DISSERTATION

TOP-DOWN INFLUENCES ON BISTABLE PERCEPTION REVEALED BY EVENT-RELATED POTENTIALS

Submitted by

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY MICHAEL A. PITTS ENTITLED TOP-DOWN INFLUENCES ON BISTABLE PERCEPTION REVEALED BY EVENT-RELATED POTENTIALS BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

TOP-DOWN INFLUENCES ON BISTABLE PERCEPTION REVEALED BY EVENT-RELATED POTENTIALS

Electrophysiological recordings were made in 27 observers to investigate whether differences in recently identified ERP components (reversal positivity, reversal negativity, late positive component) would be revealed during naturally occurring perceptual reversals of a bistable figure. Additionally, to investigate the role of top-down control over perceptual reversals, observers were instructed to maintain three distinct intentional approaches in separate conditions: 1) 'speed-up' reversals, 2) 'hold' one of the two percepts stable, and 3) remain passive and allow reversals to occur naturally. Using a lattice of Necker cubes as a stimulus, Kornmeier and Bach (2004, 2005) reported early amplitude differences related to perceptual reversals, the reversal positivity at 120msec post-stimulus, the reversal negativity at 180-380msec, and the late positive component at 300-500msec. The current study investigated whether these event-related potentials (ERPs) of Necker cube reversals (using the same stimulus as Kornmeier and Bach) could be identified using more conservative ERP analysis techniques, and if so, where on the scalp these components could be recorded. Additionally, intention-based ERP differences were assessed by comparing P1, N1, P2, N2, and reversal negativity amplitudes across the three intention conditions. Results revealed the broad reversal-related negativity at right posterior electrode sites and the late positive component at central parietal sites, but the reversal positivity could not be identified. When perceptual reversals occurred, intention-based differences were found for the P2, N2, and reversal negativity, in which amplitudes were more negative for the intention-to-reverse condition compared to the passive condition. An N2 enhancement was also found for unintentional reversals compared to passive reversals. A trend toward amplitude enhancement of the N1 component was found for the intention-to-reverse condition compared to both of the other conditions, especially for observers who were successful at the intention task. These results support a theory of bistable perception in which *changes* in early spatial attention (indicated by N1 enhancement) lead to *changes* in selective attention (indicated by the reversal negativity), which determine how one perceives the bistable figure. Evidence from this experiment also suggests that these same attention mechanisms can be modulated by top-down intentional control. A neuroanatomical model is presented to conceptualize these findings.

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Chapter 1: INTRODUCTION

Bistable figures

Bistable figures refer to an interesting class of stimuli in which physical input to the retina remains constant, while distinct perceptual changes occur. Perceptual interpretations of bistable figures consistently change (or "reverse") between two possibilities, and these reversals in perception form the basis for the current investigation. The appearance of bistable figures in the literature can be traced back to at least 1832 when L.A. Necker reported the curious changes in appearance of a two-dimensional drawing of a rhomboid crystal (see figure 1.1). Necker noticed how the appearance of the cube could change via voluntary control and described this observation in his early report, "By being able at my will to see the solid in which position I choose, and to make this position vary at pleasure, in looking alternately with fixed attention, either to the angle A, or to the angle X" (Necker, 1832).

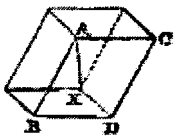
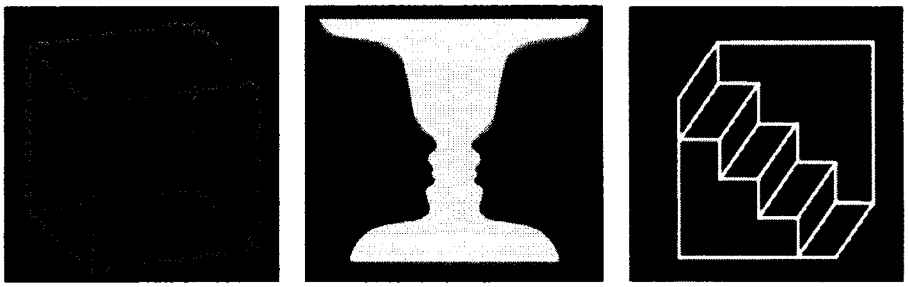


Figure 1.1. A copy of L.A. Necker's original drawing (Necker, 1832). Variations of these two-dimensional drawings later became known as "Necker cubes". Necker described the perceptual alterations he experienced by noting whether angle A or angle X appeared nearest or furthest from him.

Bistable perception may have been observed and documented as early as 300 B.C. (Boring, 1942), but it was L.A. Necker who formally introduced the now famous 'Necker cube' to the scientific community in 1832. Since then, researchers interested in sensation, perception, cognition, and consciousness have used such stimuli to study fundamental aspects of human psychological function. As the field of psychology progressed and transitioned through different epistemologies (with the exception of behaviorism), these stimuli have continued to be of interest.

On theoretical grounds, bistable perception offers a unique avenue to the study of visual awareness. Although presented with a single, physically unchanging stimulus, our visual perception alternates between two mutually exclusive interpretations (see figure 1.2 for examples). We can only be aware of one of these perceptual interpretations at any given time. Therefore, changes in perception when physical stimulation remains constant must be attributed to endogenous changes in visual processing. Experimentally, bistable stimuli offer a rare experimental advantage in that physical stimulation can remain fixed while changes in behavior or neural activity are evaluated. Understanding the neural processing that underlies bistable perception allows us to examine the stages leading to visual awareness and may help us clarify the elusive distinction between sensation and perception. Whether these alternations in visual awareness are due to passive neural fatigue-recovery cycles or more active attention shifts, we can be certain that these changes are endogenous in nature.



(a) (b) (c)

Figure 1.2. Examples of bistable stimuli. Necker's cube (a) can be perceived as having the front-face toward the top-left or the bottom-right. Rubin's face/vase (b) can be seen as two face-profiles or as one central vase. Schroeder's staircase (c) can be perceived as three upright stairs or four upside-down stairs.

Neuroanatomy and bistable perception

With the advent of electrophysiological and neuroimaging technologies, researchers have begun to investigate the underlying neural mechanisms of bistable perception. It is generally accepted that the very early stages of visual processing (retina, lateral geniculate nucleus) are devoted to relaying a spatially-preserved retinotopic map of light stimulation to the visual cortex (Hubel & Wiesel, 1972; Hubel & Wiesel, 1977; Horton & Hedley-Whyte, 1984; Tootell Hadjikhani, Vanduffel, Liu, Mendola, Sereno, & Dale, 1998; Schneider, Richter, & Kastner, 2004). Although complex and fascinating processes have been shown to occur at these early stages, this level of the visual system is primarily concerned with sensory as opposed to perceptual processes. Because sensory input remains constant with bistable figures, the first potentially relevant visual area involved is primary visual cortex (V1; striate cortex; Brodmann's Area 17). Recent electrophysiological and functional neuroimaging work have shown that no event-related hemodynamic changes occur in early visual cortex (V1 and V2) when the perception of a bistable figure changes (Leopold & Logothetis, 1999). This implies that the role of V1 and other early visual areas is to process basic physical features of the stimulus, which in the case of bistable figures, are unchanging. To further support this idea, an fMRI study found a pattern of deactivation in the thalamus and V1 during perceptual reversals (Kleinschmidt Buchel, Zeki, & Frackowiak, 1998). This may suggest that during perceptual alterations of an ambiguous visual stimulus, inhibition of incoming feature-based sensory information is required. It is not yet clear whether this decrease in thalamic and V1 activity is necessary for perceptual reversals to occur, or whether the decrease results from neural fatigue as opposed to active inhibition from higher-level visual areas.

Other neurophysiological evidence suggests that activity in extrastriate cortex may correlate with perceptual reversals and lead to perceptual awareness of each of the two percepts. For example, Logothetis and colleagues (Logothetis & Schall, 1989; Sheinberg & Logothetis, 1997; Leopold & Logothetis, 1996, 1999) have identified specific cells in the extrastriate layers of the non-human primate cortex that change their firing patterns just before a perceptual reversal occurs, and other cells that exhibit firing patterns correlated with each of the two possible percepts exclusively. Extrastriate cortex (V2, V3, V4, MT, V7, and V8; Brodmann's Areas 18 and 19) is located beyond the level of automatic sensory processing, assumed to be primary visual cortex, (Livingstone & Hubel, 1988; Lee, Mumford, Romero, & Lamme, 1998), but not at the level of cognitive or executive control, assumed to involve frontal cortical areas (Carter, Botvinick, &

Cohen, 1999; Smith & Jonides, 1999; Stuss & Alexander, 2000). It is also worth noting that neuroanatomical studies have identified axonal connections between frontal areas and extrastriate areas, as well as between primary visual cortex and extrastriate areas, but not between frontal areas and primary visual cortex (Felleman & Van Essen, 1991; Felleman, Burkhalter, & Van Essen, 1998; Barone, Batardiere, Knoblauch, & Kennedy, 2000). Thus, it seems that the critical brain areas involved in bistable perception may reside at the intersection between feedforward and feedback pathways.

Theories of bistable perception 1: Bottom-up vs. top-down

One of the reoccurring debates among psychologists who study bistable perception involves a historically-driven distinction between “bottom-up” and “top-down” effects on perceptual reversals. The convenient, yet often misleading distinction between bottom-up and top-down processing is rooted in two major schools of thought in twentieth century psychology (see Long & Toppino, 2004 for a review). Historically, the neurophysiological approach was born out of post-Gestalt thinking, and emphasizes the critical role of neural adaptation (or satiation) in accounting for the alterations of bistable percepts (Köhler, 1940; Cohen, 1959). In this view, sometimes referred to as the ‘neural-channel model’, perceptual reversals of bistable figures are caused by disparate fatigue-recovery cycles of the neural circuits underlying each of the percepts (Orbach, Ehrlich, & Heath, 1963; Toppino & Long, 1987; Long & Toppino, 2004). This theory describes figure reversals as passive, automatic, sensory-driven events that are independent of cognition. The ‘bottom-up’ thus refers to the hypothesized direction of information flow, from the retinal stimulus, to early stages of sensory processing, through various intermediate stages, and finally to perceptual and cognitive awareness.

The opposing top-down theory stems from the cognitive revolution and information processing theories of the 1960s and 1970s. From this point of view, an emphasis is placed on the active role of the observer. Processes such as memory, attention, and expectation are brought to the forefront in top-down theories (Pelton & Solley, 1968; Kawabata, 1986; Rock, Hall, & Davis, 1994; Horlitz & O’Leary, 1993; Shulman, 1993; Georgiades & Harris, 1997; Struber & Stadler, 1999; Toppino, 2003; Leopold, 2003; Meng & Tong, 2004). In contrast to the bottom-up account, top-down theories emphasize the flow of information from high-level, non-sensory systems, to lower-level perceptual processes.

As a clear example of the two competing theories, consider the following example. It has been shown that pre-exposure to unambiguous versions of bistable figures can influence subsequent perceptual interpretation of ambiguous versions (Long & Toppino, 2004). For example, if an unambiguous cube is flashed briefly, followed by an ambiguous Necker cube, observers tend to report perceiving the Necker cube in the same configuration as the unambiguous prime (Long, Toppino & Mondin, 1992). This evidence has been used to support the top-down theory, i.e. attention has been exogenously drawn to certain features and visual short term memory has been activated by the unambiguous prime. This activation of attention and memory systems then influences the perception of the ambiguous target. However, if observers are asked to adapt to an unambiguous version of the cube for an extended period of time (e.g. > 30sec), and are then presented with an ambiguous Necker cube, they most often report perceiving the cube in the opposite configuration (Long, Toppino & Mondin, 1992). This adaptation effect has been interpreted as supporting a bottom-up, or fatigue-based account of figure reversals. Thus, simply changing the duration of pre-exposure to an unambiguous version of a bistable figure allows one to support either (or neither) of the opposing theories.

Most individuals will agree, at least subjectively, that they have a degree of voluntary control over perceptual reversals, i.e. if you simply ‘try to reverse the figure’, you are often successful (see figures 1.1 and 1.2). Numerous behavioral studies have in fact shown that reversals can be influenced by the observers’ intentions (Pelton & Solley, 1968; Liebert & Burk, 1985; Kawabata, 1986; Leopold & Logothetis, 1999; Struber & Stadler, 1999; Toppino, 2003; Long & Toppino, 2004; van Ee, 2005; van Ee, van Dam, & Brouwer, 2005). In a recent study, van Ee and colleagues (van Ee, 2005; van Ee, van Dam, & Brouwer, 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, van Dam, & Brouwer, 2005). For the Necker cube, observers were able to significantly 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, although not to a statistically significant degree. From this research as well as from earlier work (e.g. Ammons, Ulrich, & Ammons, 1960; Pelton & Solley, 1968; Kawabata, 1986), it is evident that some degree of intentional control over the Necker cube reversal rate is attainable.

Interestingly, although each of the opposing theories are currently supported by behavioral evidence alone, the bottom-up approach has more often utilized neurophysiological explanations (Orbach, Ehrlich, & Heath, 1963; Toppino & Long 1987) while the top-down approach has employed abstract processing models to explain their data (Gomez et al., 1995; Grossberg & Swaminathan, 2004; Long & Toppino, 2004). One of the goals of the current investigation is to explain top-down effects on bistable perception in neurophysiological terms, and to develop a conceptual model that incorporates recent neurophysiological findings.

Theories of bistable perception 2: Attention-based environment exploration

Leopold and Logothetis (1999) proposed a theory of bistable perception that is largely non-sensory in origin. Based on perceptual research in a variety of contexts, they support a view in which perceptual reversals are the necessary consequences of a generalized high-level "exploratory" mechanism that directs spatial and selective attention in a way that forces lower-level perceptual systems to periodically "refresh". Spatial attention can be described as an increase in salience of a specific region of visual space. Selective attention involves a salience increase of certain visual features such as color, motion, or form (Sperling, Reeves, Blaser, Lu, & Weichselgartner, 2001). Although the precise neural mechanisms underlying these types of visual attention are currently unknown, their functions are critical to understanding intermediate stages of visual processing. In some theories, spatial attention is thought to influence selective attention by determining which features can be attended to and integrated into a coherent percept (Treisman & Galade, 1980; Anllo-Vento & Hillyard, 1996).

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 voluntary 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 found evidence 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 spatial and selective attention and reorganize perceptual interpretations.

As mentioned above, numerous studies have shown that perceptual reversals can be controlled voluntarily (e.g. Pelton & Solley, 1968; Liebert & Burk, 1985; Kawabata, 1986; Leopold & Logothetis, 1999; Struber & Stadler, 1999; Toppino, 2003; Long & Toppino, 2004; van Ee, 2005; van Ee, van Dam, & Brouwer, 2005; Windmann, Wehrmann, Calabrese, & Gunturkun, 2006) although it is always the case that *in*voluntary 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 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. involuntary 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. This suggests that a possible distinction exists between these two types of voluntary control at the neurophysiological level. It is possible that different visual processes are involved in increasing vs. decreasing the reversal rates of bistable stimuli, and that "shifting" vs. "sustaining" visual attention relies on distinct neural pathways. 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.

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 attention (normally 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, and that the bottom-up/top-down dichotomy is over-simplistic and misleading in relation to visual neural networks. The attention-based theory (as opposed to the bottom-up or top-down theories) is likely to be more valuable 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.

Psychophysiological measurements of bistable perception

With the recent division of the cognitive neuroscience field from traditional cognitive psychology, much work has been directed at finding neurophysiological correlates for such processes as memory, attention, and executive control. Top-down approaches no longer rely solely on abstract theoretical models of cognitive processing to explain experimental findings. By utilizing functional magnetic resonance imaging (fMRI), transcranial magnetic stimulation (TMS), magnetoencephalography (MEG), and electroencephalography (EEG) techniques, researchers have begun to measure aspects of neural activity in living human subjects while they perceive bistable stimuli (Hasson, Hendler, Bashat, & Malach, 2001; Miller, Liu, Ngo, Hooper, Riek, Carson, & Pettigrew 2000; Struber & Herrmann, 2002; Kompass, 2000). Recently, fMRI studies of bistable perception have identified areas of increased cortical activity during perceptual reversals. These areas include the ventral occipital cortex, posterior intraparietal cortex (Kleinschmidt et al., 1998), the occipital temporal gyrus, prefrontal gyrus, premotor cortex, parietal cortex (Inui et al, 2000), the superior parietal lobule, and interparietal sulcus (Slotnick & Yantis, 2005).

A weakness of fMRI technology as applied to perceptual research is the inadequate degree of temporal resolution, i.e. 1-3 seconds of temporal smear per image (Luck, 2005). From simple reaction time studies, it is well known that the entire duration of activity from visual input to behavioral response can occur in less than 1 second (Teichner & Krebs, 1974; Ratcliff, Van Zandt, & McKoon, 1999). Therefore, although we can be fairly certain that the brain areas listed above are involved in the processes of disambiguation, figure reversal, and perceptual awareness, fMRI data cannot help us evaluate the stages of visual processing with the necessary temporal precision.

Recent electrophysiological experiments have suggested that information can reach primary visual cortex as early as 56msec post-stimulus, and be projected to frontal cortical areas in less than 80msec post-stimulus (Foxe & Simpson, 2002). Lamme and Roelefsema (2000) describe how some extrastriate visual areas such as area MT are activated so quickly, that information carried in feedback loops to other visual areas may arrive at the same time as the information in the feedforward loops. In event-related potential (ERP) experiments, although no concrete distinction can be made, ‘early’ sensory components are assumed to occur in less than 100msec, while ‘late’ perceptual and cognitive components usually occur between 100-700msec post-stimulus (Luck, 2005). Visual awareness has been estimated to begin somewhere between 350-450msec post-stimulus (Verleger, 1997). The nature of bistable stimuli are such that we can only be aware of one of the two possible percepts at a given time, and therefore the processes involved in disambiguation and figure reversal must occur prior to visual awareness (i.e. prior to 350-450msec). Because the initial visual processing stages underlying bistable perception are likely to occur in less than 350msec, and EEG measurements have a temporal resolution of 1msec (compared to fMRI’s 1000-3000msec resolution), human electroencephalography is an ideal method for studying the neural basis of bistable perception.

