allow reversals to occur naturally', i.e. only ERPs associated with *involuntary* reversals have been measured so far. Numerous behavioral studies have shown that reversals can be influenced by observers' intentions (e.g. Horlitz & O'Leary, 1993; Kawabata, 1986; Leopold & Logothetis, 1999; Liebert & Burk, 1985; Long & Toppino, 2004; Meng & Tong, 2004; Pelton & Solley, 1968; Rock, Hall, & Davis, 1994; Shulman, 1993; Struber & Stadler, 1999; Toppino, 2003; van Ee, 2005; van Ee, van Dam, & Brouwer, 2005; Windmann, Wehrmann, Calabrese, & Gunturkun, 2006). In a recent study, van Ee and colleagues (van Ee, 2005; van Ee et al., 2005) measured changes in reversal rates of various bistable stimuli under conditions involving voluntary control. Observers were asked in one condition to "speed-up reversals" and in another condition to "hold one percept stable for as long as possible" (van Ee et al., 2005). For the Necker cube, observers were able to increase the reversal rate when instructed to speed-up reversals. They were also able to decrease the reversal rate when instructed to hold one percept stable. From this research as well as from earlier work (e.g. Ammons, Ulrich, & Ammons, 1960; Kawabata, 1986; Pelton & Solley, 1968), it is clear that some degree of intentional (voluntary) control over Necker cube reversal rates is attainable. What is unknown however is when and how these top-down control mechanisms influence visual processing.

The goal of the current investigation was to compare ERPs associated with *voluntary* (intentional; top-down) perceptual reversals to those associated with *involuntary* (unintentional; bottom-up) reversals. An enhancement of RN amplitude for intentional vs. unintentional reversals would suggest early top-down influences on bistable perception, and would provide further support for the selective attention shifting theory of perceptual reversals.

2. Methods

2.1. Participants

A total of 52 observers (13 male, 39 female; ages 18–22, mean age 19) were recruited from an undergraduate psychology class. Each received two research participation

credits required for their course. Eye dominance was determined via simple dichoptic tests and visual acuity was assessed via a high-contrast Bailey-Lovie acuity chart. All observers had foveal acuities of $\leq 20/40$. All procedures adhered to federal regulations and were approved by the Colorado State University institutional review board; written informed consent was obtained from each observer prior to participation in the experiment.

2.2. Stimuli

A perceptually bistable Necker lattice (provided by Kornmeier & Bach) served as the stimulus for all conditions (see Fig. 2). The Necker lattice subtended a viewing angle of $3.3^\circ \times 3.3^\circ$, and was presented on a Dell Monitor (Plug & Play Monitor on RADEON 7000, Microsoft Inc.) with a frame rate of 85 Hz. To avoid any visual persistence or effects of afterimages, the lattice image was randomly repositioned in space by 0.8° in both horizontal and vertical directions between presentations, resulting in five spatial variants. Observers maintained fixation on a small (0.2°) fixation cross in the center of the monitor which was visible throughout all stimulus presentations and inter-stimulus intervals (ISIs).

2.3. EEG recording

EEG scalp voltages were recorded using a Geodesic EEG System, NetAmps 200 [Electrical Geodesics Inc. (EGI)]. A 128-channel HydroCel Geodesic Sensor Net (EGI) held each electrode in place. Each carbon-fiber electrode consisted of a silver-chloride carbon fiber pellet, a lead wire, a gold plated pin, and a potassium chloride soaked sponge. This electrode configuration effectively blocks out electrochemical noise and minimizes triboelectric noise. Signals were amplified via an AC-coupled, 128-channel high-input impedance amplifier (NetAmps 200, EGI). Amplified analog voltages, hardware band-pass-filtered at 0.1–100 Hz, were digitized at a sampling rate of 500 Hz. A vertex electrode served as the ground for all recordings. All sensors were individually adjusted by the experimenter until the impedance of each was less than 50 k Ω . Impedances were also checked halfway through the experiment, and were adjusted if necessary.

2.4. Procedure

Observers were comfortably seated 1.4 m from the computer monitor in order to maintain an approximately constant retinal image size of the stimulus. Prior to any recordings, observers viewed a static version of the Necker lattice stimulus. If an observer was initially unable to perceive both perceptual interpretations, the experimenter helped guide the observer by tracing the outline of the alternative percept on the computer monitor until the observer could easily perceive both configurations.

Because reversal rates are known to increase during initial exposure to a novel bistable stimulus (Long & Toppino, 2004) practice trials were administered. The 180 practice trials (60 of each of the three intention conditions) served to familiarize the observers with the intention conditions, as well as the timing of stimulus presentation, the importance of fixating on the fixation cross, and the operation of the response box.

During all practice and experimental trials, the stimulus was flashed on the screen for 800 ms followed by a 400 ms ISI. Observers were instructed to either (a) press a response button indicating that their perception of the stimulus had reversed compared to the previous trial (reversal trials), or (b) wait for the next stimulus to appear without responding in the case of a non-reversal of the image (stability trials). Adopting the protocol used by Kornmeier and Bach (2004), the ISI was extended to 1000 ms following trials that elicited a perceptual reversal. Fig. 3 shows the stimulus presentation protocol. To obviate any effects of eye movements (Georgiades & Harris, 1997; Long & Toppino, 2004), participants maintained their gaze on a centrally located fixation cross. All stimuli were viewed monocularly with the dominant eye to eliminate binocular depth cues that can occasionally lead to ‘flatter’ appearances of these two-dimensional stimuli.

For all experimental trials, the stimulus was presented 150 times per block, resulting in blocks lasting approximately 6 min. Short breaks after each block helped to alleviate observer fatigue. Two blocks were run for each of the three intention conditions, resulting in 300 trials per condition. Prior to each experimental block, observers were provided written instructions on the monitor to maintain one of three intentional approaches: (1) try to increase reversals as much as possible (2) try to hold your perception stable as long as possible, or (3) remain passive, and allow reversals to occur naturally. EEG was recorded throughout the six experimental blocks, which were counterbalanced (in two sets of three) across intention conditions. Each experimental session lasted approximately 1.5 h.

2.5. Event-related potentials analyses

Following procedures of Kornmeier and Bach (2004), ERPs were time-locked to stimulus onset, baseline corrected at -200 to 0 ms, and low-pass filtered at 25 Hz. Trials were discarded from analysis if they contained an eye blink or eye movement artifact ($\text{EOG} > 70 \mu\text{V}$), or more than 20% of electrode channels exceeded defined signal amplitudes (average amplitude $>200 \mu\text{V}$, or transit amplitude $>100 \mu\text{V}$). On average, 26% of trials per individual were rejected due to a combination of these artifacts. Averaged-referenced ERPs were computed for each channel by calculating the differences between each channel and a spherical interpolation of the average of all 128-channels.

In order for a participant's data to be included in further analyses, at least 30 non-discarded trials per condition were required. This criterion ensured a reasonable signal/noise ratio in the averaged ERP waveforms. For the analysis of the passive condition ERPs (the replication phase), data from 11 observers were excluded based on this criterion. For analysis of the voluntary control ERPs, data from an additional 14 observers were excluded. It is worth noting that meeting the criterion of 30 trials per condition was influenced by task performance as well as production of artifacts. For example, in the ‘try to stabilize’ condition, eight of observers performed the task so well that too few reversals occurred for attainment of reasonable ERP signal/noise ratios.

Recordings were sorted by intention-perception combinations and averaged for each individual observer. This resulted in six ERP traces, i.e. one reversal and one stability waveform (defined by button-press vs. no button-press) for each of the three intention conditions (defined by the instructions given prior to each block). Nine pairs of electrode sites were chosen for statistical analysis: left, right, and center pairs at frontal, central, and posterior locations. Choice of electrode sites for analysis was based on three factors: 1) The reversal negativity component has been previously identified in posterior scalp regions (Kornmeier & Bach, 2004, 2005; Pitts et al., 2007), 2) The LPC is maximal

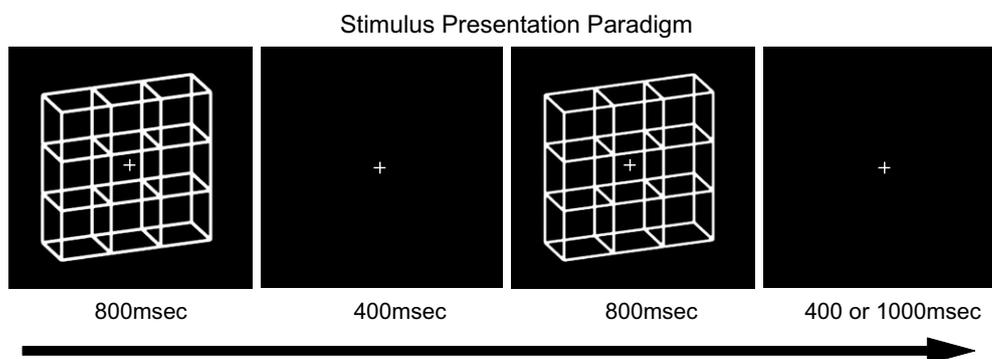


Fig. 3. To allow time-locking of the EEG recording to the stimulus rather than to the response, and to entrain the moment of perceptual reversals to an externally observable event, i.e. stimulus onset, stimuli were continuously flashed on-and-off in 800 ms stimulus/400 ms ISI presentations (adopted from Kornmeier & Bach, 2004). Observers indicated reversals by a button-press, which extended the ISI to 1000 ms before the next 800–400 ms cycle resumed.

at central and posterior scalp sites (Ji, Porjesz, Begleiter, & Chorlian, 1999) and 3) Frontal activity has been implicated in the voluntary control over perceptual reversals (Windmann et al., 2006). Fig. 4 shows the positions of these nine pairs of electrodes (see Luu & Ferree, 2005 for HydroCel/10-10 international conversions). For statistical analyses, amplitudes were averaged within each pair of electrode sites.

In the first phase of analyses, only data from the passive condition were used. Mean amplitudes of reversal and stability ERPs for each individual observer ($N = 44$) were measured for the RN (150–350 ms) and LPC (350–650 ms) relative to baseline (–200 to 0 ms). The variability of the mean amplitudes was estimated by 2×9 repeated-measures ANOVAs with the factors perception (stability or reversal) and scalp location (frontal-left, frontal-center, frontal-right, central-left, central-center, central-right, posterior-left, posterior-center, posterior-right). Post hoc t -tests were then conducted to evaluate the differences between reversal and stability ERP amplitudes at specific scalp locations during the RN and LPC time windows.

In the second phase of analyses, no significant differences were found across intention conditions for the stability ERPs, therefore difference waves (reversal ERPs minus stability ERPs) were derived and used in all subsequent analyses. This reduced the number of factors in the ANOVAs, and allowed a clearer graphical depiction of the scalp locations of the components of interest. Mean amplitudes

of RN (150–350 ms) and LPC (350–650 ms) were measured relative to baseline (–200 to 0 ms). For the RN component, a 3×3 repeated-measures ANOVA with the factors intention (try-to-reverse, try-to-stabilize, or passive) and scalp location (posterior-left, posterior-center, posterior-right) was used to measure the effect of intention. For the LPC, a second 3×3 repeated measures ANOVA with the factors intention and scalp location (central-left, central-center, central-right) was used to measure the effect of intention. To measure the effect of intention on a possible frontal counterpart to the RN (the frontal reversal positivity or FRP; discussed below), a third 3×3 ANOVA was conducted. The bon ferroni correction was applied to correct for multiple significance testing (critical p values = .016), and the greenhouse-geisser correction was used to account for non-sphericity.

3. Results

3.1. Behavioral results

Consistent with Kornmeier and Bach (2004, 2005) and Pitts et al. (2007), all observers reported perceiving reversals only at stimulus onset and never within the 800 ms duration of stimulus presentation. Reversal rates for the first phase of analyses (passive condition; $N = 44$) were 27%. These rates are consistent with previous research (Long & Toppino, 2004) in which reversals normally occur once every 3–4 s (25–33%). Reversal rates for the second phase of analyses ($N = 27$) differed across the three intention conditions as expected: passive (26%); intention-to-reverse (29%); intention-to-stabilize (23%). The effect of intention on reversal rate approached significance, $F(2, 78) = 3.095$, $p = .051$, and reversal rates in the intention-to-reverse condition were significantly higher than in the intention-to-stabilize condition (tested with Tukey's HSD multiple comparison test; $p = .039$). Fig. 5 shows the number of reversals reported in each of the three intention conditions for the original 52 observers as well as the more restricted set of 27 observers whose data were used for the analyses of the intention-based effects. The similarities between the two plots indicates that the exclusion criterion of 30 trials per condition did not artificially create a group who differed behaviorally.

Of the original 52 observers, 30 were able to successfully control reversal rates by intention (i.e. rates increased when the intention was to reverse, and decreased when the intention was to stabilize compared to the passive control condition). Of the 27 observers whose data passed the criterion for ERP analyses, 15 were able to successfully control reversal rates by intention. Six of these observers showed reduced reversal rates in both intention conditions compared to the passive condition. One observer experienced an increase in reversal rates for both intention conditions. Five of these observers exhibited reversal rates that were opposite of their intentions. Fig. 6 shows percentages of intention successes/failures for the original 52 observers

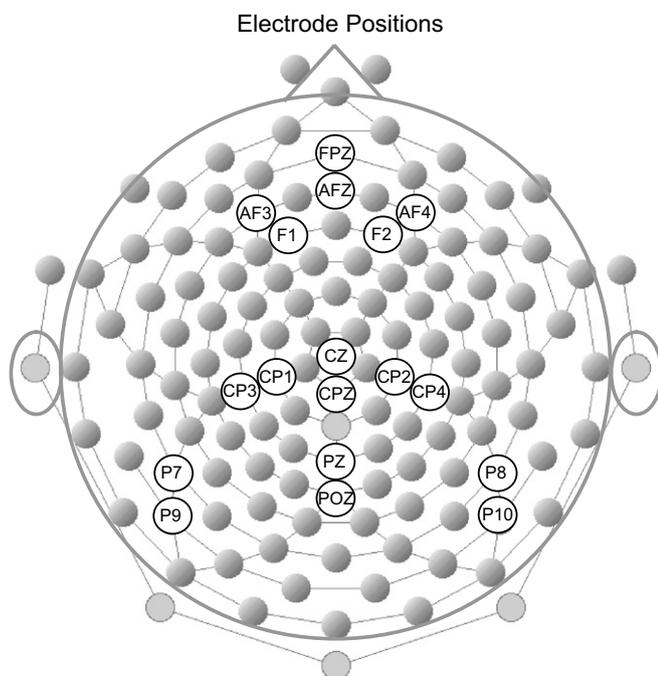


Fig. 4. Positions of electrodes used for statistical analyses. ERPs were averaged within each of the 9 electrode pairs: frontal-left (AF3&F1); frontal-center (FPZ&AFZ); frontal-right (AF4&F2); central-left (CP1&CP3); central-center (CZ&CPZ); central-right (CP2&CP4); posterior-left (P7&P9); posterior-center (PZ&POZ); and posterior-right (P8&P10).