Event-related potentials (ERPs) and time-locking

Early ERP studies of bistable perception identified a late positive component, or LPC (originally described as P300-like) related to perceptual reversals (Basar-Eroglu, Struber, Stadler, & Kruse 1993; Isoglu-Alkac, Basar-Eroglu, Ademoglu, Demiralp, Miener, & Stadler, 1998). The LPC (or P300) is thought to represent higher-level cognitive processes (Picton, 1992; Annlo-Vento & Hillyard, 1996; Luck, 2005) and does not seem to be related to early or intermediate-level perceptual processing. In these experiments, static bistable stimuli were presented, and observers were asked to press a button when a perceptual reversal occurred. The EEG recordings were then time-locked to the subject's response, and average ERP waves were derived.

The problem with the method employed in these earlier studies was the potential variability inherent in the mathematical averaging technique. Recordings that are time-locked to the response require looking backwards in time. This method is likely to obscure any smaller ERP components because of the inherent variability in reaction times across trials and observers. Kornmeier and Bach (2004) ran experiments with unambiguous stimuli to test this potential methodological concern. These researchers found that presenting temporally discontinuous stimuli and time-locking recordings to stimulus onset produces much sharper and more clearly defined ERP components (Kornmeier & Bach, 2004). A similar attempt at utilizing a discontinuous technique had previously been made with bistable stimuli (O'Donnell, Hendler, & Squires, 1988), but inter-stimulus intervals (ISIs) of 3.3 seconds proved too long for any reversal-related components to emerge.

By formulating this new paradigm, Kornmeier and Bach (2004, 2005) identified two early ERP components related to endogenous perceptual reversals of a Necker cube-like stimulus. Their paradigm consisted of discontinuous stimulus presentations at durations short enough to prevent reversals from occurring within a single presentation (800msec), and interstimulus intervals (ISIs) short enough to maintain normal reversal-rates but long enough to allow the visual ERP waves to return to baseline (400msec). The short ISI is crucial to maintaining adequate reversal rates, as Leopold et al. (2002) reported that periodic removal of the stimulus could slow and even stop reversals from occurring. Based on previous studies (Bach & Meigen, 1992), Kornmeier and Bach (2004, 2005) combined nine Necker cubes into a “Necker lattice” in order to amplify the ERP signals (figure 1.3). Furthermore, in some conditions, Kornmeier and Bach (2004) presented versions of the Necker lattice that were made unambiguous by shading certain regions and therefore altering depth cue information. They compared ERPs of these exogenous reversals of unambiguous stimuli to ERPs of endogenous reversals of ambiguous stimuli. Kornmeier and Bach (2004) also included a response manipulation in which for half of the trials, observers were instructed to press a button when reversals occurred, and in the other half of the trials to press a button when stability occurred. Comparing results from these two conditions revealed any motor preparation influences on the ERP waves. Kornmeier and Bach found no effects based on the manipulation of response, and therefore combined these conditions for subsequent analyses.

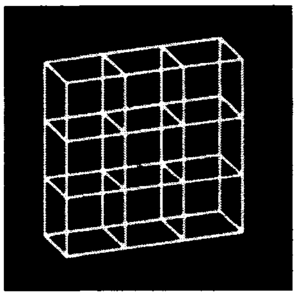


Figure 1.3. The Necker lattice is composed of nine Necker cubes stacked on top of each other (Kornmeier & Bach, 2004). To reverse this image, view the lattice as ‘one big cube’. The front-face can either appear to pop-out in the top-left or the bottom-right.

In their first experiment under this new paradigm, Kornmeier and Bach (2004) identified an ERP component related to endogenous reversal of the Necker lattice. They characterized this component by computing difference waves from stability trials and reversal trials. The largest difference between the two waveforms occurred at 250msec post-stimulus and the authors coined the term “reversal negativity” to define this effect. They found a similar reversal negativity in response to exogenous reversals of unambiguous lattices, but this component peaked 50msec earlier. They also found increased positivities for reversal trials at 470msec post-stimulus, and interpreted these as analogous to the P300-like components (or LPC) reported in earlier studies (Basar-Eroglu et al., 1993; Isoglu-Alkac et al., 1998). In a second study using the same paradigm, an earlier reversal component was identified, the “reversal positivity'”, which occurred 120msec post-stimulus (Kornmeier & Bach, 2005). Only ambiguous lattices were used in this study, and the reversal negativity as well as the late positive component were once again identified.

In a recent study aimed at determining the generalizability of these ERP differences to other types of bistable stimuli, Pitts, Nerger, and Davis (2007) reported P1 (≈120msec), N1 (≈175msec), and reversal negativity (170-370msec) effects related to perceptual reversals. The authors argued that these electrophysiological differences closely mimicked differences reported in the visual attention ERP literature, and may reflect common underlying attention-based mechanisms.

Spatial and selective attention ERPs

Numerous studies have demonstrated that the occipital P1 and N1 amplitudes are dependent on spatial attention (e.g. Luck, Hillyard, Mouloua, Woldorff, Clark, & Hawkins, 1994; Mangun, 1995; Clark & Hillyard, 1996; Hillyard & Anllo-Vento, 1998; Hillyard, Vogel & Luck, 1998). For example, Luck et al (1994) employed cueing paradigms to manipulate observers' attention to particular spatial locations. P1 and N1 amplitudes for attended vs. unattended locations were compared to P1 and N1 amplitudes for neutral trials, in which attention was more broadly allocated. Unattended stimuli led to decreases in P1 amplitude, while attended stimuli led to increases in N1 amplitude. Interestingly, reversal compared to stability waveforms reported in Kornmeier and Bach (2004, 2005) as well as in Pitts, Nerger, and Davis (2007) closely resemble Luck et al's (1994) attended vs. unattended waveforms, respectively. In stable trials, spatial attention can be assumed to be sustained, whereas in reversal trials, spatial attention has arguably shifted. This is not necessarily equivalent to attending vs. not attending, but may instead reflect a difference between sustaining vs. shifting spatial attention.

Although it is difficult to localize the neural generators of ERP components, recent attempts have been made to identify the neurophysiological sources of the P1 and N1 components. Such approaches include combining ERP and fMRI techniques in a single study (Martinez, DiRusso, Anllo-Vento, Sereno, Buxton, & Hillyard, 2001; Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2001), combining ERP and PET measurements (Woldroff, Fox, Matzke, Lancaster, Veeraswamy, Zamarripa, Seabolt, Glass, Gao, Martin, & Jerabek 1997), combining ERP and MEG measurements (Hopf, Vogel, Woodman, Heinze, & Luck, 2002), analyzing scalp current density mappings (Gomez Gonzalez, Clark, Fan, Luck, & Hillyard, 1994; Johannes, Munte, Heinze, & Mangun, 1995), and modeling spatiotemporal dipoles (Gomez Gonzalez et al, 1994; Clark & Hillyard, 1996; Anllo-Vento, Luck & Hillyard, 1998; Di Russo et al, 2001). All of these approaches have provided converging evidence that the generator of the occipital P1 is located in extrastriate cortex, either in dorsal or ventral regions, depending on the particular techniques used. The N1 generators on the other hand have been localized to the ventral pathway, in particular the occipitotemporal cortex, although one study (Martinez et al, 2002) suggests that negativities ranging from 160msec to 260msec may reflect delayed V1 activity that is influenced by reentrant feedback from higher visual areas. Enhancement of P1 and/or N1 amplitudes therefore may reflect an initial change in extrastriate cortex activity, and a later change in occipitotemporal cortex activation.

Kornmeier and Bach (2004) coined the term reversal negativity to describe the broad negative difference in the ERP waves (from ≈180-380msec post-stimulus) that occurs for reversal trials compared to stability trials. They argued that this component was distinct from the selection negativity (SN) component. The SN has been described as a selective attention-dependent ERP component (Hillyard & Anllo-Vento, 1998). If observers are instructed to pay attention to a certain stimulus feature such as color, orientation, or shape, a broad negativity (beginning at 180-200msec, and persisting for another 200msec) can be identified when comparing trials in which the attended feature appears to trials in which it does not appear (Anllo-Vento & Hillyard, 1996; Smid, Jakob & Heinze, 1997; Valdes-Sosa, Bobes, Rodriguez, & Pinilla, 1998; Martin-Loeches, Hinojosa, & Rubia, 1999; Michie, Karayanidis, Smith, Barrett, Large, O'Sullivan, & Kavanagh, 1999; Smid, Jakob & Heinze, 1999). In some of these studies (Smid, Jakob, & Heinze, 1997; Mitchie et al, 1999; Smid, Jakob, & Heinze, 1999), participants were instructed to respond when the to-be-attended feature appeared. Kornmeier and Bach (2004) suggested that the reversal negativity was distinct from the SN because the reversal negativity was identified both in trials in which the target (i.e. what the observers responded to) was perceptual reversal and in trials in which the target was perceptual stability, i.e. the reversal negativity is target-independent, whereas the SN may reflect target-selection. Anllo-Vento and Hillyard (1996) however, designed a clever experiment in which attended location-feature combination trials were separable from target trials. They then compared target to non-target ERPs and showed that the SN is not dependent on target-selection, and that the earliest target-related ERP differences occur later than 325msec post-stimulus. This target-independent feature of the SN was later confirmed by studies with similar experimental designs (Valdes-Sosa et al, 1998; Martin-Loeches, Hinojosa, & Rubia, 1999). Because of the striking similarity (in polarity, scalp topography, and latency) between the SN and the reversal negativity, as well as the assumed independence of the SN and target-selection components, a more parsimonious explanation would suggest a common underlying mechanism.

Purpose

The first goal of this project is to identify the reversal positivity, the reversal negativity, and the LPC of perceptual reversals, and to determine from where on the scalp these potentials can be recorded. Kornmeier and Bach (2004, 2005) only measured electrical activity at the scalp from nine electrode sites. The current experiment will utilize a high-density EEG system which includes 128 electrode sites. Increasing the number of recording sites will allow an enhancement in scalp topography analysis, and may reveal a precise scalp location for which these reversal-related components are most easily identified.

In addition to increasing the number of recording channels, the current study will conduct more conservative ERP analyses on the data compared to the seminal studies of Kornmeier and Bach (2004, 2005). In these earlier studies, Kornmeier and Bach chose a difference wave approach in their analysis, which is beneficial in certain circumstances, but may lead to unwarranted interpretations in other situations (Luck, 2005). Kornmeier and Bach defined the reversal positivity and reversal negativity by computing difference waves and identifying the largest excursions within broad time windows. For statistical purposes, defining a long-duration component such as the reversal negativity (or SN) by analyzing the amplitude at the point of maximal difference may contribute to an artificial inflation of differences. A more conservative method for analyzing these components is to calculate the mean amplitude across the entire time windows of each component (for difference waves, this is essentially an area under the curve measure). This later approach was taken in the current study, and should help clarify whether these reversal-related components can be reliably identified. Any ERP differences found in the current investigation will also be compared to spatial and selective attention ERPs in scalp topography, polarity, and latency in order to assess attention-based theories of bistable perception. To summarize, the first experimental question of the current study is: Can the reversal positivity, reversal negativity, and LPC be identified using more conservative statistical analyses, and if so, where on the scalp can these differences be detected?

The second purpose of this investigation is to assess the influence of top-down *intentional* control on reversal-related ERPs. Although the reversal components identified by Kornmeier and Bach (2004, 2005) occurred early in visual processing, this does not necessarily support the bottom-up theory of bistable perception. In all conditions, Kornmeier and Bach (2004, 2005) instructed observers to maintain a passive perceptual approach, i.e. to allow reversals to occur naturally. From the behavioral and neuropsychological studies sited above, it is clear observers can exert some degree of intentional control over perceptual reversals simply by ‘trying to speed-up reversals’ or ‘trying to hold one percept stable’. If observers are asked to invoke this type of top-down control on their perception of the Necker cube, will the amplitudes of any of the visual ERP components be affected, and if so when (in msec post-stimulus), where (in scalp topography terms), and how (in which direction, and in which intentional conditions)? By manipulating the instructions to participants before each block of trials, we will be able to measure any ERP changes specifically related to intentional influences on bistable perception.

Chapter 2: METHODS

Participants

A total of 54 observers (13 male, 41 female; ages 18-22, mean age 19) were recruited from an undergraduate psychology class, and received credits toward their grade for participating. Eye dominance was determined via simple dichoptic tests and visual acuity was assessed via a high-contrast Bailey-Lovie acuity chart. Only observers with uncorrected or corrected foveal acuities ≤ 20/40 were allowed to participate in the experiment (two participants were excluded based on this criterion). 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.

Stimuli

A perceptually bistable Necker lattice (see figure 1.3) served as the stimulus for all conditions (provided by Kornmeier and Bach). The Necker lattice subtended a viewing angle of 3.3° x 3.3°, and was presented on a Dell Monitor

(Plug & Play Monitor on RADEON 7000, Microsoft Inc.) with a frame rate of 85Hz. 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).

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 bandpass-filtered at 0.1-100Hz, were digitized at a sampling rate of 500Hz. 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 50kΩ.

Procedure

Observers were comfortably seated 1.4 meters from the computer monitor in order to maintain an approximately constant retinal image size. 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. All observers were able to perceive the lattice in both orientations.

Because reversal rates are known to increase during initial exposure to a novel bistable stimulus (Long & Toppino, 2004) practice trials were administered. Before each practice block, participants were asked to 'try to reverse their perception as often as possible', 'try to hold one of the percepts stable for as long as possible', or 'maintain a passive approach'. Each block of practice trials included 30 stimulus presentations, and lasted approximately 1.5min. All participants practiced the passive condition first, the intention-to-reverse condition second, and the intention-to-stabilize condition third. Each of the three intentional condition practice blocks was then repeated in the same order. The total number of practice trials was 180, and the entire practice session lasted approximately 9min. The practice trials 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 800msec followed by a 400msec 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 1000msec following trials that elicited a perceptual reversal. Figure 2.1 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.

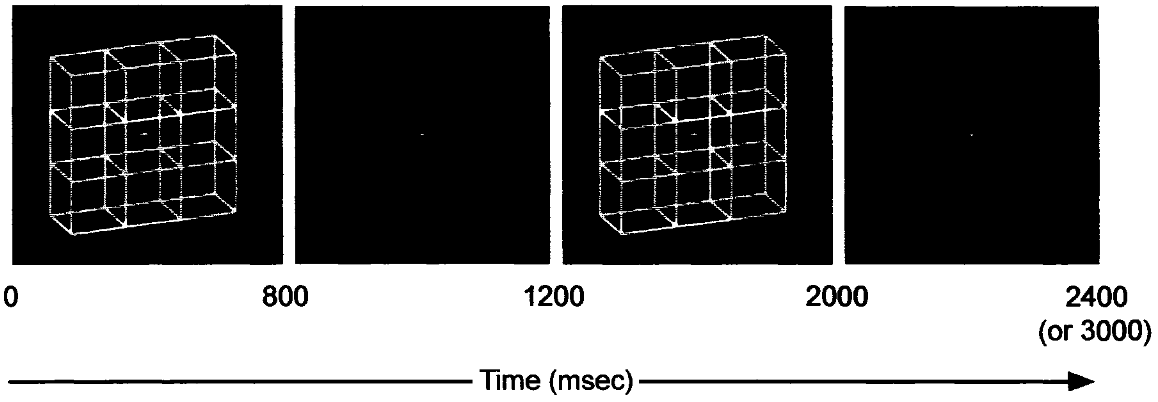


Figure 2.1. To allow time-locking of the EEG recording to the stimulus rather than to the response, and to entrain the moment of perceptual reversals to an externally observable event, i.e. stimulus onset, stimuli were continuously flashed on-and-off in 800msec stimulus / 400msec ISI presentations (adopted from Kornmeier & Bach, 2004). Observers indicated reversals by a button-press, which extended the ISI to 1000msec before the next 800-400msec cycle resumed.

For all experimental trials, each stimulus was presented 150 times per block, resulting in blocks lasting approximately 6min. Short trial blocks with breaks after each 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 instructions 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 across intention conditions. Each experimental session, including vision testing, net application, practice, and experimental trials, lasted approximately 1.5hrs.

Event-related potentials analyses

ERPs were time-locked to stimulus onset, baseline corrected at -200 to 0msec, and low-pass filtered at 25Hz (following procedures of Kornmeier & Bach, 2004). Trials were discarded from analysis if they contained an eye blink or eye movement artifact (EOG > 70µV), or more than 20% of electrode channels exceeded defined signal amplitudes (average amplitude > 200µV, or transit amplitude > 100µV). On average, 26% of trials per individual were rejected due to a combination of these artifacts. In addition, 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. Data from 27 observers were excluded based on this criterion. 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, 8 of the 27 excluded observers performed the task so well that too few reversals occurred for attainment of reasonable ERP signal/noise ratios. All subsequent analyses were conducted on data from the remaining 27 observers. Of the 27 observers, 19% of trials were rejected due to 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.

To answer the first set of questions, i.e. can the previously reported reversal components be identified and where on the scalp can they be recorded, comparisons between ERP waves of reversal and stability trials in the passive condition will be made. To answer the second, and more novel set of questions, comparisons between the ERP waves of the three intentional conditions will be made. To complicate matters, we can never have complete control over reversals of bistable stimuli. When we try to reverse our perception as often as possible, it will inevitably remain stable some of the time. Similarly, when we try to stabilize one percept, it will inevitably reverse once in a while. Because of this fundamental aspect of intentional control of bistable perception, we are essentially left with six different ERP waveforms to compare, i.e. three intentions x two perceptions. If any differences are found for the first set of questions, the ERP waveforms for perceptual reversal and perceptual stability will differ substantially. Asking, "Are there intention-based ERP differences, *regardless* of perception?" therefore requires a collapsing of two very different ERP waveforms in the average. For this reason, the second experimental question must be divided into two more precise questions: "*When we perceive a reversal*, are there intention-based ERP differences?", and "*When we perceive stability*, are there intention-based ERP differences?" By making comparisons of the ERPs in this manner, neural responses to the same stimulus and the same perception will be compared with the only difference being the intention of the observer. Amplitude differences in neural responses to the same input and the same state of visual awareness may therefore reveal when, where, and how top-down intentional control influences bistable perception.