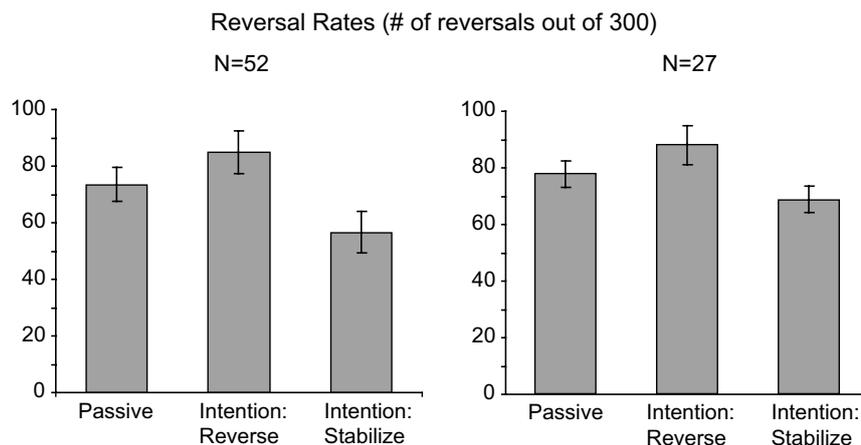


Fig. 5. Mean number of reversals (out of 300 total stimulus presentations) for the three intention conditions. The left plot shows the reversal rates for the original 52 observers while the right plot shows rates for the 27 observers whose data was used for the ERP analyses. Error bars represent ± 1 standard error of the mean (SEM).

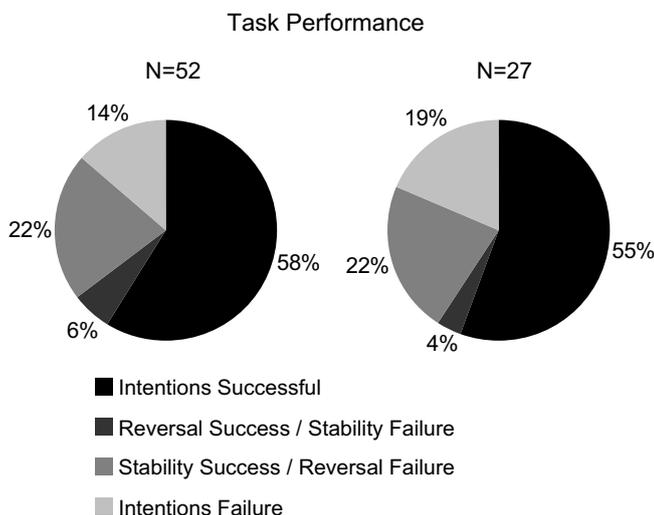


Fig. 6. Percentages of intention successes/failures for the original 52 observers and the 27 observers whose data was used for ERP analyses. Successful intentions are defined as reversal rate increases when intended and decreases when intended. Intention failures are defined as reversal rates increases when the intention was to decrease, and decreases when the intention was to increase. There were partial successes, in which one of the two intentions was carried out successfully while the other was not, i.e. reversal success/stability failure, and vice versa. All increases/decreases are relative to the passive condition reversal rate. The legend denotes the four combinations of successful vs. unsuccessful intentions.

as well as the 27 who met the analysis criterion for intention-based effects. It is important to note that 80% of the original 52 observers were able to successfully reduce reversal rates in the intention-to-stabilize condition, and 64% of these observers were able to successfully increase reversal rates in the intention-to-reverse condition.

Reaction times to reversals were not significantly different across intention conditions, and were never longer than 1200 ms (stimulus presentation plus ISI durations): Passive ($M = 543$ ms; $SEM = 35$), intention-to-reverse ($M = 525$ ms; $SEM = 36$), intention-to-stabilize ($M = 567$ ms;

$SEM = 37$). Most responses occurred within the timeframe of the stimulus presentation (800 ms), and 10% (Passive), 9% (Intention-to-reverse), and 13% (Intention-to-stabilize) of responses were made during the subsequent ISI.

3.2. Electrophysiological results

Fig. 7 shows the grand average reversal and stability ERPs for the passive condition ($N = 41$) at nine scalp locations: left, central, right \times frontal, central, posterior. Amplitude (μV) is plotted as a function of time (msec post-stimulus), and positive is plotted up and negative down. Examples of the reversal negativity (RN) and late positive component (LPC) are indicated on these plots. A frontal reversal positivity (FRP) was also evident and occurred during the same timeframe as the posterior reversal negativity (RN). Unlike Kornmeier and Bach (2005), an early posterior reversal positivity (120 ms) was not found.

Topographic maps of reversal minus stability ERPs are provided in Fig. 8. These maps incorporate recordings from all 128 channels and reveal the scalp topography of amplitude differences between reversal and stability ERPs across several intervals of time (150–500 ms in 50 ms steps). As depicted in Fig. 8, the RN (dark blue) began between 150 and 200 ms, and was lateralized to the right posterior scalp. The LPC began at approximately 350 ms, and was localized to central scalp locations.

The ANOVA for RN (and FRP) amplitude in the passive condition confirmed a main effect of perception, $F(1, 40) = 6.306$, $p = .016$ and a perception \times scalp location interaction, $F(8, 320) = 3.775$, $p < .001$. Post hoc t -tests revealed that the mean RN amplitudes for reversal ERPs were significantly more negative than stability ERPs at right posterior scalp locations, $t(40) = 3.431$, $p = .0014$. No significant differences were found at central or left posterior sites, supporting the right posterior lateralization of this component (see Fig. 8). Post hoc t -tests for the FRP component confirmed that reversal ERPs at left frontal,

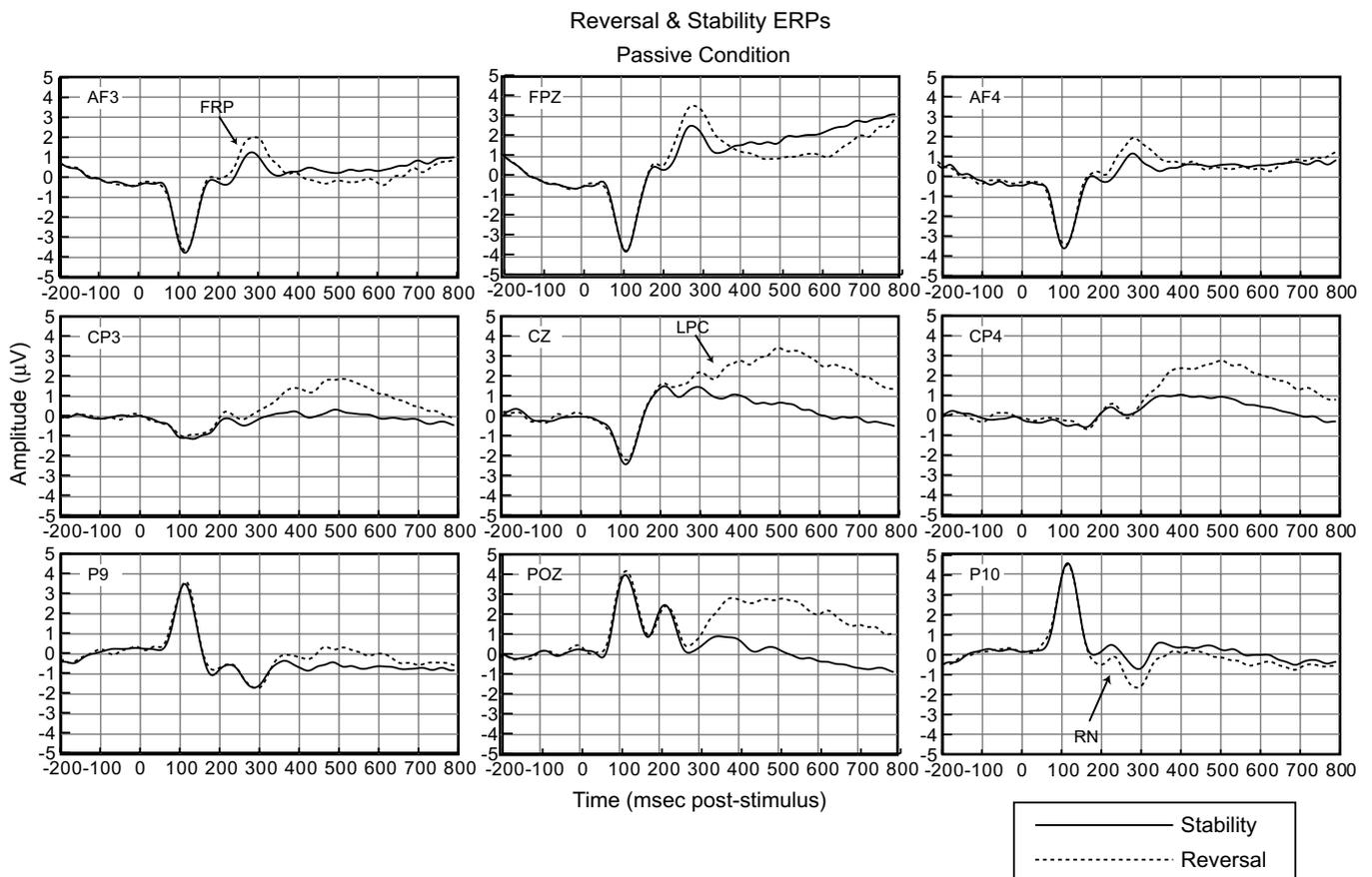


Fig. 7. Grand average ($N = 41$) reversal and stability ERPs in the passive condition. Amplitude is plotted as a function of time post-stimulus. Solid lines represent stable perceptions and dotted lines represent reversals in perception. Examples of the reversal negativity (RN), frontal reversal positivity (FRP), and late positive component (LPC) are indicated with labels and arrows.

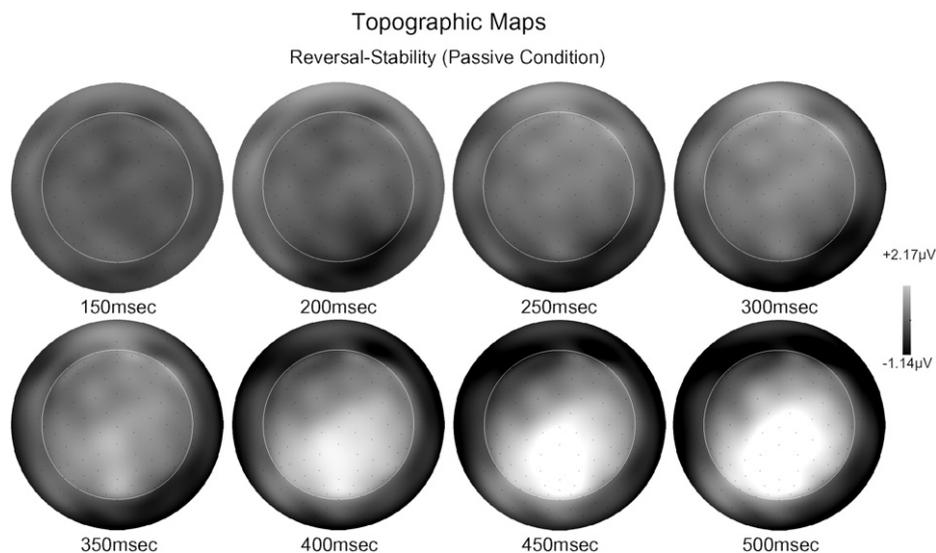


Fig. 8. Grand average ($N = 44$) topographic maps of reversal-stability differences for the passive condition. Each map depicts a time interval separated by 50 ms from left to right. Left/right on the plots corresponds to left/right scalp regions, and top/bottom corresponds to frontal/posterior scalp regions. Red indicates a positive difference and blue a negative difference. The RN begins between 150–200 ms, lasts until approximately 350 ms, and shows a right posterior distribution. The LPC begins at approximately 350 ms, lasts beyond 650 ms, and shows a central (slightly posterior) distribution.

$t(40) = 2.116$, $p = .040$, central frontal, $t(40) = 2.986$, $p = .0048$, and right frontal sites $t(40) = 2.808$, $p = .0076$ ($M = .857$; $SD = 1.545$) were more positive than stability ERPs at those same locations.

The ANOVA for LPC amplitude revealed a main effect of perception, $F(1,40) = 37.755$, $p < .001$ and a perception \times scalp location interaction, $F(8,320) = 15.204$, $p < .001$. Post hoc t -tests at central electrode sites confirmed that reversal ERP amplitudes at left central $t(40) = 5.062$, $p < .0001$, central central, $t(40) = 8.671$, $p < .0001$, and right central sites, $t(40) = 6.114$, $p < .0001$, were significantly more positive than stability ERPs at those same locations.