To evaluate the first experimental question, recordings from the passive condition were sorted into reversal and stability waveforms and averaged for each individual. Based on Kornmeier and Bach's (2004, 2005) findings, three groups of posterior electrode sites were chosen for analysis: a central posterior group, channels 75 (Oz), 70 (O1), 83 (O2), 74, 82; a left posterior group, channels 69, 65 (PO7), 59, 68, 64, 58 (T5-P7); and a right posterior group, channels 89, 90 (PO8), 91, 94, 95, 96 (T6-P8), (see Luu & Ferree, 2005 for conversions from EGI hydrocel nets to the international 10-20 system). Figure 2.2 shows the positions of the electrodes within each group. For statistical analyses, amplitudes were averaged within the three clusters of electrode sites, i.e. the central, left, and right posterior groups.

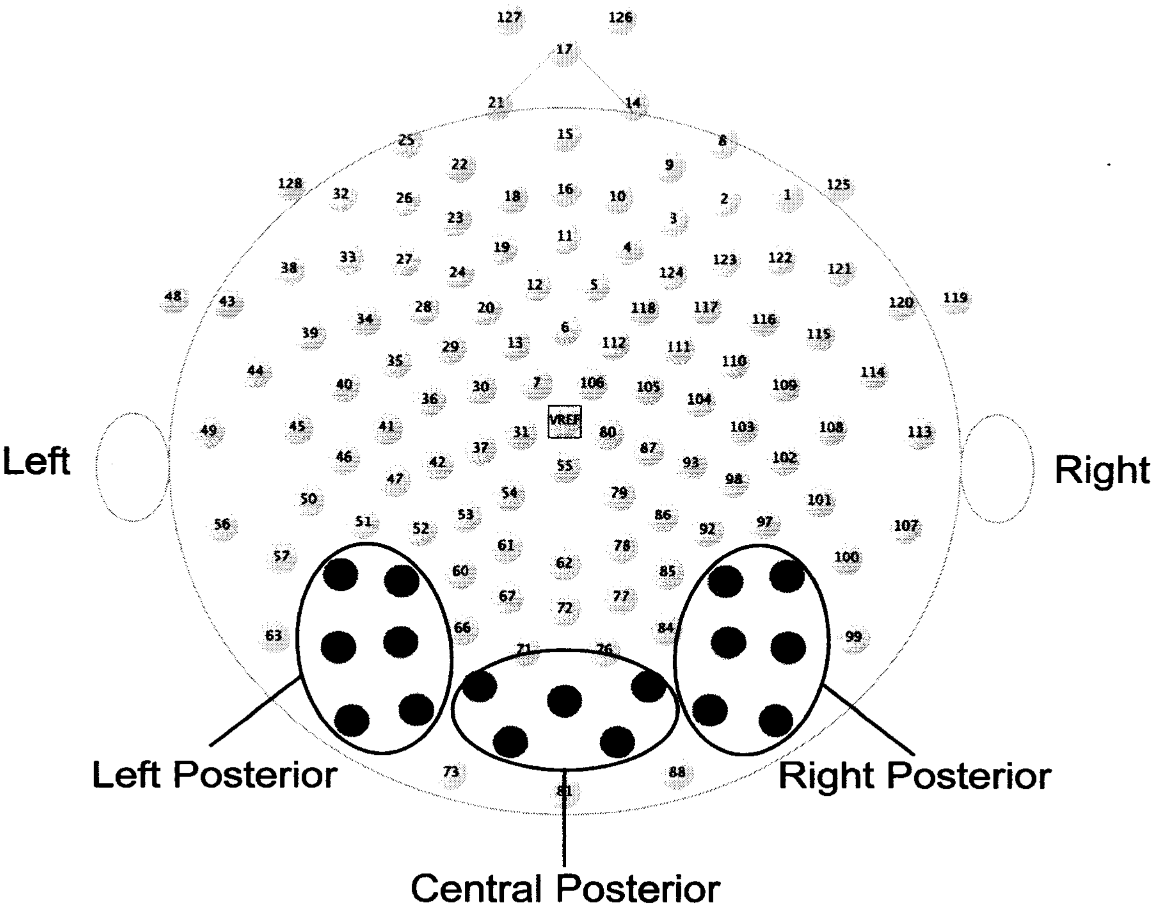


Figure 2.2. Electrode positions of the Hydrocel 128-channel electrogeodesic sensor net as seen from above. The electrodes selected for analysis of the RP and RN components are shown in dark gray. The three groups of sites, central, left, and right posterior are labeled, and ERPs were averaged within each group for statistical purposes.

Amplitudes of the three ERP components identified by Kornmeier and Bach (2004, 2005), the reversal positivity (RP), the reversal negativity (RN), and the late positive component (LPC), were measured by extracting the mean voltages across specified time windows. The mean amplitude approach offers several advantages over the approach taken by Kornmeier and Bach (2004, 2005). Kornmeier and Bach (2004, 2005) defined reversal-related components by computing difference waves (reversal-stability) and selecting the largest amplitude excursions for analysis. They then compared the peak amplitudes of the difference waves to zero, i.e. no difference, in their statistical analyses. The first concern with this approach is that by analyzing the amplitude at the point of maximal difference, an artificial inflation of differences is likely to occur. Second, by computing a difference and then comparing this value to 0, only one measure of variability is attained for statistical analysis. A more conservative and arguably more accurate method for analyzing these components is to calculate the mean amplitude across the entire time window of the component (for difference waves, this is essentially an area under the curve measure as opposed to a peak amplitude measure). Also, by comparing the mean amplitudes of reversal and stability waveforms, a more accurate assessment of variability can be achieved. For these reasons, mean amplitude measures were used in the current study to evaluate reversal-related differences in the ERP waveforms for the passive condition.

The reversal positivity (RP) was measured by comparing the mean amplitude of the reversal and stability waveforms within a ±20msec time window around the latency of the grand average P1 peak, which occurred at 118msec post-stimulus. Individual ERP waveforms were inspected to ensure that the time window captured the P1 peak. Kornmeier and Bach (2005) identified the RP in their difference waves by selecting the most positive amplitude within a ±20msec time window around the point of maximal difference, which occurred at 120msec post-stimulus. Thus, while the mean and peak amplitude measures of the RP are different, comparisons between the two studies are still possible. The reversal negativity (RN) was measured by comparing the mean amplitude of the reversal and stability waveforms from 170-370msec post-stimulus. This time window was chosen to allow comparisons to the selection negativity (SN; a broad negative component related to selective attention), but also permits comparisons to Kornmeier and Bach's (2004, 2005) findings. Kornmeier and Bach (2004, 2005) found that the RN began at about 160msec and peaked at 250 ±20msec in their difference waves. This time window of 170-370msec therefore captures the same component and allow comparisons across studies. The late positive component (LPC) was defined as the mean amplitude across a time window of 300-500msec post-stimulus, and was also similar in latency to the late component reported by Kornmeier and Bach (2004). Due to the more central-parietal scalp distribution of P3-like components, a different set of electrode sites was employed to measure the LPC: channels 55 (CPz), 62 (Pz), 72 (POz), 54, 61, 67 (PO3), 77 (PO4), 79, and 78. Figure 2.3 shows the positions of these electrodes. Recordings from these central-parietal sites were averaged for analysis purposes.

The variability of the mean amplitudes for the RP and RN components was estimated by 2x3 repeated-measures ANOVAs with the factors perception (reverse or stable), and scalp location (central, left, or right posterior). The scalp location factor was included to allow an assessment of where these components could be identified. Kornmeier and Bach (2004, 2005) were able to identify the reversal-related components in left, central, and right occipital and parietal locations, although as mentioned previously, this identification was accomplished

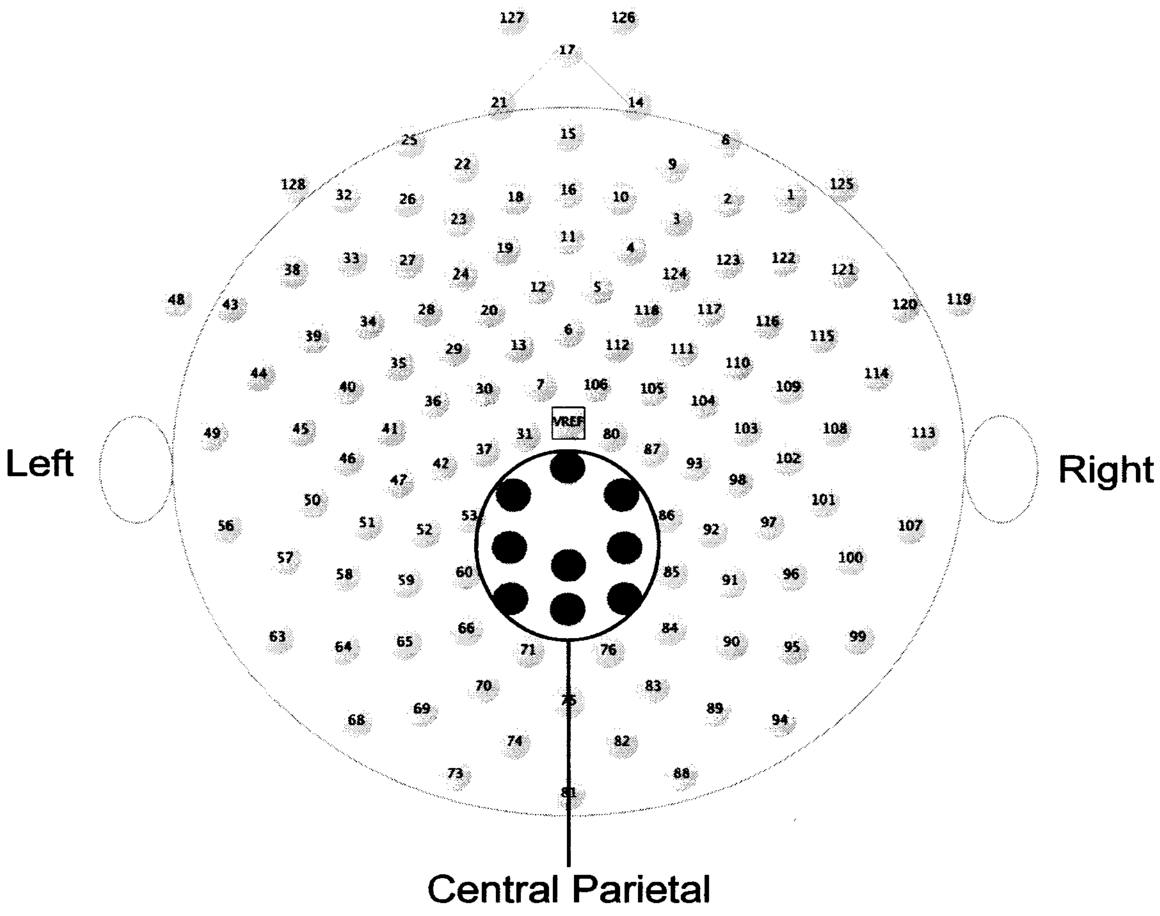


Figure 2.3. Electrodes chosen for analysis of the LPC are marked in dark gray. ERPs from these channels were averaged for statistical purposes.

with difference wave peak amplitude analyses, not mean amplitude measures, and a limited number of recording sites. If no scalp distribution differences exist, a main effect of perception should be found. If scalp location differences exist however, an interaction between perception and scalp location would be expected. A main effect of scalp location is not necessarily important for this analysis, because ERP amplitudes from both perceptions are averaged together to measure this effect, and the focus of the first experimental question is on ERP *differences* between reversal and stability perceptions. Three a priori t-tests (one for each scalp location) were performed to analyze whether the mean amplitude for reversals was significantly different than the mean amplitude for stability, i.e. to determine what differences were driving the main effects and/or interactions. A one-way ANOVA was used to measure mean amplitude differences between reversal and stability in the LPC, as only one scalp location was selected for analysis.

To address the second experimental question, (when reversals occur, are there ERP differences based on intention; and when stability occurs, are there ERP differences based on intention), 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). Although a frontal-posterior attention network is the assumed anatomical substrate that mediates voluntary shifts in visual attention, previous studies have shown that associated changes in brain activity are more pronounced in posterior regions (Yamaguchi, Yamagata, & Kobayashi, 2000; Slotnick & Yantis, 2005), i.e. where frontal-posterior synapses reside, as opposed to anterior regions, i.e. where goal-directed attentional shifts are ‘controlled’ or ‘initiated’. Based on this factor, as well as an inspection of the grand averages, two groups of electrode sites were chosen for analysis: a central occipital group, channels 75 (Oz), 70 (O1), and 83 (O2); and a central parietal-occipital group, channels 62 (Pz), 72 (POz), 67 (PO3), 77 (PO4), 71, and 76. Figure 2.4 shows the positions of the electrodes

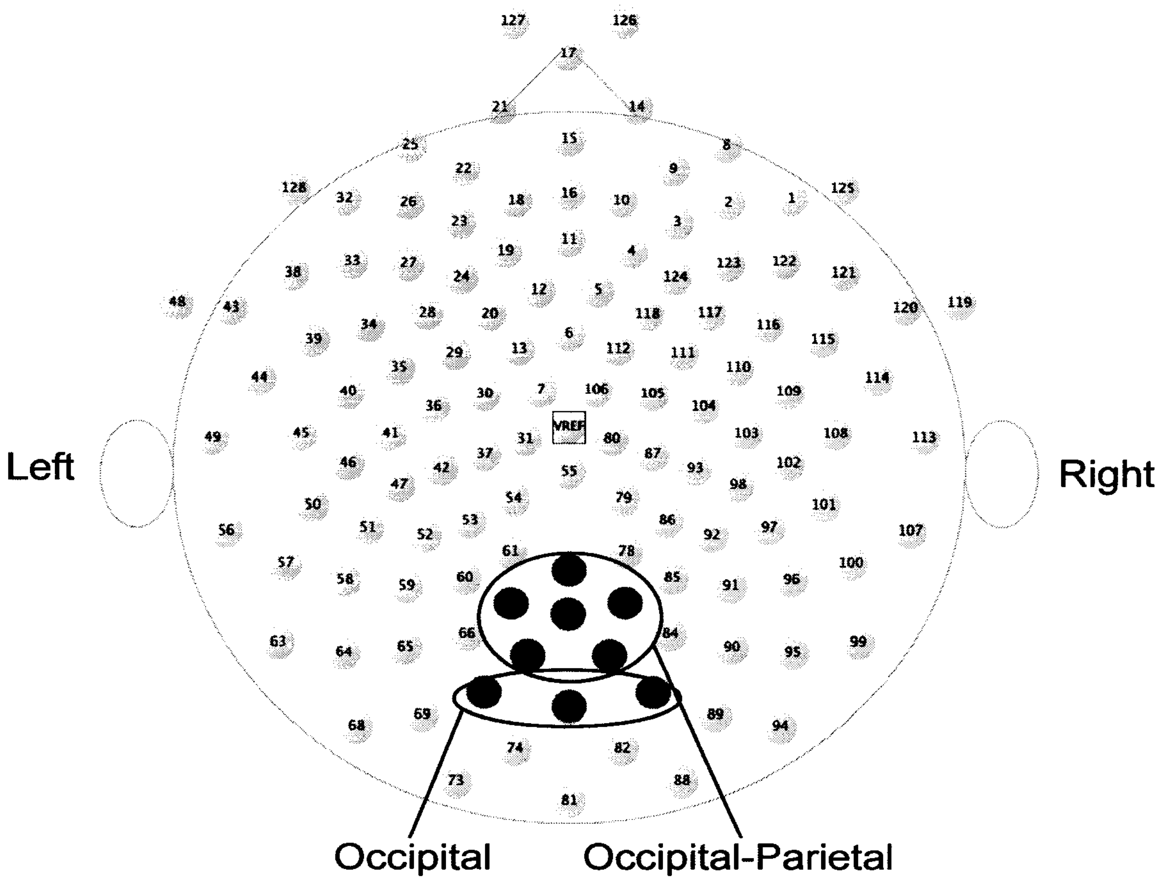


Figure 2.4. Electrode positions used for analysis of the second experimental question are marked in dark gray. The two clusters of sites in which ERPs were averaged for analysis are circled, i.e. the occipital and occipital-parietal groups.

within these two groups. For statistical analyses, amplitudes were averaged within the two clusters of electrode sites.

Because this was the first study to investigate the effects of intention on perceptual reversals, amplitudes of all four of the prominent visual ERP peaks, the P1, N1, P2, and N2 were measured. Based on the results of the analysis of the passive condition (i.e. from the first experimental question of this study), the mean amplitudes of the reversal negativity (RN) and late positive component (LPC) were measured as well. The P1, N1, P2, and N2 peak amplitudes for each individual were measured relative to baseline (-200-0msec) by selecting the maximum/minimum amplitude within a ±40msec time window around the grand average peaks: P1=118msec, N1=178msec, P2=218msec, N2=280msec. All individual ERP waveforms were inspected to ensure that each peak maxima was captured by the ±40msec time window. If the time window was too wide, i.e. it captured a previous or subsequent peak maxima, the window was narrowed on an individual basis. The mean amplitudes of the RN (170-370msec) and LPC (300-500) were measured in the same way as in the analysis of the first experimental question (described above).