For the second phase of analyses, difference waves (reversal minus stability) across the three intention conditions were compared. The scalp distributions and timing of the RN, FRP, and LPC for the three intention conditions are shown in the topographic maps in Fig. 9. The RN (dark blue) appears as early as 150 ms in the intention-to-reverse condition, and is larger in amplitude compared to the other two conditions for the entire duration of the component (until approx 350 ms). In addition, the RN appears to be lateralized to the right posterior scalp in all three intention conditions. The LPC (dark red) develops as early as 300 ms in the passive and intention-to-reverse conditions, although the scalp distributions appear to differ. The passive condition LPC has a traditional central-posterior focus whereas the intention-to-reverse LPC develops into a horseshoe-like distribution (see Fig. 9; middle column; 350–400 ms). It is possible that because the RN component is larger and persists longer in the intention-to-reverse condition, and because the two components are opposite in polarity, their potentials may have canceled at overlapping scalp regions (i.e. central-posterior) between 350 and 450 ms, therefore creating this horseshoe-like distribution (see Fig. 9). The LPC appears later in the intention-to-stabilize condition compared to the other two conditions, but has a similar distribution to the passive condition LPC by 450 ms. By 500 ms, the distributions of the LPC in all three conditions are quite similar. Fig. 9 illustrates that differences in ERPs based on intention (top-down control) exist, occur early (150 ms), and can be quite dramatic (350 ms).

Fig. 10 shows the grand average ERPs at left-frontal (AF3), central-central (CZ), and right-posterior (P10) electrode sites for the three different intention conditions (arranged in 3 columns). These sites were chosen based on the scalp distribution plots from Fig. 9, i.e. these are the locations where the RN, FRP, and LPC amplitudes are maximal. An example of the reversal negativity (RN) is labeled on the P10 plot in the intention-to-reverse condition, an example of the late positive component (LPC) is labeled on the CZ plot in the passive condition, and an example of the frontal reversal positivity (FRP) is labeled on the AF3 plot in the intention-to-reverse condition.

Difference waves (reversal minus stability) from one of the two electrodes in each pair (frontal, central, posterior \times left, right, central) are plotted in Fig. 11. The RN, LPC, and FRP are marked with arrows in this figure. Because the RN and LPC overlap in time but present distinct scalp distributions, the RN effect is best isolated and

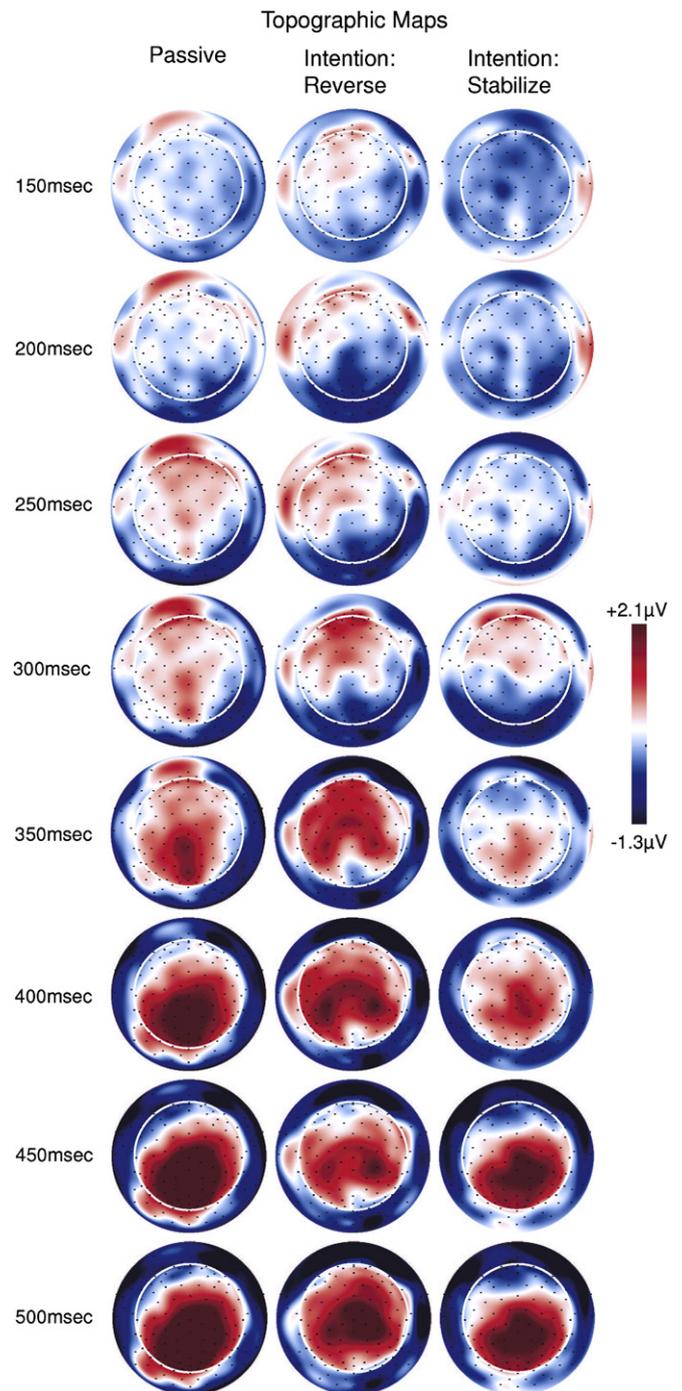


Fig. 9. Grand average ($N = 27$) topographic maps of reversal-stability differences. Passive condition plots are shown in the left column, intention-to-reverse in the middle column, and intention-to-stabilize in the right column. Each row depicts a time interval separated by 50 ms. Red indicates a positive difference and blue a negative difference. The RN appears earliest in the intention-to-reverse condition and is also higher in amplitude compared to the other two conditions. The LPC appears earlier in the passive and intention-to-reverse conditions compared to the intention-to-stabilize condition. Clear differences based on intention can be seen at 350 ms, but also exist as early as 200 ms post-stimulus. Differences between the three intention conditions continue until approximately 500 ms where the scalp distributions of the LPC become roughly equivalent.