The variability of the peak (P1, N1, P2, N2) and mean (RN, LPC) amplitudes for each of these six components was estimated by 2x2x3 repeated-measures ANOVAs with the factors perception (reverse or stable), scalp location (central occipital or central parietal-occipital), and intention (try to reverse, try to stabilize, or passive). Although multiple estimations of variance increase the chance of making a type I error, the relationship among separate ERP components remains uncertain. Including 'component' as a fourth factor (with six levels) in an ANOVA would maintain a family-wise error rate of .05, but averaging together amplitudes of these separate components does not make theoretical sense when evaluating the effects of the other three factors. Therefore, in this analysis, separate ANOVAs were conducted for each component, and p values for all comparisons are provided in the results section as well as in the appendices.

Because ERP differences based on perception are known to occur (from Kornmeier & Bach, 2004, 2005; Pitts, Nerger, & Davis, 2007), a main effect of intention is not necessarily critical or expected. A main effect of perception might be found, but again, this effect is not critical to answering this experimental question, as measurements from all three intentions are averaged together in such an analysis. The main effects and interactions involving the scalp location factor are also not critical, as post-hoc tests can be used to assess where the differences exist. The relevant aspect of these ANOVAs is the potential interaction between perception and intention. If a perception x intention interaction is found, post-hoc comparisons will be made to assess how intention influences reversal and stability ERP waveforms separately at each scalp location.

Chapter 3: RESULTS

Behavioral Results

Consistent with Kornmeier and Bach (2004, 2005) and Pitts, Nerger, and Davis (2007), all observers reported seeing reversals only at stimulus onset and never within the 800msec duration of stimulus presentation. Reversal rates differed across the three intention conditions as expected: passive (26%); intention-to-reverse (29%); intention-to-stabilize (23%). Figure 3.1 shows the number of reversals reported in each of the three intention conditions.

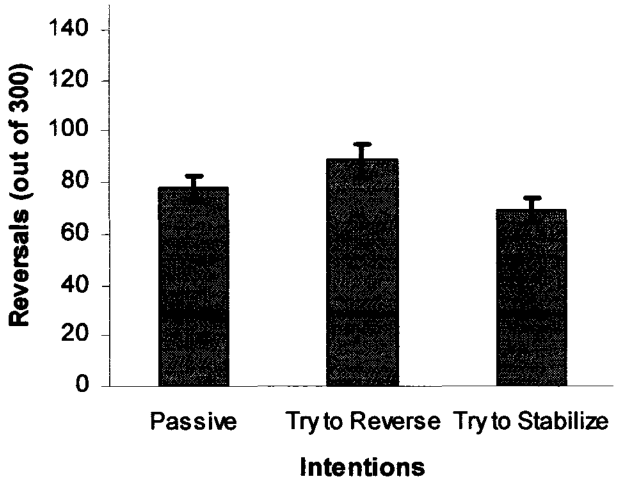


Figure 3.1. Mean number of reversals (out of 300 total stimulus presentations) across observers for the three intention conditions. Error bars represent ±1 standard error of the mean (SEM).

Fifteen of the twenty seven observers 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). Five of the observers showed reduced reversal rates in both intention-to-stabilize as well as intention-to-reverse conditions, compared to the passive condition. Only one observer experienced an increase in reversal rates for both intention-to-reverse and intention-to-stabilize conditions compared to the passive condition. Interestingly, six of the twenty seven observers exhibited reversal rates that were completely opposite of their intentions, i.e. rates decreased when they tried to increase reversals, and increased when they tried to decrease reversals. Figure 3.2 provides percentages of intention successes/failures. As this chart shows, 77% of observers were able to successfully reduce reversal rates in the intention-to-stabilize condition, while 59% of 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 1200msec (stimulus presentation plus ISI durations): Passive (M = 543msec; SEM = 35), intention-to-reverse (M = 525msec; SEM = 36), intention-to-stabilize (M = 567msec; SEM = 37). Most responses occurred within the timeframe of the stimulus presentation (800msec), and 10% (Passive), 9% (Intention-to-reverse), and 13% (Intention-to-stabilize) of responses were made during the ISI.

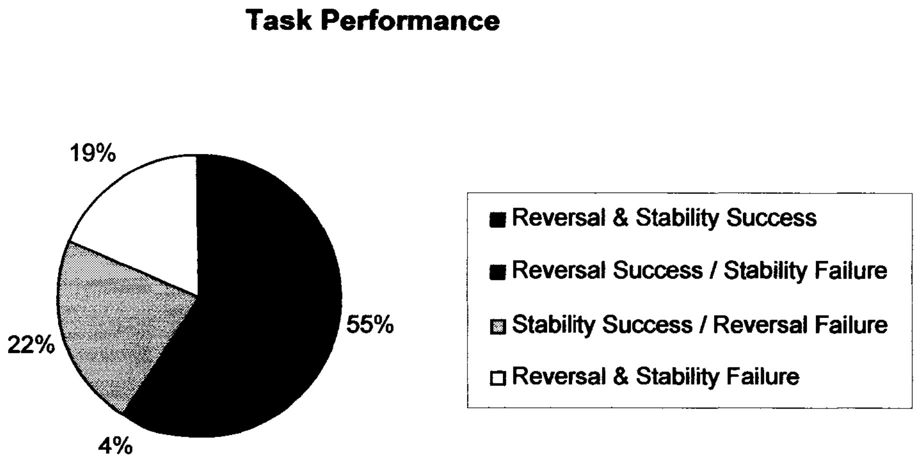


Figure 3.2. Percentages of intention successes/failures for the 27 observers. Successful intentions are defined as reversal rate increases when intended and decreases when intended. Intention failures are defined as reversal rates increases when the intention was to decrease, and decreases when the intention 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 vise versa. All increases/decreases are relative to the passive condition reversal rate. The legend above denotes the four combinations of successful vs. unsuccessful intentions.

Electrophysiological Results

Figures 3.3, 3.4, and 3.5 show the grand average ERPs for reversal and stability trials in the passive condition at central, left, and right posterior electrode sites respectively. These waveforms were used to evaluate the reversal positivity (RP) and reversal negativity (RN) components. Figure 3.6 shows the grand average ERPs for reversal and stability in the passive condition at central-parietal sites. These waveforms were used to measure the late positive component (LPC). For figures 3.3-3.6, reversal ERPs are depicted in gray, stability ERPs in black, and amplitude (µV) is plotted as a function of time (msec post-stimulus). In all graphs, positive amplitude is plotted up, and negative amplitude down.

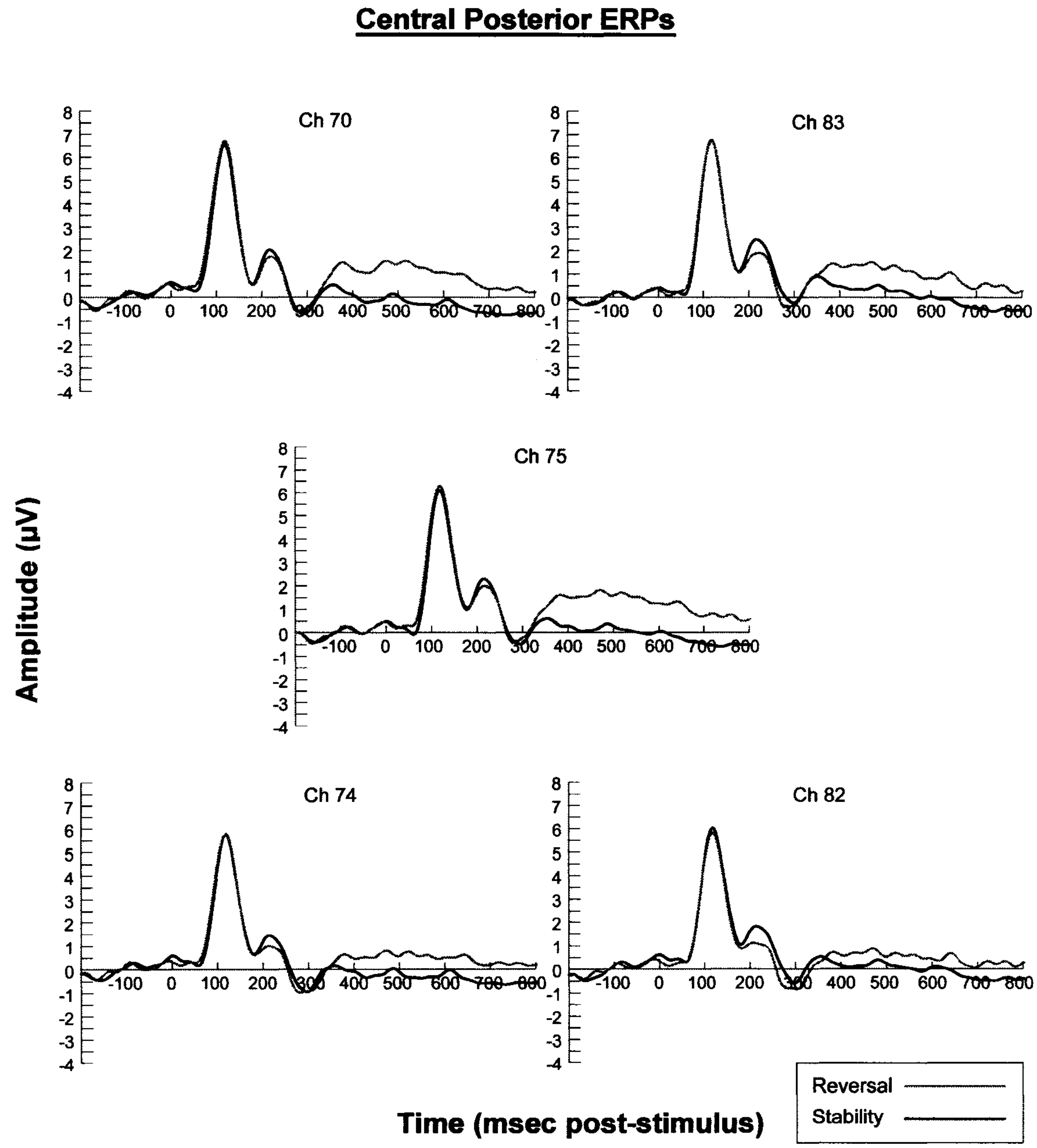


Figure 3.3. Grand average ERPs (N=27) from 5 central posterior electrode sites (marked on the sensor layout in Fig 2.2) for perceptual reversal (gray lines) and perceptual stability (black lines) in the passive condition. All graphs show amplitude (µV) plotted as a function of time (msec post-stimulus). A reversal negativity (170-370msec) can be seen in channel 82 (and possibly channels 74 & 83), and the LPC (300-500msec) can be seen in all five channels.

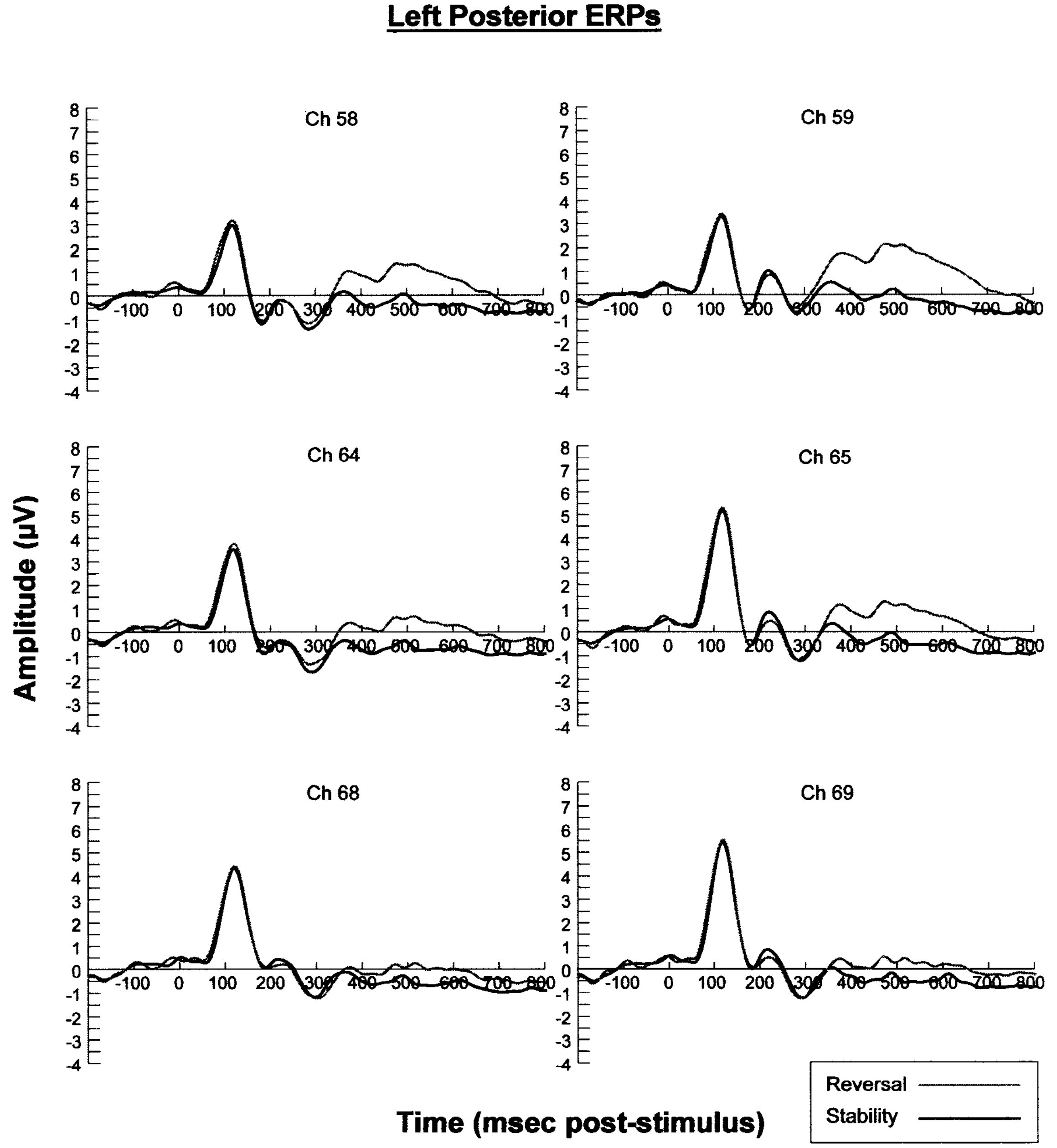


Figure 3.4. Grand average ERPs (N=27) from 6 left posterior electrode sites (marked on the sensor layout in figure 2.2) for perceptual reversal (gray lines) and perceptual stability (black lines) in the passive condition. All graphs show amplitude (µV) plotted as a function of time (msec post-stimulus). The reversal negativity (170-370msec) is absent from all channels. The LPC (300-500msec) can be seen in channels 58, 59, 64, and 65, and seems to contain two distinct peaks.

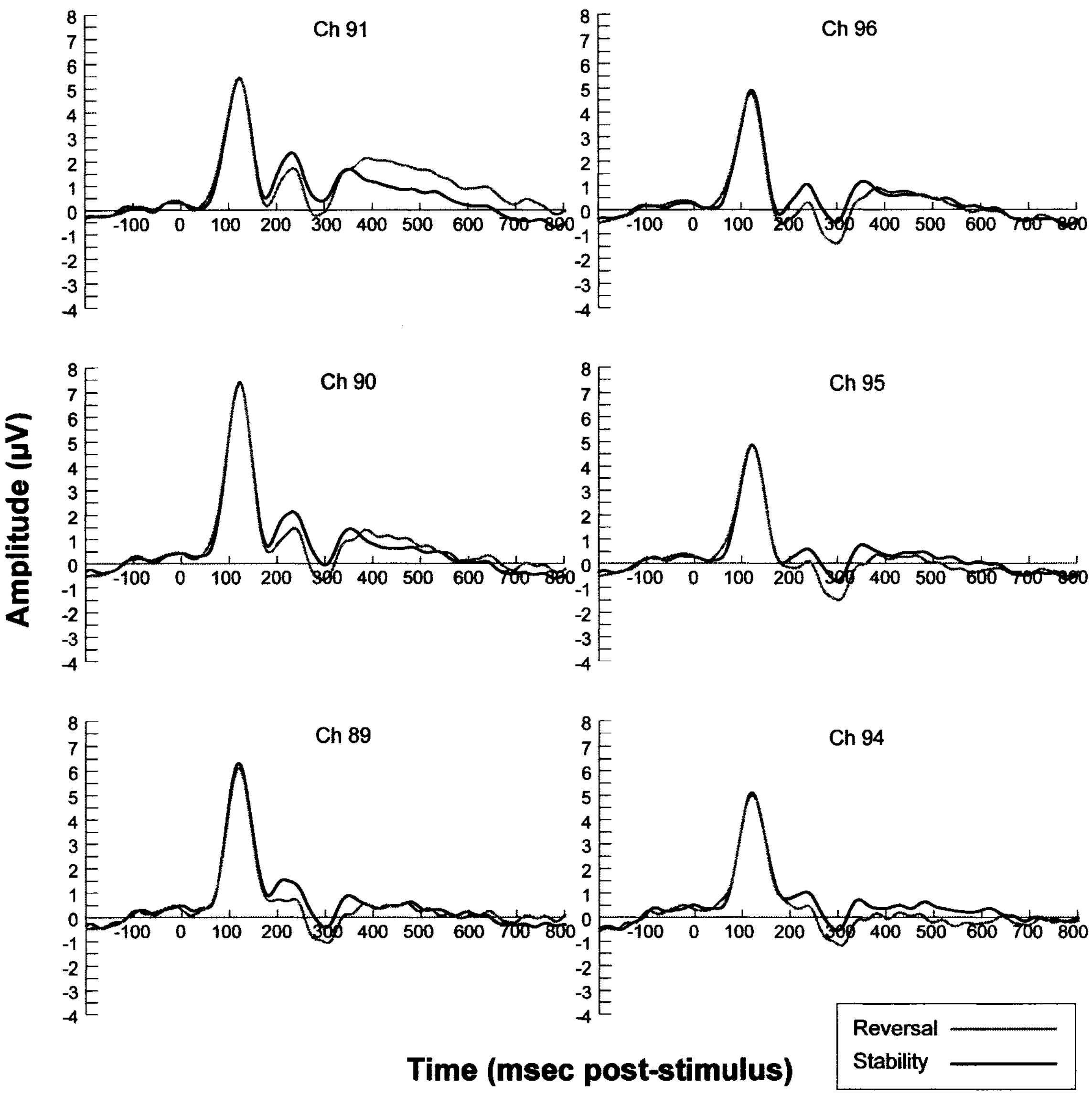

Right Posterior ERPs

Figure 3.5. Grand average ERPs (N=27) from 6 right posterior electrode sites (marked on the sensor layout in figure 2.2) for perceptual reversal (gray lines) and perceptual stability (black lines) in the passive condition. All graphs show amplitude (µV) plotted as a function of time (msec post-stimulus). The reversal negativity (170-370msec) can clearly be identified in all six channels. Interestingly, the LPC (300-500msec) is small and/or absent in these recordings.

Central Parietal ERPs

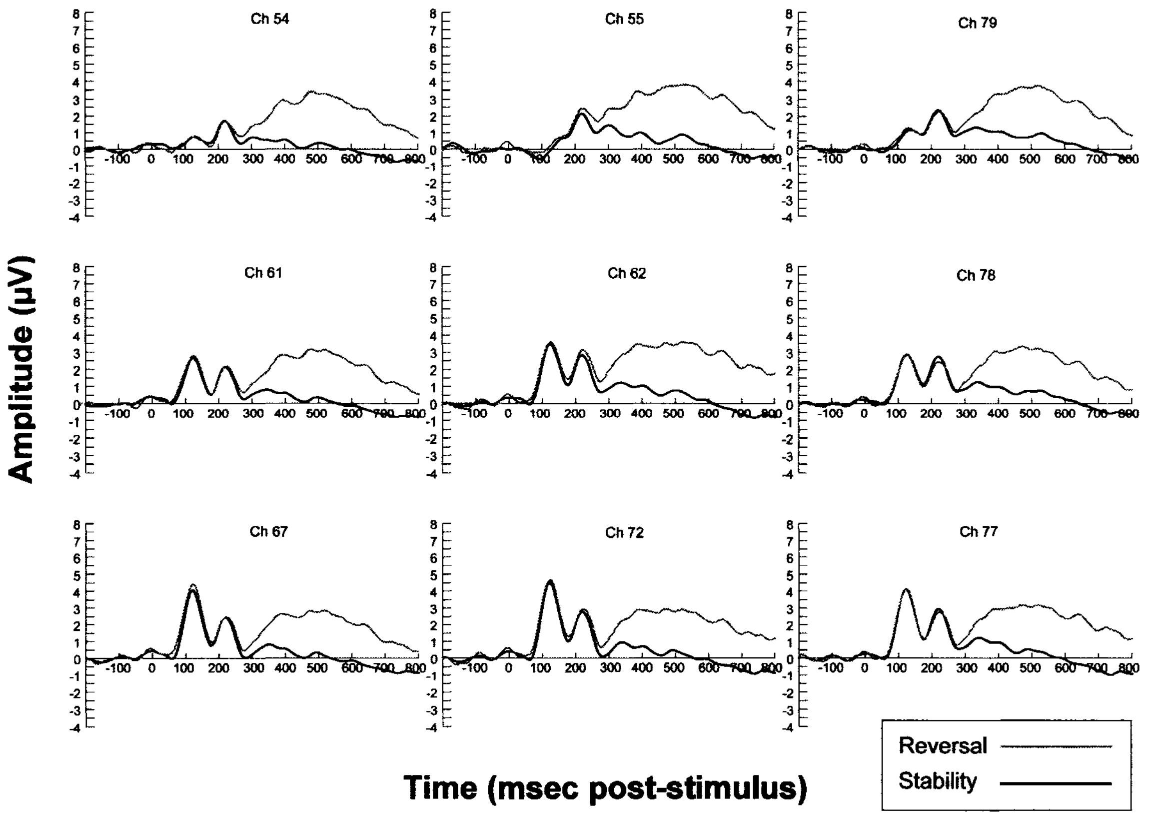


Figure 3.6. Grand average ERPs (N=27) from 9 central parietal electrode sites (marked on the sensor layout in figure 2.3) for perceptual reversal (gray lines) and perceptual stability (black lines) in the passive condition. All graphs show amplitude (µV) plotted as a function of time (msec post-stimulus). The LPC (300-500msec) can be clearly identified in all channels.

For the RP, no main effect of perception was found, F(1,26) =.115, p = .738, and no interaction between perception and scalp location was found, F(2,26) = .534, p = ..589. A main effect of scalp location was found, F(1,26) = 19.256, p<.001, although this effect was not of primary interest to this study. The scalp location effect was driven by larger P1 amplitudes in central and right posterior sites compared to left posterior sites. This amplitude difference can be observed by comparing the P1 peaks in figures 3.3 and 3.5 (central and right) to the P1 peaks in figure 3.4 (left). Figures 3.3, 3.4, and 3.5 show no indication of a reversal-related difference in the time frame of the RP (98-138msec).

For the RN component, no main effect of perception was found, F(1,26) = 1.035, p = .318, although a significant interaction between perception and scalp location was found, F(2,26) = 3.89, p = .027. Mean RN amplitudes for reversal and stability at central, left, and right electrode sites are shown in figure 3.7. From this figure, it is clear that the largest difference between reversal and stability ERP amplitudes occurs at right posterior sites, and the difference is small or non-existent at left and central posterior sites.

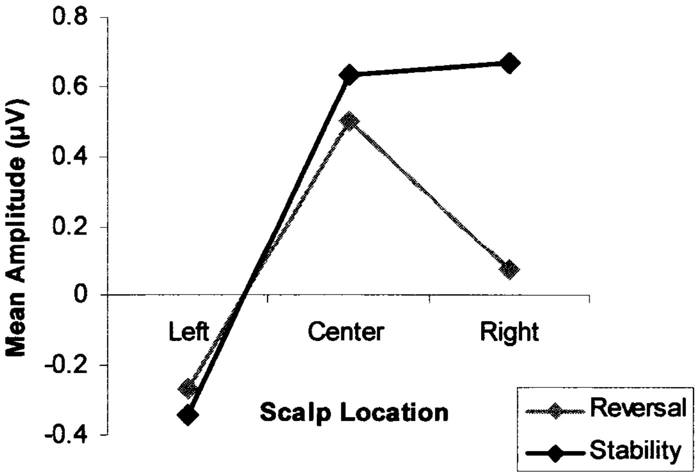


Figure 3.7. Mean amplitude of the RN (170-370msec) plotted as a function of scalp location. Reversal amplitudes are plotted in gray, and stability amplitudes are plotted in black. The largest difference between reversal and stability was found at right posterior sites.

The RN can also be seen in all right posterior sites in figure 3.5 (from 170-370msec), and there is a slight indication of similar differences at central sites shown in figure 3.3. T-tests assessed the differences between reversal and stability at each scalp location and confirmed that the RN is present at right posterior sites, $t(26) = 2.26$, $p < .05$, but not central, $t(26) = .50$, $p > .05$, or left posterior sites, $t(26) = .28$, $p > .05$.

The LPC component was assessed by a one-way ANOVA, and a main effect of perception was found, $F(1,26) = 40.07$, $p < .001$. This difference between reversal and stability waveforms from 300-500msec post-stimulus can be seen in all nine central-parietal channels shown in figure 3.6.

Difference waves were computed for all of the channels included in the analysis of the passive condition and are presented in figures 3.8-3.11. All difference waves show reversal minus stability ERPs, and amplitude difference (μV) is plotted as a function of time (msec post-stimulus). The significant RN can be seen in figure 3.10 (right posterior), and the significant LPC can be seen in figure 3.11 (central-parietal).

Central Posterior Difference Waves

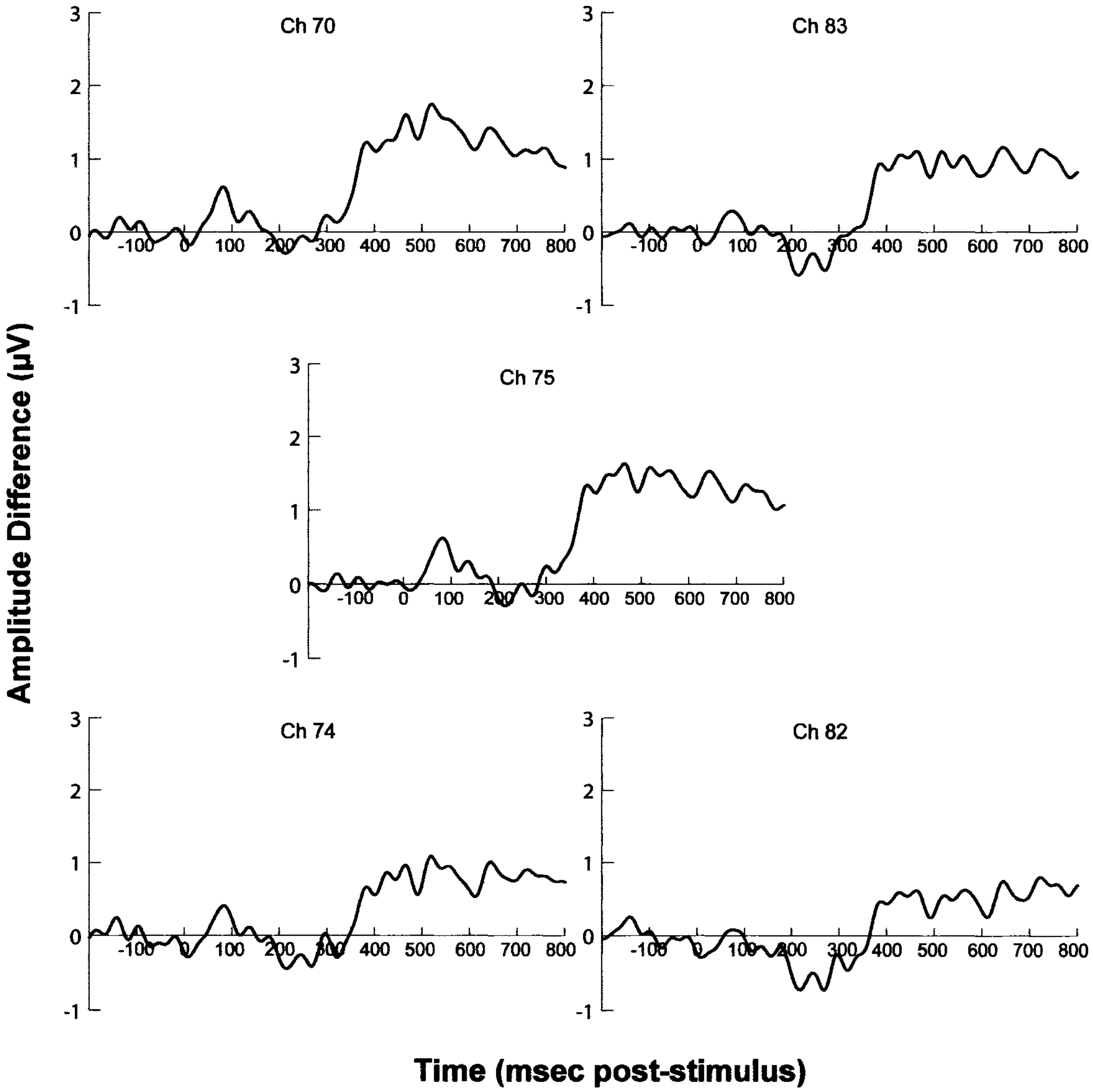


Figure 3.8. Grand average difference waves (reversal minus stability) from 5 central posterior electrode sites (marked on the sensor layout in figure 2.2) in the passive condition. All graphs show amplitude difference (µV) plotted as a function of time (msec post-stimulus). A reversal negativity (170-370msec) can be seen in channel 82 (and possibly in channels 74 and 83), and the LPC (300-500msec) can be seen in all five channels.

Left Posterior Difference Waves

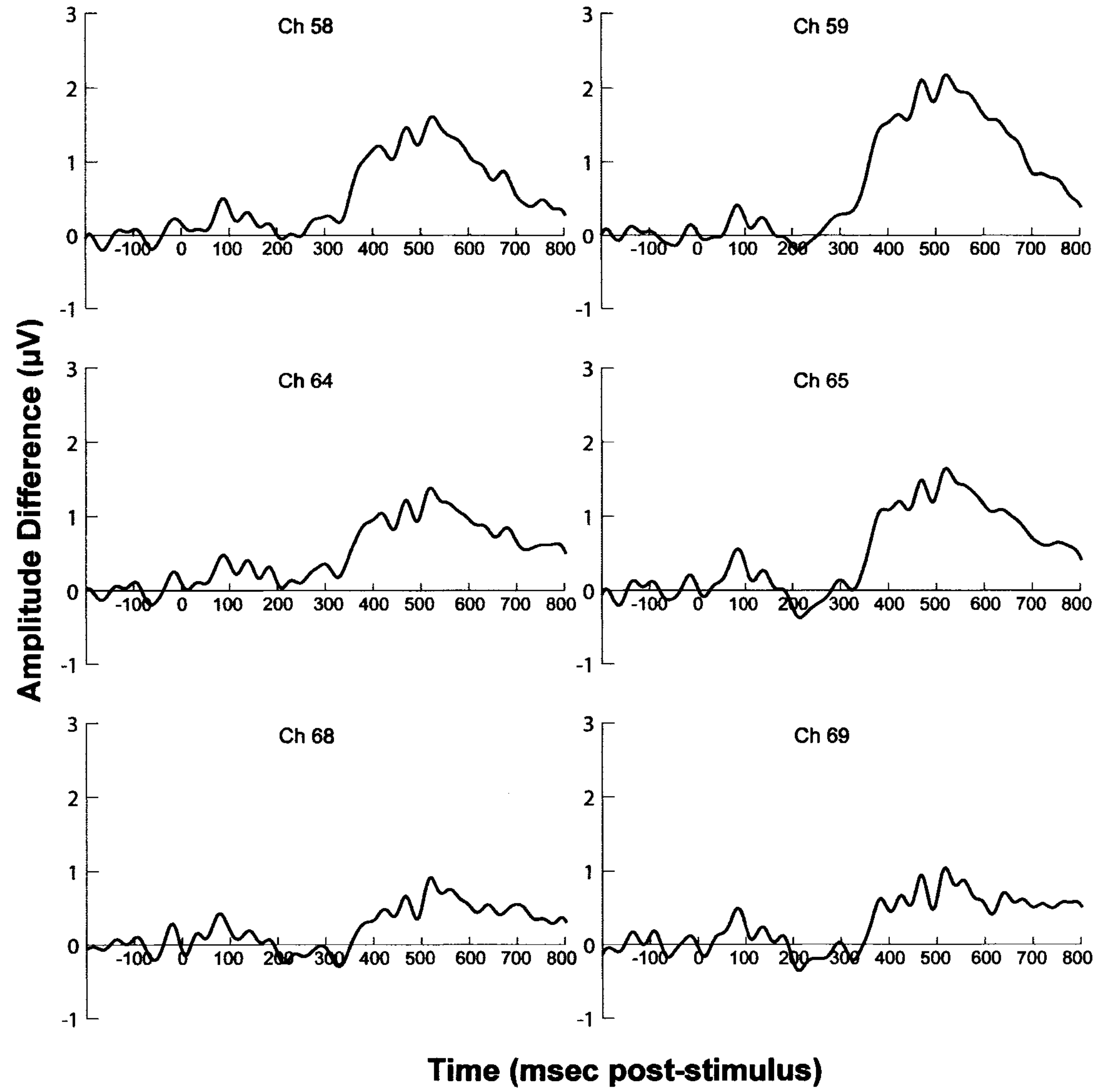


Figure 3.9. Grand average difference waves (reversal minus stability) from 6 left posterior electrode sites (marked on the sensor layout in figure 2.2) in the passive condition. All graphs show amplitude difference (µV) plotted as a function of time (msec post-stimulus). The reversal negativity (170-370msec) is absent from all channels. The LPC (300-500msec) can be seen in all six channels.