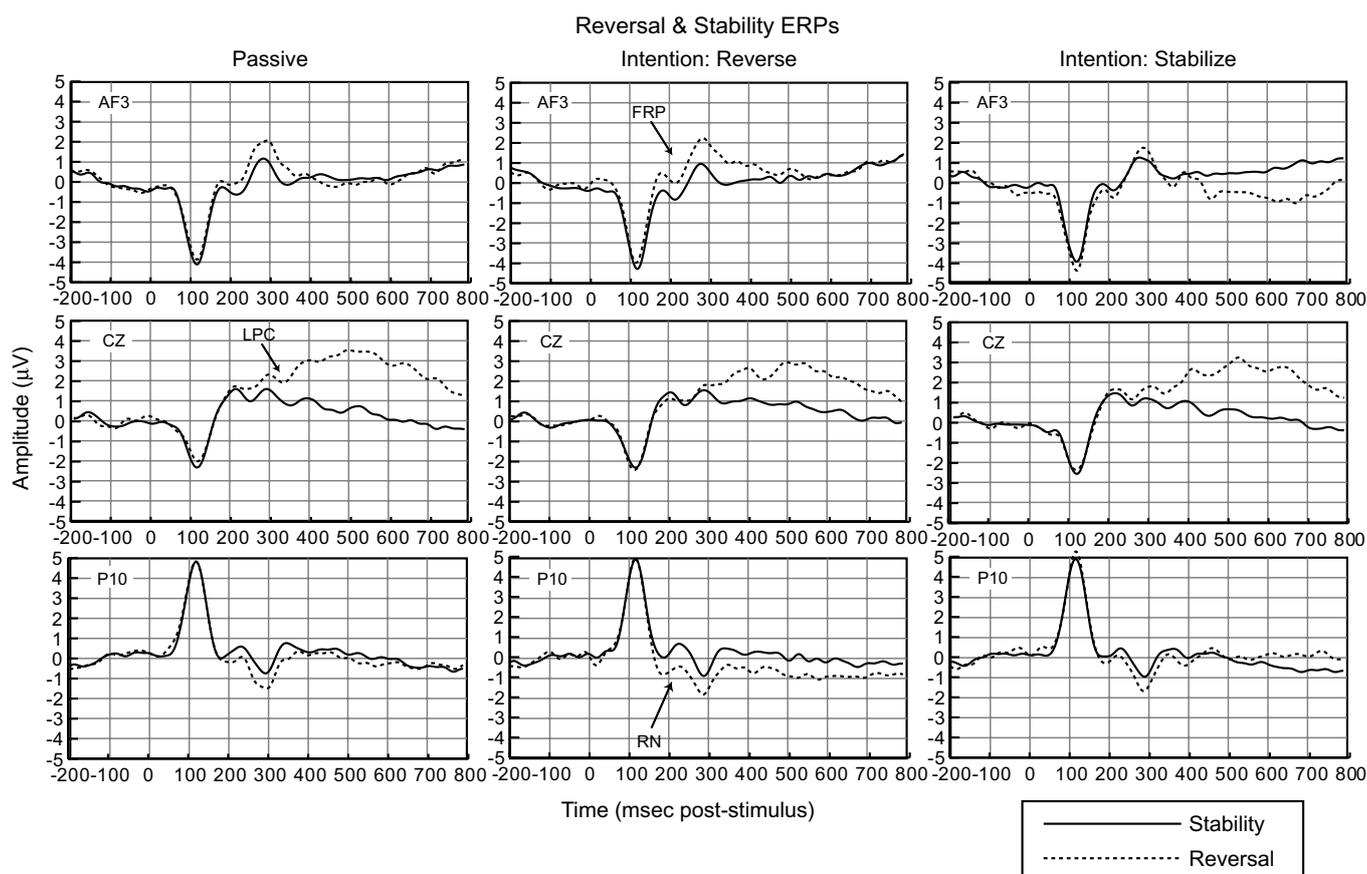


Fig. 10. Grand average ERPs ($N = 27$) for perceptual reversals and stability in the three intention conditions at left-frontal (AF3), central (CZ), and right-posterior (P10) scalp locations. Amplitude is plotted as a function of time post-stimulus. Solid lines represent stable perceptions and dotted lines represent reversals in perception. Passive condition ERPs are shown in the left column, intention-to-reverse in the middle column, and intention-to-stabilize in the right column. Examples of the reversal negativity (RN), frontal reversal positivity (FRP), and late positive component (LPC) are indicated with labels and arrows.

measured at right-posterior sites, and the LPC effect is best isolated and measured at central-central sites.

The ANOVA for the RN (150–350 ms) revealed a main effect of intention, $F(2, 52) = 4.873$, $p = .013$, and no intention \times scalp location interaction, $F(4, 104) = 1.955$, $p = .107$. RN amplitudes in the intention-to-reverse condition were more negative than amplitudes in the passive condition, $t(26) = 2.891$, $p = .0077$ at right posterior scalp locations. The ANOVA for the FRP component showed a trend towards a main effect of intention, $F(2, 52) = 3.300$, $p = .048$, and no intention \times scalp location interaction, $F(4, 104) = .478$, $p = .713$. FRP amplitudes were more positive in the intention-to-reverse condition compared to the intention-to-stabilize condition at left frontal sites, $t(26) = 3.447$, $p = .0019$, and at central frontal sites, $t(26) = 2.771$, $p = .0102$.

The ANOVA for the LPC (350–650 ms) did not show a main effect of intention, $F(2, 52) = 1.141$, $p = .327$, or an intention \times scalp location interaction, $F(4, 104) = 1.338$, $p = .270$. However, a post hoc t-test comparing mean amplitudes of the early phase of the LPC (350–500 ms) between passive and intention-to-stabilize conditions, revealed greater amplitudes for the passive condition,

$t(26) = 2.230$, $p = .0346$, although not significant when compared to the adjusted alpha level of .016.

4. Discussion

With the first phase of analyses, we were able to replicate some of the findings of Kornmeier and Bach (2004, 2005). The reversal negativity (RN) and late positive component (LPC) were both identified in the passive condition. However, no early posterior reversal positivity (120 ms) was found in the current study. A possible frontal counterpart to the RN, the frontal reversal positivity or FRP was also identified in the current study. Due to the timing, scalp distribution, and inversion of polarity, it is possible that the FRP and RN are generated by the same dipolar source. Also, if the RN and selection negativity (SeN) are equivalent, the FRP may be equivalent to the selection positivity (SeP) identified in previous studies (Anllo-Vento & Hillyard, 1996; Anllo-Vento et al., 1998). Further work incorporating dipole analysis and/or fMRI techniques as well as task that allows a direct comparison between selective attention shifting and reversal components is required to

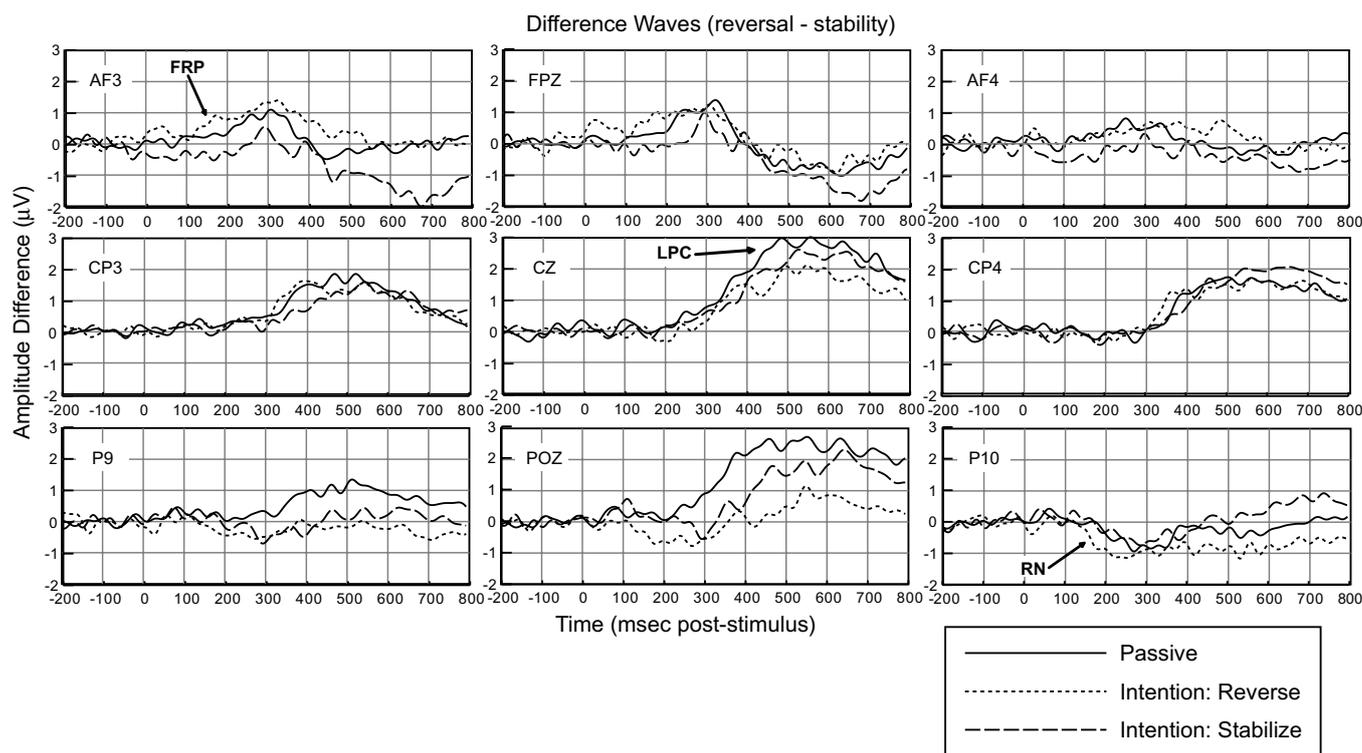


Fig. 11. Grand average difference waves (reversal minus stability) for each of the three intention conditions (solid lines, passive; dotted lines, intention-to-reverse; dashed lines, intention-to-stabilize) at nine different scalp locations. Amplitude difference is plotted as a function of time post-stimulus. The enhanced RN for the intention-to-reverse condition can be seen at all three posterior sites, while the enhanced LPC for the passive condition can be seen at POZ, CZ, and P9. Arrows and labels indicate where statistical tests confirmed differences in mean amplitude for the RN (electrode P10), LPC (electrode CZ), and FRP (electrode AF3).

localize the source of these components and validate these claims of functional equivalence.

In the second and more novel phase of the experiment, we were able to demonstrate for the first time an early influence of top-down control on perceptual reversals. This top-down modification of visual processing occurs at least as early as 150 ms post-stimulus (the onset of the RN component). RN amplitude was enhanced in the intention-to-reverse condition compared to the passive control condition. This intention-based effect on the RN component lends support to the selective attention theory of bistable perception (discussed below). The effects on the LPC indicate differences in post-perceptual processing. Specifically, the LPC was delayed in the intention-to-stabilize condition compared to both of the other conditions. These changes in the LPC most likely represent differences in the expected probability of having to update visual short term memory (VSTM).

Our behavioral data showed unexpected variability among observers in their ability to control reversal rates through intention. In this study, observers completed 60 practice trials per intention condition. It is possible that some observers require more extensive training in order to develop an ability to control reversal rates. If this top-down control is mediated by frontal lobe mechanisms, however, it is interesting to consider the age range of the population studied in this experiment (18–22 yrs), and

take into account the accumulating evidence that the frontal lobes are not fully developed until later in adulthood, i.e. later than 20 years of age (Fuster, 2002; Giedd et al, 1999; Gogtay et al, 2004; Jernigan, Trauner, Hesselink, & Tallal, 1991; Sowell, Thompson, Holmes, Jernigan, & Toga, 1999; Sowell, Thompson, Tessner, & Toga, 2001). Fuster (2002) suggests that the developmentally-late myelination and increase in white matter volume of the lateral prefrontal cortex is related to the late acquisition of attention-related cognitive functions such as the organization of goal directed behaviors. If frontal lobe attention networks are part of the systems that develop later in adulthood, it is possible that half (or more) of the participants in this study had not yet fully developed the ability to control their selective attention in order to change the reversal rates. Further research incorporating groups of observers in different age categories may help explore this possibility.

4.1. The role of selective attention in perceptual reversals

The enhancement of RN amplitude by top-down voluntary control suggests a critical role for selective attention in bistable perceptual reversals. Involuntary shifts in selective attention have been previously indicated in the mediation of perceptual reversals (Pitts et al., 2007). Drawing from a wide variety of perceptual rivalry research, Leopold

and Logothetis (1999) proposed an “environment exploration” theory to explain how and why these changes in perception occur. They support a view in which perceptual reversals are the necessary consequences of a generalized high-level “exploratory” mechanism that directs selective attention in a way that forces lower-level perceptual systems to periodically “refresh”. Selective attention involves a salience increase of certain visual features such as location, color, motion, or form (Sperling, Reeves, Blaser, Lu, & Weichselgartner, 2001). In some theories, attention to location is thought to influence attention to features in those locations by determining which features can be attended to and integrated into a coherent percept (Anllo-Vento & Hillyard, 1996; Treisman & Galade, 1980). In the current context, attending to certain locations within a bistable figure, may allow features at those locations to be preferentially processed, and therefore interpreted by mechanisms at later stages in the visual system as ‘nearest’ or ‘in the foreground’.

The exploratory mechanism described by Leopold and Logothetis (1999) is neither purely sensory nor purely motor, but rather a mechanism in which the ultimate goal is to “use” and “act upon” environmental information. By continually reorganizing and refreshing perceptual processing, accurate interpretation of visual input is improved. In normal everyday situations, this central mechanism (most likely a fronto-parietal network) works with eye movement centers (the frontal eye fields) to mediate a continuous exploration of the visual scene. In this model, visual attention is most easily controlled through eye movements, and objects of interest are usually disambiguated quickly and effortlessly. In bistable perception experiments, in which observers must fixate on a central location, covert attention (without eye movements) may still be altered by this central exploratory mechanism. Due to the ambiguity of the stimuli, the visual scene requires continual exploration, and reversals in perceptual interpretation consistently occur. Although this is all assumed to work largely in an unconscious, automatic fashion, voluntary control over bistable perceptual reversals may work through this same mechanism. For example, Leopold and Logothetis (1999) note the similarities between control over bistable perception and other voluntary behaviors, specifically in regards to the improvement over time with practice and learning.

Recent fMRI studies have provided evidence supporting the view that intentional reversals of bistable stimuli are mediated through attentional mechanisms (Slotnick & Yantis, 2005). A comparison of brain activity during Necker cube reversals vs. simple left-right attention shifts revealed similar areas of neural activation. Transient increases of activity in the superior parietal lobule and intraparietal sulcus occurred for both voluntary shifts in spatial attention as well as voluntary reversals of the Necker cube (Slotnick & Yantis, 2005). It is possible that when observers attempt to control perceptual reversals of bistable stimuli, they are tapping into this normally automatic, exploratory, perceptual-refresh mechanism in order

to change selective attention and reorganize perceptual interpretations.