Right Posterior Difference Waves

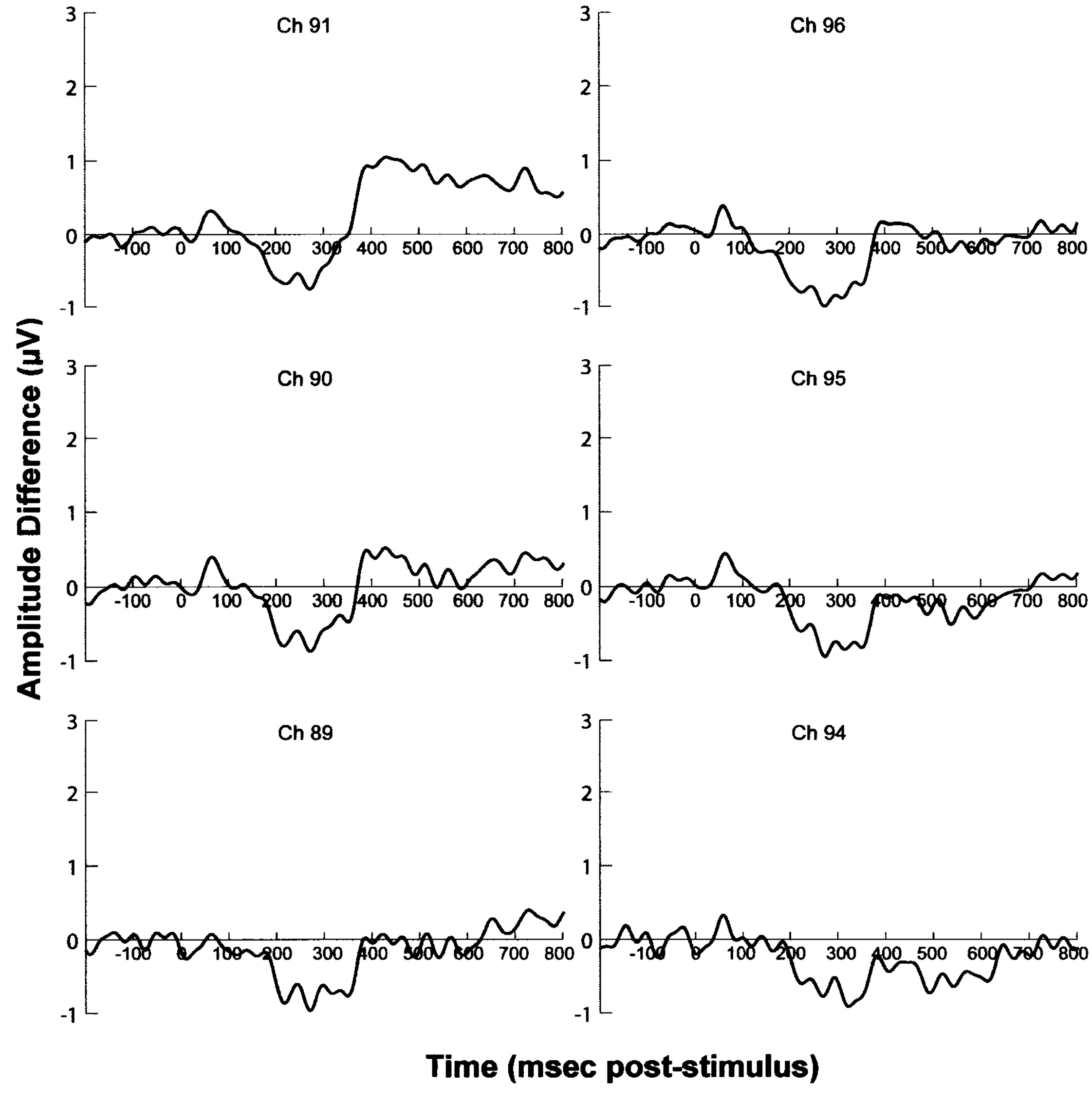


Figure 3.10. Grand average difference waves (reversal minus stability) from 6 right posterior electrode sites (marked on the sensor layout in figure 2.2) in the passive condition. All graphs show amplitude difference (µV) plotted as a function of time (msec post-stimulus). The reversal negativity (170-370msec) can clearly be identified in all six channels. Interestingly, the LPC (300-500msec) is absent from most of these channels.

Central Parietal Difference Waves

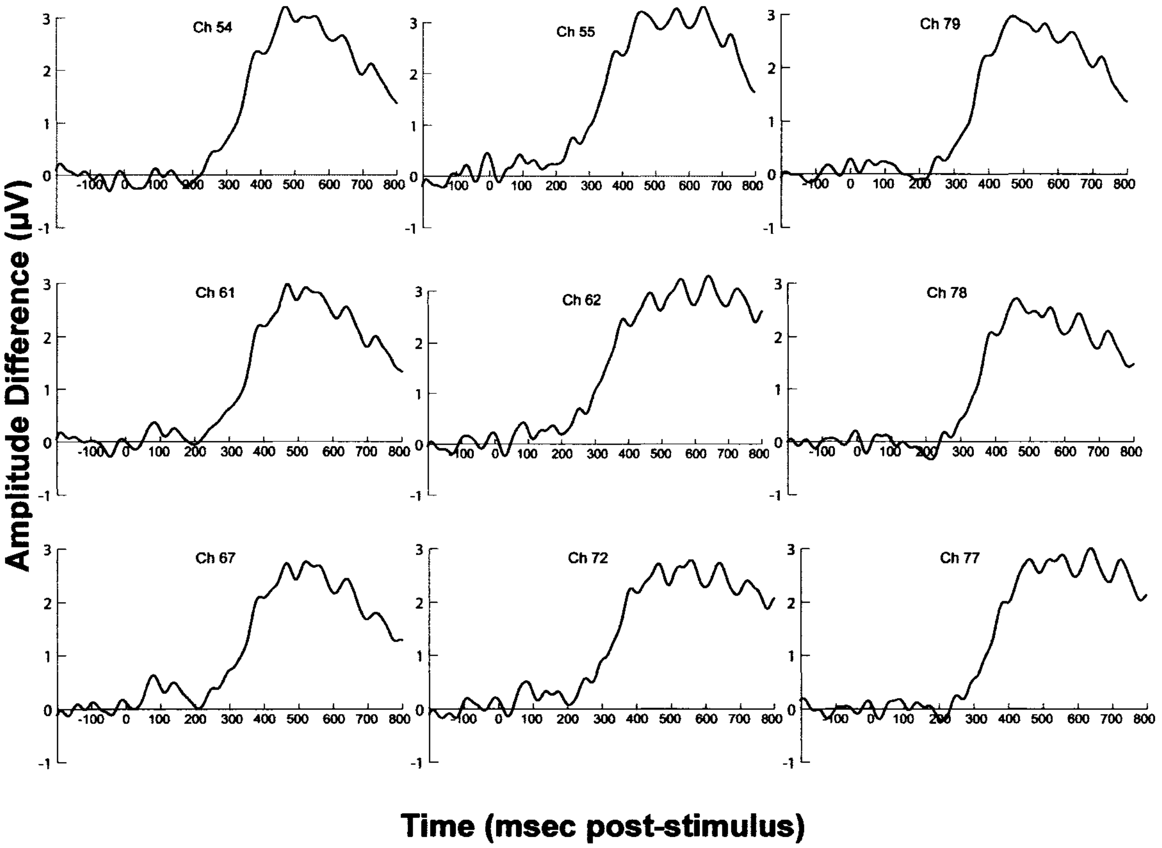


Figure 3.11. Grand average difference waves (reversal minus stability) from 9 central parietal electrode sites (marked on the sensor layout in figure 2.3) in the passive condition. All graphs show amplitude difference (μV) plotted as a function of time (msec post-stimulus). The LPC (300-500msec) can be clearly identified in all channels, and appears to begin earlier in some channels (≈200msec).

To assess whether intention had an effect on the visual ERPs, the peak amplitudes of the P1, N1, P2, N2, and mean amplitudes of the RN and LPC were measured. 2x3x2 ANOVAs (perception x intention x scalp location) were employed to assess main effects and interactions for each of these five components. Grand average ERPs are plotted in figures 3.12-3.15. For all figures, the passive condition ERPs are plotted as a solid lines, the intention-to-reverse ERPs as a dotted lines, and the intention-to-stabilize ERPs as dashed lines. Figure 3.12 and 3.13 show the three different intention ERPs for perceptual reversals while figures 3.14 and 3.15 show the three intention ERPs for perceptual stability.

For the P1 amplitude, no interaction between perception and intention was found, F(2,26) = .145, p = .866, although a significant main effect for perception was found, F(1,26) = 5.083, p = .033. This main effect is not relevant to the second experimental question, because amplitudes from all three intentions are averaged together, but this difference may indicate a reversal positivity (RP), which was not found in the analysis of the first experimental question.

No interaction between perception and intention was found for the N1 peak, F(2,26) = 1.016, p = .369, but once again, a main effect of perception was found, F(1,26) = 5.748, p = .024. This main effect most likely represents the beginning of the reversal negativity (RN) component, since the N1 peak occurred at 178msec, and the RN component ranges from 170-370msec.

Occipital Perceptual Reversal ERPs

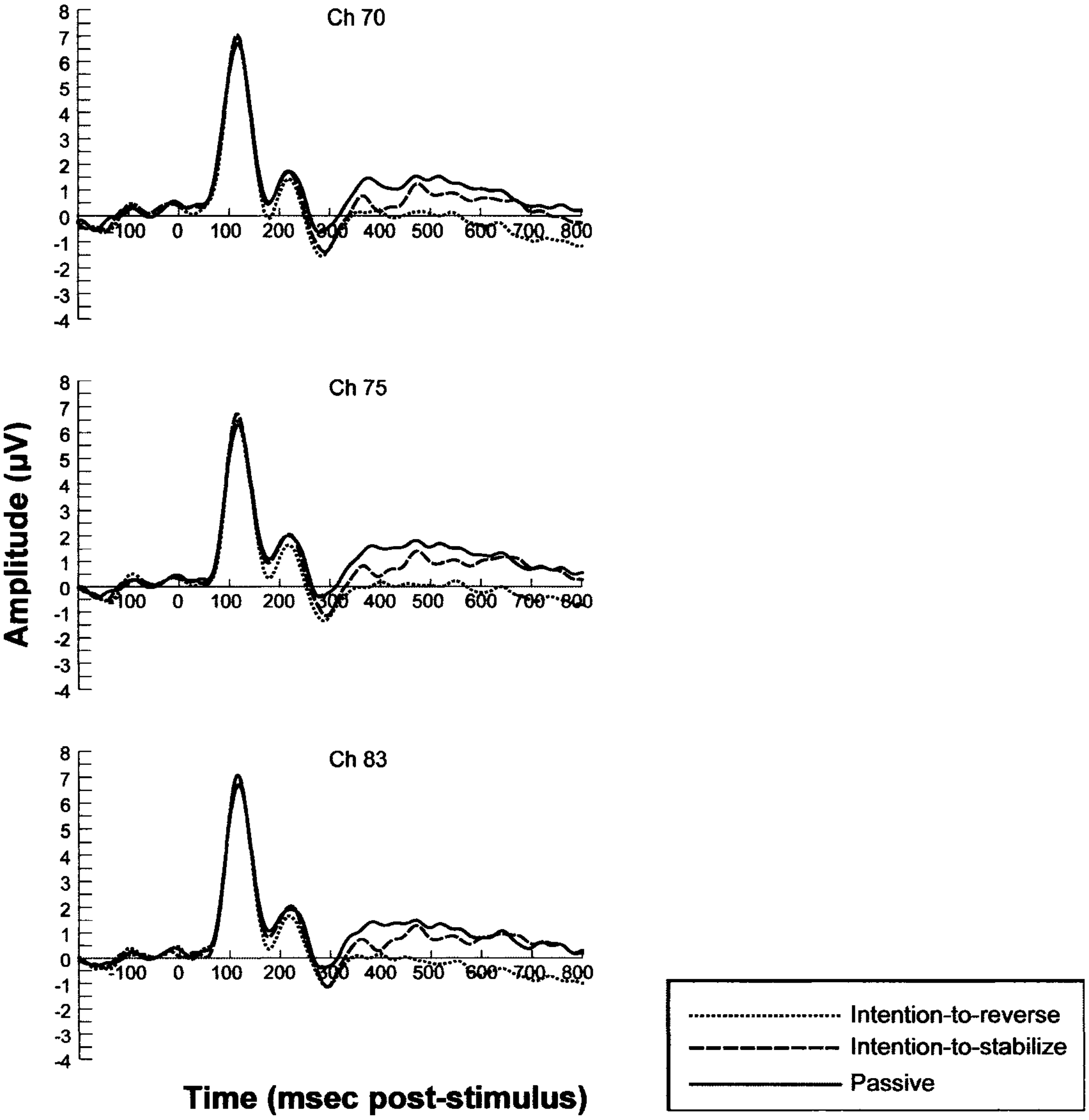


Figure 3.12. Grand average ERPs (N=27) from 3 occipital electrode sites (marked on the sensor layout in figure 2.4) for perceptual reversals in the three intention conditions. Intention-to-reverse ERPs are shown as dotted lines, intention-to-stabilize as dashed lines, and the passive condition as solid lines. All graphs show amplitude (µV) plotted as a function of time (msec post-stimulus). Note that the overlaid waveforms represent responses to the same stimulus and same perception (reversal), with the only difference being the observers' intentions. Intention-based differences begin at the N1 peak, and continue through the P2, N2, and LPC peaks.

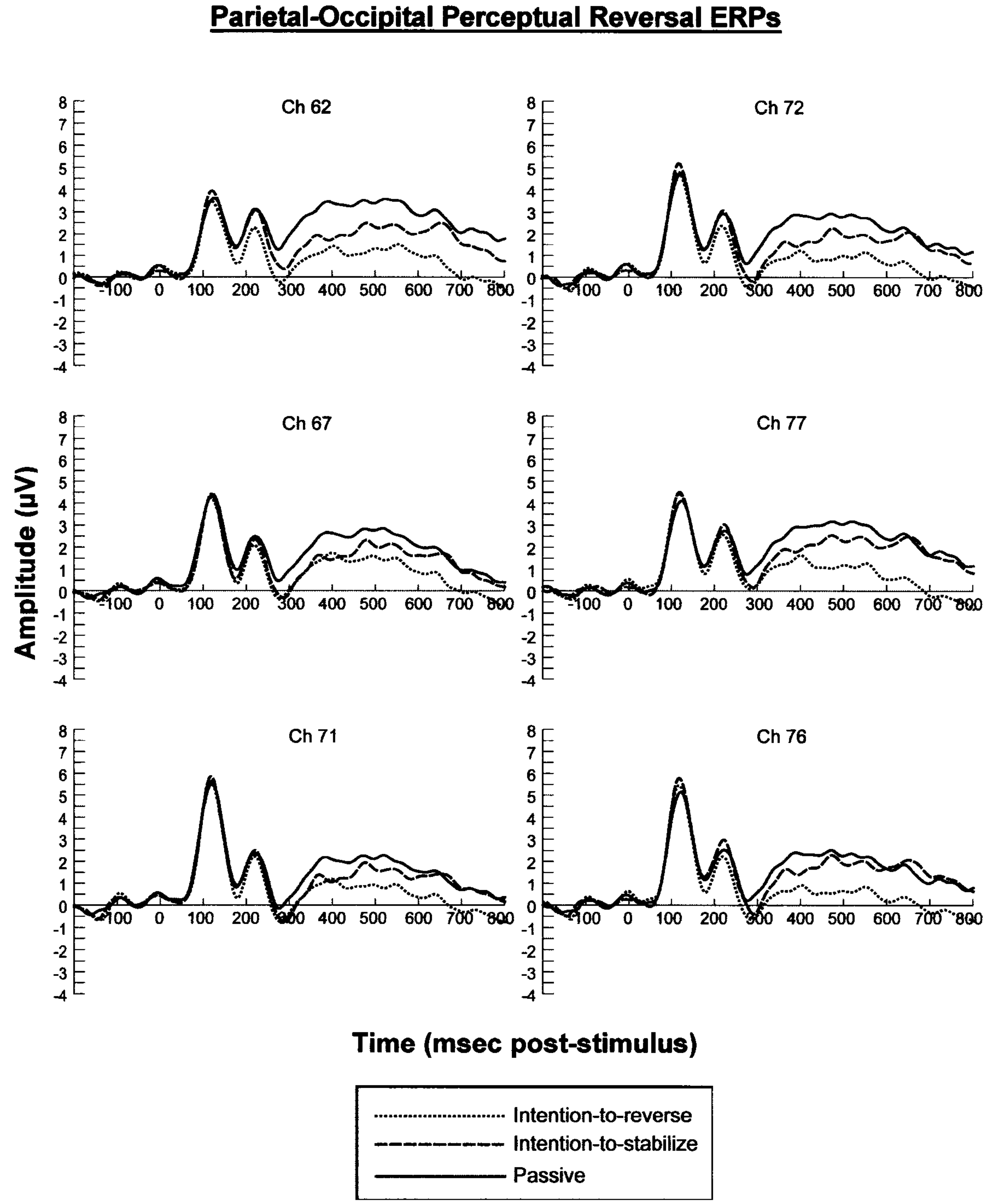


Figure 3.13. Grand average ERPs (N=27) from 6 occipital-parietal electrode sites (marked on the sensor layout in figure 2.4) for perceptual reversals in the three intention conditions. Intention-to-reverse ERPs are shown as dotted lines, intention-to-stabilize as dashed lines, and the passive condition as solid lines. All graphs show amplitude (µV) plotted as a function of time (msec post-stimulus). Note that the overlaid waveforms represent responses to the same stimulus and same perception (reversal), with the only difference being the observers' intentions. Intention-based differences begin at the N1 peak, and continue through the P2, N2, and LPC peaks.

Occipital Perceptual Stability ERPs

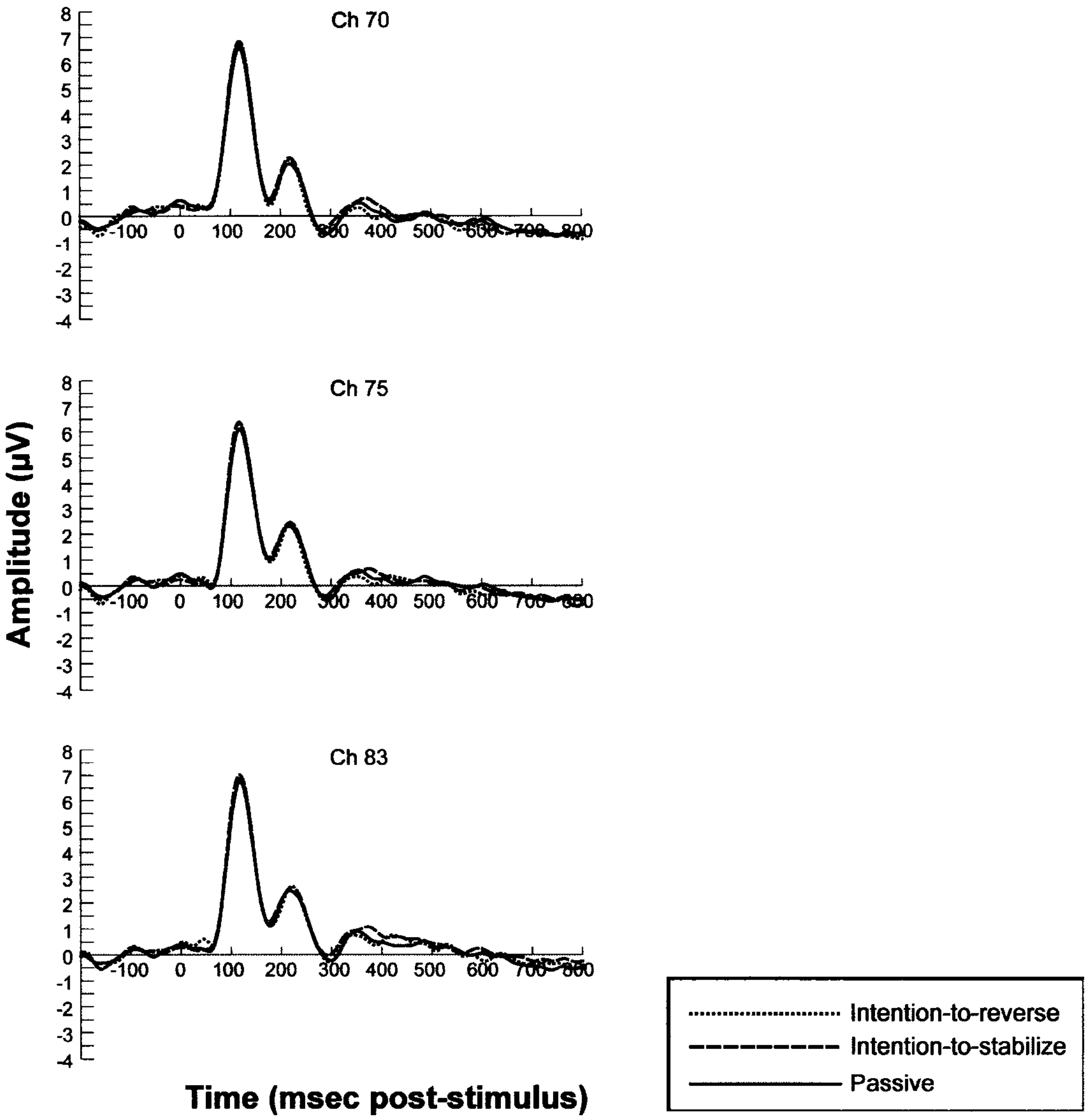
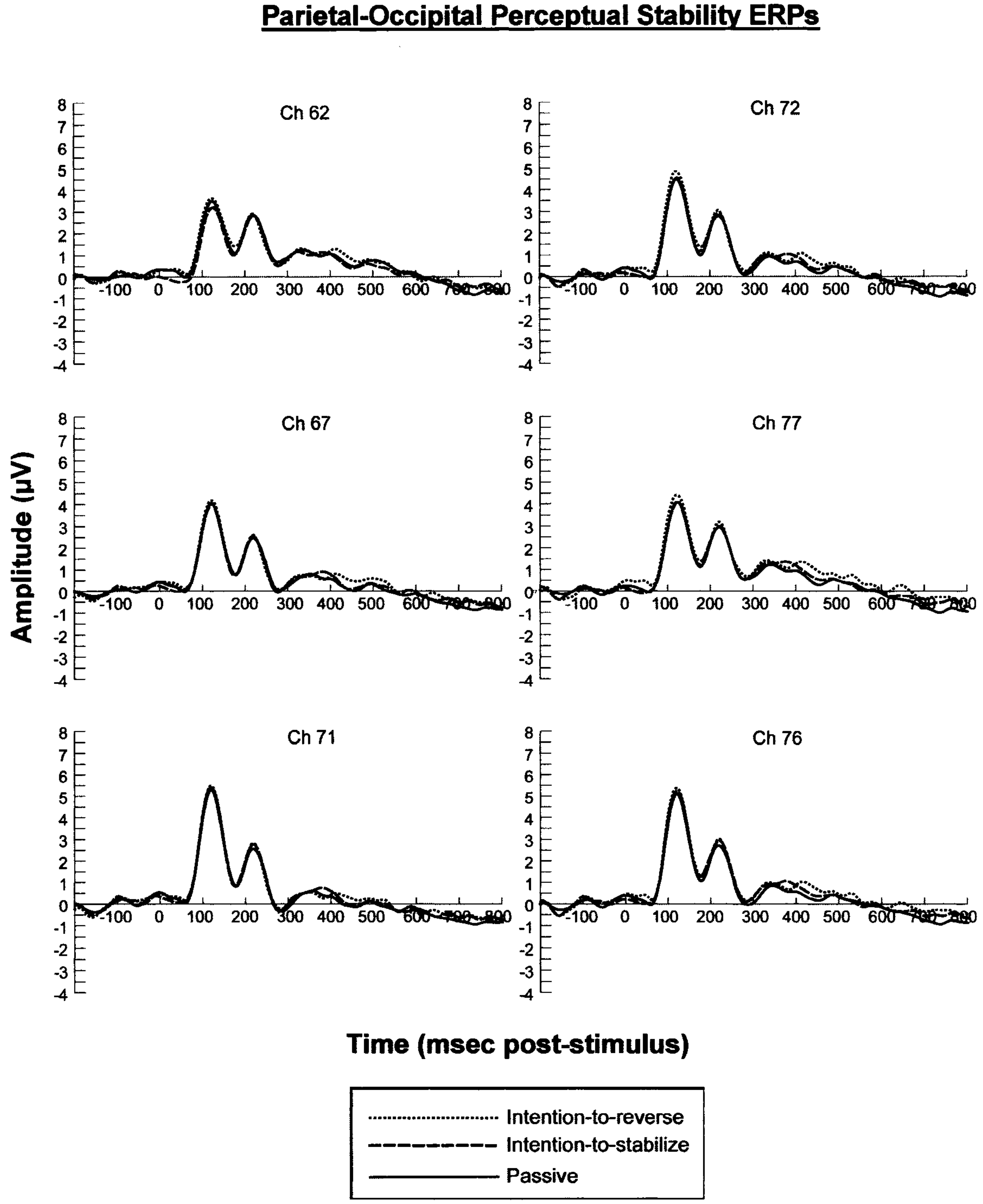


Figure 3.14. Grand average ERPs (N=27) from 3 occipital electrode sites (marked on the sensor layout in figure 2.4) for perceptual stability in the three intention conditions. Intention-to-reverse ERPs are shown as dotted lines, intention-to-stabilize as dashed lines, and the passive condition as solid lines. All graphs show amplitude (µV) plotted as a function of time (msec post-stimulus). No intention-based ERP differences were found when perceptual stability occurred.



Parietal-Occipital Perceptual Stability ERPs

Ch 62

Ch 72

Ch 67

Ch 77

Ch 71

Ch 76

Figure 3.15. Grand average ERPs (N=27) from 6 occipital-parietal electrode sites (marked on the sensor layout in figure 2.3) for perceptual stability in the three intention conditions. Intention-to-reverse ERPs are shown as dotted lines, intention-to-stabilize as dashed lines, and the passive condition as solid lines. All graphs show amplitude (µV) plotted as a function of time (msec post-stimulus). No intention-based differences were found when perceptual stability occurred.

An intention x perception interaction was found for the P2 peak, $F(2,26) = 3.326$, $p = .048$. T-tests revealed that when perceptual reversals occurred, the P2 amplitude of the intention-to-reverse ERPs was significantly reduced compared to the passive condition ERPs at both occipital, $t(26) = 2.26$, $p < .05$, and parietal-occipital, $t(26) = 2.55$, $p < .05$, locations. The intention-to-reverse P2 amplitudes were also significantly reduced compared to the intention-to-stabilize amplitudes at parietal-occipital sites, $t(26) = 2.54$, $p < .05$, and were close to significantly reduced at occipital sites, $t(26) = 1.74$, $p < .10$.

An intention x perception interaction was also found for the N2 peak, $F(2,26) = 5.146$, $p = .009$. T-tests determined that when perceptual reversals occurred, N2 amplitudes at both occipital and occipital-parietal sites were reduced for the intention-to-reverse condition, $t(26) = 4.01$, $p < .001$; $t(26) = 4.23$, $p < .001$, *and* the intention-to-stabilize condition, $t(26) = 3.39$, $p < .01$; $t(26) = 3.15$, $p < .01$, compared to the passive condition. Interestingly, significant N2 main effects were found for perception, $F(1,26) = 5.863$, $p = .023$, and intention, $F(2,26) = 4.802$, $p = .012$. The differences found in the t-tests reveal the specific factors driving the main effect of intention, but one can nevertheless make the claim that regardless of perception, intention affects the amplitude of the N2 component.

A significant interaction between intention and perception was found for the RN, $F(2,26) = 3.875$, $p = .027$. T-tests showed that the mean amplitude of the RN was significantly enhanced (more negative) for the intention-to-reverse ERPs compared to the passive condition ERPs at both occipital and occipital-parietal locations, t(26) = 2.98, p < ..001; t(26) = 3.66, p < .001 respectively. Because the measurement of the RN (170-370msec) spans across the latencies of the N1 (178msec), P2 (218msec), and N2 (280msec) peaks, significant amplitude enhancements of the RN and more negative amplitudes of any of these three peaks may not necessarily be independent. This issue is addressed in the discussion section.

Analysis of the LPC revealed main effects of intention, F(2,26) = 3.726, p = .031, perception, F(1,26) = 6.245, p = .019, and location, F(1,26) = 12.366, p = .002. An interaction between intention and perception was also found, F(2,26) = 7.832, p = .001. T-tests revealed, similar to the other components, no intention-based amplitude differences when perceptual stability occurred. When reversals occurred however, the LPC amplitude was significantly larger in the passive condition compared to the intention-to-reverse condition at occipital, t(26) = 3.77, p < .001, and parietal-occipital, t(26) = 4.61, p < .001, locations. For the parietal-occipital cluster, LPC amplitude was also significantly larger in the passive condition compared to the intention-to-stabilize condition, t(26) = 2.69, p < .05.

A summary of the intention-based ERP differences is shown in figures 3.16 and 3.17. Difference waves (reversal-stability) were computed for each of the three intention conditions, and are plotted for all occipital (figure 3.16) and occipital-parietal (figure 3.17) sites used in this analysis. As in previous figures, the passive condition ERPs are plotted as solid lines, the intention-to-reverse as dotted lines, and the intention-to-stabilize as dashed lines. The enhancement of the RN for the intention-to-reverse condition can be seen in nearly all of the sites

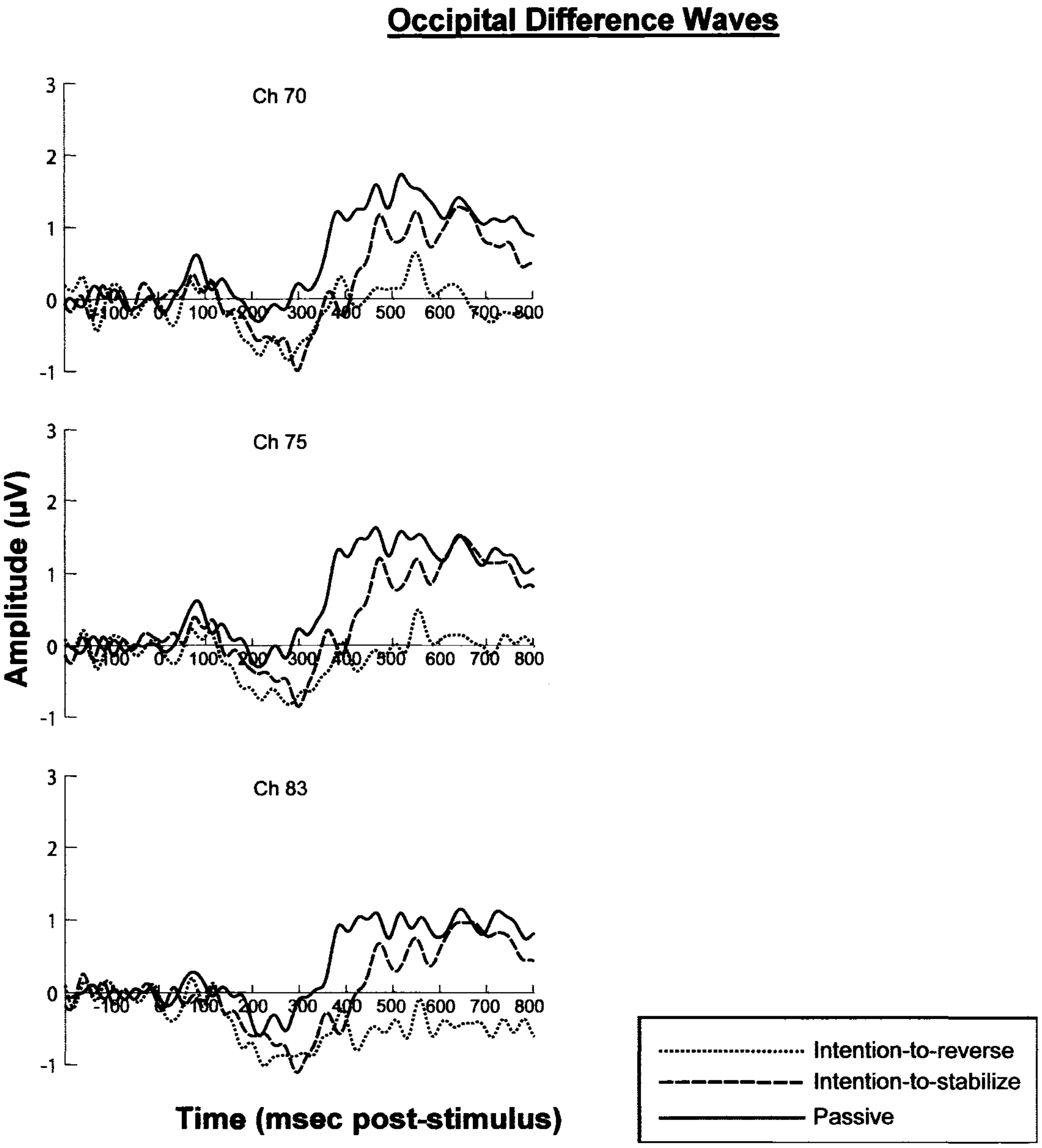


Figure 3.16. Grand average difference waves (reversal minus stability) from three occipital electrode sites (marked on the sensor layout in Fig 2.4) in the three intention conditions. Intention-to-reverse difference waves are shown as dotted lines, intention-to-stabilize as dashed lines, and the passive condition as solid lines. All graphs show amplitude difference (µV) plotted as a function of time (msec post-stimulus). Intention-based differences begin at approx. 170msec. The reversal negativity (170-370msec) is largest for the intention-to-reverse condition, and smallest for the passive condition. Interestingly, the LPC (300-500msec) is largest for the passive condition and smallest for the intention-to-reverse condition.

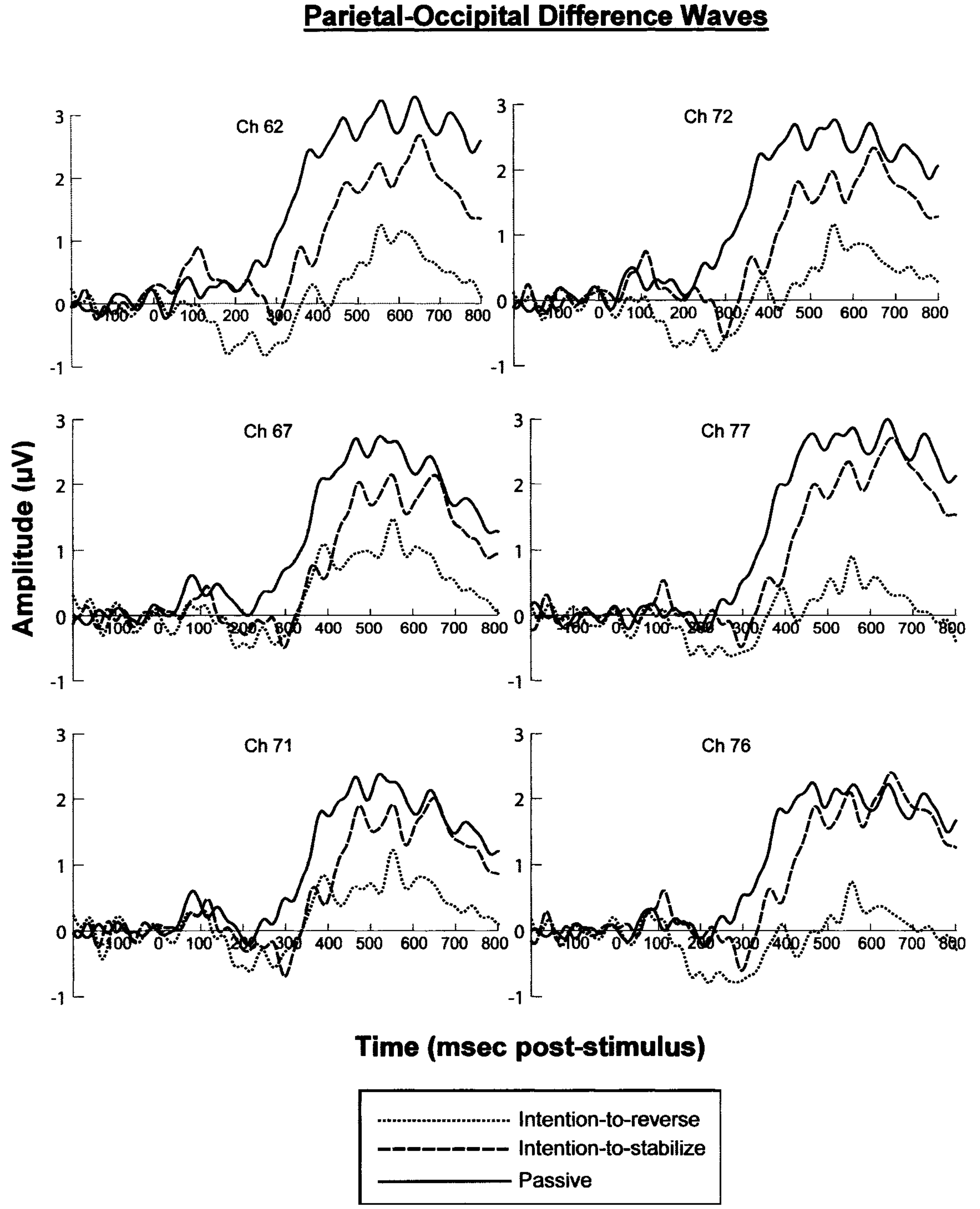


Figure 3.17. Grand average difference waves (reversal minus stability) from six parietal-occipital electrode sites (marked on the sensor layout in Fig 2.4) in the three intention conditions. Intention-to-reverse difference waves are shown as dotted lines, intention-to-stabilize as dashed lines, and the passive condition as solid lines. All graphs show amplitude difference (μV) plotted as a function of time (msec post-stimulus). Intention-based differences begin at approx. 110msec. The reversal negativity (170-370msec) is largest for the intention-to-reverse condition, and smallest for the passive condition. The LPC (300-500msec) is largest for the passive condition and smallest for the intention-to-reverse condition.

shown in figures 3.16 and 3.17. It is also clear from these figures that the LPC is largest in the passive condition and smallest in the intention-to-reverse condition.