As mentioned above, numerous studies have shown that perceptual reversals can be controlled voluntarily (e.g. Horlitz & O’Leary, 1993; Kawabata, 1986; Leopold & Logothetis, 1999; Liebert & Burk, 1985; Long & Toppino, 2004; Meng & Tong, 2004; Pelton & Solley, 1968; Rock et al., 1994; Shulman, 1993; Struber & Stadler, 1999; Toppino, 2003; van Ee, 2005; van Ee et al., 2005; Windmann et al., 2006) although it is always the case that *involuntary* reversals continue to occur as well. Slotnick and Yantis (2005) argue that these unintentional reversals are evidence that attention cannot account for all perceptual shifts in bistable perception, and that perceptual fatigue may also play a role. If Leopold and Logothetis’s (1999) theory is correct however, it may be unnecessary to rely on the notion of perceptual fatigue at all. When observers in Slotnick and Yantis’s (2005) experiment (as well as in the current study) experienced unintentional shifts in perception, the unconscious, automatic exploratory mechanism may have been responsible. In many trials, observers were able to control the attentional shifts mediated by this mechanism, but when the task’s demands conflicted with the system’s pre-existing strategy of continuously refreshing perception (especially when the stimulus remained ambiguous) reversals occurred largely on their own, i.e. unintentional reversals.

In a recent neuropsychological study, Windmann et al. (2006) found an interesting dissociation of voluntary control abilities in patients with frontal lobe damage that may lend support to Leopold and Logothetis (1999) attention-based theory. When asked to hold one percept of the Necker cube stable, patients with frontal lobe damage performed just as well as normals, i.e. they were able to decrease the reversal rate successfully. However, when asked to speed-up reversals, patients with frontal lobe damage were unable to increase the reversal rate beyond baseline (passive condition) levels (Windmann et al., 2006). Earlier neuropsychological studies reported similar findings (Ricci & Blundo, 1990), and Meenan and Miller (1994) postulated a right frontal lobe lateralization of a perceptual switching mechanism to account for this difference. Thus, a possible distinction exists between these two types of voluntary control at the neurophysiological level. Our results support this idea since ERP differences were found across intention conditions for perceptual reversals, but not for perceptual stability. It is likely that distinct neural pathways are involved in increasing vs. decreasing the reversal rates of bistable stimuli, and that these processes are analogous to “shifting” vs. “sustaining” visual attention. Hence, patients with frontal lobe damage may have lost the ability to tap into this attention-based perceptual refresh mechanism described by Leopold and Logothetis (1999), but maintained the ability to sustain visual attention.

Finally, similarities between the RN and SeN components suggest common underlying mechanisms. The scalp

topography (occipital-parietal; posterior), timing (150–350 ms), and polarity (negative) of both components are equivalent. It is worth noting however, that the RN is obtained by subtracting reversal (shifting) from stability (sustaining) waveforms while the SeN is obtained by subtracting attended from unattended waveforms. Research in our laboratory aimed at evaluating the relationship between these two components is currently underway.

How does the attention-based environment exploration theory fit in with previous bottom-up or top-down theories? The environment exploration theory postulates a critical role for selective attention (often categorized as a high-level, top-down process), but the shifting of attention in this theory is described as largely involuntary and automatic (terms usually reserved to support bottom-up accounts). It seems as though a critical revision in conceptualization of feedforward and feedback networks involved in visual processing is required (Lamme & Roelfsema, 2000), and that the bottom-up/top-down dichotomy is over-simplistic and misleading in relation to visual neural networks. Due to its greater precision in describing the complex interactions between high-level and low-level processes, the attention-based theory (as opposed to the bottom-up or top-down theories) is likely to be more satisfactory in explaining the data from the current investigation due to its greater precision in describing the complex interactions between high-level and low-level processes.

4.2. Alternative explanations

While data from the current investigation arguably support selective attention theories of bistable perception, it is worth considering alternative explanations. For example, bottom-up theories often describe perceptual reversals as the necessary consequence of fatigue/recovery cycles of the underlying perceptual mechanisms (Cohen, 1959; Köhler, 1940; Long & Toppino, 2004; Orbach, Ehrlich, & Heath, 1963; Toppino & Long, 1987). If distinct neuronal populations represent each of the two possible perceptions, one population of cells will eventually become fatigued enough to cause a shift in competitive weights toward the other population. While the other neural population is ‘winning’ this perceptual competition, the cells in the first population recover, and when the second set of cells is fatigued enough, competitive weights are once again shifted in favor of the first population. Previous neurophysiological evidence may seem to support this theory at first glance. For example, Logothetis and colleagues (Leopold & Logothetis, 1996, 1999; Logothetis & Schall, 1989; Sheinberg & Logothetis, 1997) have identified specific cells in the extrastriate layers of the non-human primate cortex that exhibit firing patterns correlated with each of the two possible percepts exclusively. However, these studies have also identified cells that change their firing patterns just before a perceptual reversal occurs. If these results are interpreted in the context of the selective attention theory of bistable perception, the cells that changed their firing patterns just

before a perceptual reversal might be correlated with shifts in selective attention and act as a kind of filter to determine which sets of cells are activated at the next level (and therefore which of the two perceptions are favored).

A recent behavioral experiment has suggested that fatigue-based influences on bistable perception only occur after extended adaptation periods (Long & Moran, 2007). In this study, observers were exposed to unambiguous versions of a “rotating” Necker cube for either brief (2 s) or extended durations (150 s) followed by the ambiguous version. A reverse-bias effect was found for extended durations, i.e. observers were more likely to report opposite perceptual configurations of the ambiguous version following exposure to the unambiguous version, supporting the notion of perceptual fatigue. A positive-bias effect was found for brief durations, i.e. observers were more likely to report the same perceptual configurations of the ambiguous versions following exposure to the unambiguous version, supporting the notion of perceptual priming (also see Long, Toppino, & Mondin, 1992). These results suggest that perceptual fatigue may play a role in perceptual reversals, but only when cell populations are fatigued for extended durations. In the current study, reversals occurred, on average, every 3–5 exposures (or every 3.6–6 s). If distinct cell populations represent each of the two percepts, it seems as though more time would be required to instantiate neural fatigue.

It may also be argued that shifts in selective attention are correlated with perceptual reversals, but occur *after* some other process (such as perceptual fatigue/recovery cycles, or random shifting of competitive weights) determines how the figure is disambiguated. In this view, the function of selective attention can be conceptualized as ‘accessing’ one of the two neural representations that has already won the competition, rather than acting on the representations in order to bias the percept. If this is the case however, it is unclear how voluntary control (top-down influence) affects perception. It seems unlikely that in the intention-to-reverse condition top-down mechanisms could increase neural fatigue or decrease neural recovery times of selected populations of cells in order to increase perceptual reversals. Further research is required in order to pinpoint exactly how (and where/when in the visual hierarchy) top-down mechanisms alter neural processing, and whether selective attention or some other process mediates this type of top-down voluntary control.

5. Conclusions

The current investigation demonstrated that top-down mechanisms can influence perception of bistable figures at least as early as 150 ms post-stimulus onset (indicated by amplitude enhancements of the RN component) and that post-perceptual processing is effected by top-down control (indicated by LPC amplitude differences). The specific neural mechanisms that mediate this top-down control remain a topic of debate. Further research is necessary to clarify

the spatial-temporal characteristics of these mechanisms and to determine their precise functional interactions with lower-level visual mechanisms.

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