Appendix A (tables A.1-A.15) includes the ERP amplitude values taken from each individual observer's average ERP waveforms for all conditions. The title of each table indicates the ERP component measured, and the scalp locations from which the amplitude values were obtained are indicated above each data column (tables A.1 and A.2) or in the title (tables A.3-A.15). The condition columns are labeled: PassRev or PassStab (passive condition [Pass]; perceptual reversal [Rev] or stability [Stab]), TRevRev or TRevStab ('try-to-reverse' condition [TRev]; perceptual reversal [Rev] or stability [Stab]), and TStabRev or TStabStab ('try-to-stabilize' condition [TStab]; perceptual reversal [Rev] or stability [Stab]).

Appendix B (tables B.1-B.9) show all statistical results from the ANOVAs, including effect size and power estimates, as well as other main effects and interactions not discussed above. Tables B.1-B.3 include results from experimental question one while tables B.4-B.9 include experimental question two results. Tables B.10-B.24 in appendix B show the results from the t-tests performed to assess question one (tables B.10-B.12) and two (tables B.13-B.24).

Chapter 4: DISCUSSION

The first goal of this investigation was to identify the reversal positivity (RP), the reversal negativity (RN), and the late positive component (LPC) of perceptual reversals, and to determine from where on the scalp these potentials can be recorded. More conservative analysis techniques were used in this study compared to previous studies (Kornmeier & Bach, 2004; 2005), i.e. mean amplitude comparisons between conditions as opposed to difference wave peak amplitudes compared to zero. The second purpose of this investigation was to assess the influence of top-down *intentional* control on reversal-related ERPs. Amplitudes of the P1, N1, N2, P2, RN, and LPC components were compared across three intentional conditions, i.e. intention-to-reverse, intention-to-stabilize, and a passive control condition.

In regards to the first set of questions, two of the three previously reported reversal-related components were successfully identified: the RN, and the LPC. The RP was not identified using more conservative ERP analysis techniques than Kornmeier and Bach (2004, 2005). Also, the RN was only identifiable in right posterior regions, and not central or left posterior regions.

To answer the second, and more novel set of experimental questions, comparisons between the three intention conditions were made separately for perceptual reversals and perceptual stability. When perceptual stability occurred, no ERP differences based on the observers' intentions were evident. However, when reversals occurred, a number of interesting differences were identified. First, the amplitude of the RN was enhanced for trials in which observers were instructed to intentionally induce reversals compared to trials in which observers remained passive. Related to this finding (the temporal overlap is discussed below) P2 and N2 amplitudes were more negative for intentional reversals compared to the passive reversals. N2 amplitudes were also enhanced for unintentional reversal trials (i.e. trials in which observers tried to hold their perception stable, but the figure reversed) compared to the passive condition. N1 amplitudes were not significantly different across intention conditions, but a trend toward an intentional-reversal enhancement was evident. No P1 effects based on intention were found, although a main effect of perception (a P1 enhancement for reversals) occurred when all three intentions were averaged together. The LPC was largest in the passive condition, and smallest in the intentional reversal condition.

General Reversal Components

The reversal positivity (RP) component most likely reflects a change in spatial attention as numerous studies have reported very similar amplitude enhancements in relation to spatial attention manipulations (Hillyard & Anllo-Vento, 1998; Hillyard, Vogel & Luck, 1998; Luck et al, 1994; Mangun, 1995; Clark & Hillyard, 1996). Although Kornmeier and Bach identified the RP in their second study (2005), no such effect was found in the passive condition of the current study. As discussed earlier, the timing and scalp topography of the RP is equivalent to well-known visual P1 component. Differences in P1 amplitude are often difficult to detect, as the differences are usually quite small (Luck, 2005). In order to identify P1 amplitude differences, many trials are required in order to attain an adequate signal/noise ratio. In the current study, an average of 90 trials per condition were used to compute each individual's ERP (although a few participants came close to the 30 trial minimum in some conditions), whereas, Clark and Hillyard (1996) for example, used 1300 trials per condition to compute each individual's ERP waveform. For comparison purposes, Kornmeier and Bach (2004) averaged 120 trials per condition. If the reversal positivity was not identified because of an inadequate number of trials, it would make sense that averaging together all reversal trials from the three intentional conditions might improve the signal/noise ratio and lead to a positive finding. A main effect of perception for the P1 was in fact found when all three intention conditions were combined. So, although the reversal positivity was not statistically significant in the passive condition, it may still exist when measured under higher signal/noise ratios.

The reversal negativity (RN) was identified in the current study, although only in right posterior sites. This component has now been identified in four separate experiments by two different research groups (Kornmeier & Bach, 2004, 2005; Pitts, Nerger, & Davis, 2007; and the current study). The right-lateralized location of this component is consistent with the Pitts, Nerger, and Davis (2007) study, in which the RN was noticeably larger in right posterior regions for Rubin's face/vase and Schroder's staircase stimuli. As described above, the timing, scalp topography, and polarity of the RN closely resemble the selection negativity (SN) reported in previous visual attention studies (Anllo-Vento & Hillyard, 1996; Smid, Jakob & Heinze, 1997; Valdes-Sosa et al, 1998; Martin-Loeches, Hinojosa, & Rubia, 1999; Michie et al, 1999; Smid, Jakob & Heinze, 1999). Arguably, the RN is analogous to the SN, and reflects selective attention to specific features of the bistable stimulus, which biases the visual system to interpret the input in one way or the other. As a simple demonstration of how spatial and selective attention may act to influence bistable perception, one can view the Necker lattice (figure 1.3) and make alternating eye movements from the bottom-right corner of the lattice to the top-left corner. Most often, these eye movements result in perceptual reversals in which the gaze-directed corner seems to pop-out into the foreground. Eye movements essentially determine which area of the image is processed by the fovea, and can therefore influence the focus of spatial and selective attention in a bottom-up fashion. Although eye movements were eliminated in the current study, one can easily imagine covert spatial and selective attention working in a similar manner.

The occurrence of these two early ERP differences suggests a critical role for spatial and selective attention in bistable perceptual reversals. Early processing of the bistable stimulus may be equivalent for reversal and stability trials in V1, but enhanced or suppressed in extrastriate cortex depending on spatial attention factors (as indicated by P1 and N1 differences). Following this initial change in extrastriate activity, cortical regions in the ventral pathway (the occipitotemporal gyrus and inferior temporal gyri) are then affected by the allocation of spatial attention and show differences in activation for reversal/stability trials. This later difference may be indexed by the reversal negativity.

In order to disambiguate a bistable figure, it can be assumed that spatial and selective attention are required regardless of whether the figure appeared the same or different on the previous trial. The reversal positivity and reversal negativity identified in Kornmeier and Bach (2004, 2005) and Pitts, Nerger, and Davis (2007) must therefore reflect *changes* in spatial and selective attention, i.e. attention to certain locations and features of the bistable figure in one trial followed by attention to different locations and features in the subsequent trial. This interpretation supports the notion that early spatial attention alteration (indexed by the reversal positivity or P1 and N1 amplitudes) modulates later feature selection (indexed by the reversal negativity or SN), which determines how the bistable image is perceived. It is likely that the recognition of reversals is dependent on these early attentional changes and occurs during or after the reversal negativity (or SN).

The late positive component (LPC) was unequivocally identified, and was the largest of the three reversal-related components. Anllo-Vento and Hillyard (1996) argued that the LPC is related to target selection. This interpretation is consistent with the current study, since perceptual reversals were the target to which observers were instructed to respond. Interestingly though, Kornmeier and Bach (2004) found the LPC for reversals even when the task was switched and observers had to respond to stability. Other explanations for this P300-like component involve a categorical probability factor, in which P300 amplitude is enhanced for lower probability stimuli (Duncan-Johnson & Donchin, 1977). This would be consistent within the context of the current study, since reversal trials always occur less frequently than stability trials, and are therefore the less probable perception. Various other interpretations of the LPC or P300 components have been proposed, such as its amplitude enhancement for unexpected stimuli or novel stimuli (Courchesne, Hillyard, & Galambos, 1975) or unpredictable, infrequent, task-relevant shifts (Squires, Squires, & Hillyard, 1975). The LPC differences based on intention (see figures 3.12, 3.13, 3.16, and 3.17) may help shed some light on the functional significance of this component. The LPC was largest in the passive condition, and smallest in the intention-to-reverse condition. If the amplitude of the LPC is dependent on expectancy (i.e. larger for unexpected events), or probability (i.e. larger for less frequent stimuli), a larger amplitude may be predicted in the passive condition compared to the intention-to-reverse condition. However, reversals that occur in the intention-to-stabilize condition (i.e. unintentional reversals) should predictably lead to even larger LPC amplitudes than the passive condition if the LPC is based on expectancy or probability. This was not the case in the current study, although a peak-to-peak measurement (from N2 to the first peak of the LPC) may have led to different conclusions, i.e. equal amplitudes for the passive and intention-to-stabilize conditions, and significantly lower amplitudes for the intention-to-reverse condition (see figures 3.12 and 3.13). It is also possible that the target-based explanation of the LPC can be rectified if reversals are always the perceptual target of interest, regardless of the response task. Whatever the eventual explanation for the LPC effects turns out to be, we can be fairly certain that this component is generated at a processing stage beyond visual awareness because in order to have target-based, probabilistic, expectancy, or predictability sensitivity, the stimulus must have already been disambiguated.

As in the Kornmeier and Bach studies (2004, 2005), the nature of the participant's task inevitably introduced a motor component to reversal trials and not to stability trials. This response-based difference should not be of concern for the current investigation because motor-related potentials occur later and are recorded from frontal and central scalp locations while the components of interest in this study occur early and were recorded at posterior electrode sites. Furthermore, Kornmeier and Bach (2004) tested for this potential confound by changing the button-press task in half of the trials (respond to stability vs.

respond to reversals) and found no differences in the response vs. non-response ERP waveforms.

Intention-based ERP effects

The behavioral results clearly indicate that much variability exists across individuals' abilities to control reversal rates through intention. Of the 27 observers, only 15 were able to successfully increase and decrease reversals when instructed to do so. Of the remaining 12 observers, 5 were able to decrease reversal rates in the intention-to-stabilize condition, but were unable to increase reversal rates in the intention-to-reverse condition; 1 was able to increase reversal rates in the intention-to-reverse condition, but was unable to decrease reversal rates in the intention-to-stabilize condition, and 6 were completely unsuccessful in both intention conditions (figure 3.2).

It is also 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 (Jernigan, Trauner, Hesselink, & Tallal, 1991; Giedd, Blumenthal, Jeffries, Castellanos, Liu, Zijdenbos, Paus, Evans, & Rapoport, 1999; Sowell, Thompson, Holmes, Jernigan, & Toga, 1999; Sowell, Thompson, Tessner, & Toga, 2001; Fuster, 2002; Gogtay, Giedd, Lusk, Hayashi, Greenstein, Vaituzis, Nugent, Herman, Clasen, Toga, Rapoport, & Thompson, 2004). 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 about half of the participants in this study had not yet developed the ability to control their visual spatial and/or selective attention in order to change the reversal rates through intentional control. Further research is necessary to evaluate this possibility. The current results do support the notion that intentional control of reversals vs. stability are mediated by separate mechanisms, as no intention-based ERP differences were found when perceptual stability occurred, while intention-based differences were identified when perceptual reversals occurred. This finding is consistent with the dissociation of intentions reported by Windmann et al (2006).

Although not statistically significant in this study, a trend toward N1 enhancement for intention-to-reverse conditions compared to both of the other conditions was suggested. This N1 enhancement most likely represents shifts in spatial attention (Hillyard & Anllo-Vento, 1998; Hillyard, Vogel & Luck, 1998; Luck et al, 1994; Mangun, 1995; Clark & Hillyard, 1996). Spatial attention effects on N1 amplitude have also been shown to occur at electrode sites contralateral to the attended location (Anllo-Vento & Hillyard, 1996). Unfortunately, the task employed in the current study does not permit an analysis of ERPs separately for each of the two perceptual interpretations of the bistable stimulus. Observers simply responded when a reversal occurred regardless of whether the lattice switched from a bottom-right to top-left orientation or from a top-left to bottom-right orientation. Hence, the two reversal directions as well as the two stability directions were averaged together. Averaging reversals in both directions may obscure some of the effects of spatial attention alteration. Studies currently underway in our laboratory are attempting to separate the two types of directional reversals by modifying the behavioral task of the observers.

Regardless of the substantial variability in task performance in the intention conditions, a significant enhancement of the reversal negativity was found for the intention-to-reverse condition compared to the passive condition. There were also significant differences in the P2 and N2 amplitudes between the same two conditions. Recall however that the latencies of the P2 (218msec) and N2 (280msec) peaks lie within the same time window as the reversal negativity (170-370msec). It is possible that activation of a single, temporally broad component resulted in amplitude differences at both of these peaks. If the reversal negativity is in fact equivalent to the selection negativity, the single component explanation is most parsimonious, although distinct overlapping components could lead to similar results (Luck, 2005). The selective attention explanation would imply that when observers tried to reverse their perception through intentional control, a change in selective attention to particular features of the stimulus occurred. This change in selective attention was possibly preceded by a change in spatial attention, although the N1 enhancement in this study was not statistically significant. If this interpretation is accurate, voluntary control of perceptual reversals is mediated by visual spatial and selective attention networks that can be cognitively directed to switch more frequently. In this context, failure to increase reversals would essentially mean a failure to activate a shift in spatial and/or selective attention.

Upon carefully inspection of the ERP waveforms, one additional effect must be addressed. Figures 3.12 and 3.13 show an N1 enhancement for the intention-to-reverse condition and an N2 enhancement for both intention-to-reverse and intention-to-stabilize conditions compared to the passive condition. If this distinction is supported with subsequent research, the interpretation of the N2 effects must be reevaluated. The N2 differences may not necessarily represent changes invoked by the temporally broad reversal negativity. In this alternative account, N1 enhancements for the intention-to-stabilize condition would represent voluntary control over covert spatial attention, while the N2 enhancements might represent intentional effort in general. Further research is required to dissociate the effects on these ERP components.

Attention-based theory of bistable perception

Results from the current study, along with accumulating evidence from various other psychophysiological studies (see Leopold & Logothetis, 1999 for a review) implicate a critical role of visual spatial and selective attention in the disambiguation and perceptual alternation of bistable stimuli. When observers are instructed to intentionally speed-up the reversal rate, it is possible that spatial attention is shifted at stimulus onset or even before the stimulus appears in order to achieve perceptual reversals. This shift in spatial attention then influences which features are selectively attended to, and eventually leads to a change in visual awareness of a physically unchanging stimulus. These same shifts in spatial and selective attention may also be critical for the disambiguation of everyday objects in our environment.

The bottom-up / top-down distinction is of little utility theoretically if a top-down mechanism such as attention influences visual perception at a very early stage (<120msec). Exactly how the fronto-parietal attention network changes visual processing at various stages remains unclear, i.e. whether more cells or a different set of cells are recruited or the activity of the same group of cells is enhanced or temporally synchronized with groups of cells in other areas. In order to directly evaluate fatigue-based vs. attention-shifting-based accounts of bistable perception, an experiment must be designed in which each potential process is measured independently. Even if ERPs are measured in a priming vs. adaptation experiment similar to the one described above (Long, Toppino, & Mondin, 1992), it would be difficult to distinguish between involuntary shifts in attention due to a forced directing of attention during adaptation and shifts in perception due to neural fatigue during adaptation. It may, however, be possible to compare ERP traces in an involuntary attention-shifting experiment and a fatigue-inducing adaptation experiment to ERPs in an involuntary perceptual reversal experiment (e.g. passive reversal ERPs or unintentional reversal ERPs). If involuntary attention-shifting ERPs are more closely correlated with passive or unintentional reversal ERPs, a case could be made for the automatic environment exploration mechanism. If the ERPs associated with fatigue-induced shifts are more closely correlated with passive or unintentional reversal ERPs, the neural fatigue-recovery cycle account for shifts in bistable perception would be supported. Further research is required in order fully support the attention-based account of perceptual reversals of bistable figures.

Models of bistable perception

In a thorough review of bottom-up vs. top-down theories of bistable perception, Long and Toppino (2004) proposed a tentative hybrid model which incorporates both feedforward (bottom-up) and feedback (top-down) visual processing mechanisms. This hybrid model is reproduced in figure 4.1. In this model, elementary features are extracted in early stages of visual processing, and interactions between feedforward and feedback pathways occur in two intermediate levels. The bistable stimulus is disambiguated in the second (representational) intermediate level.

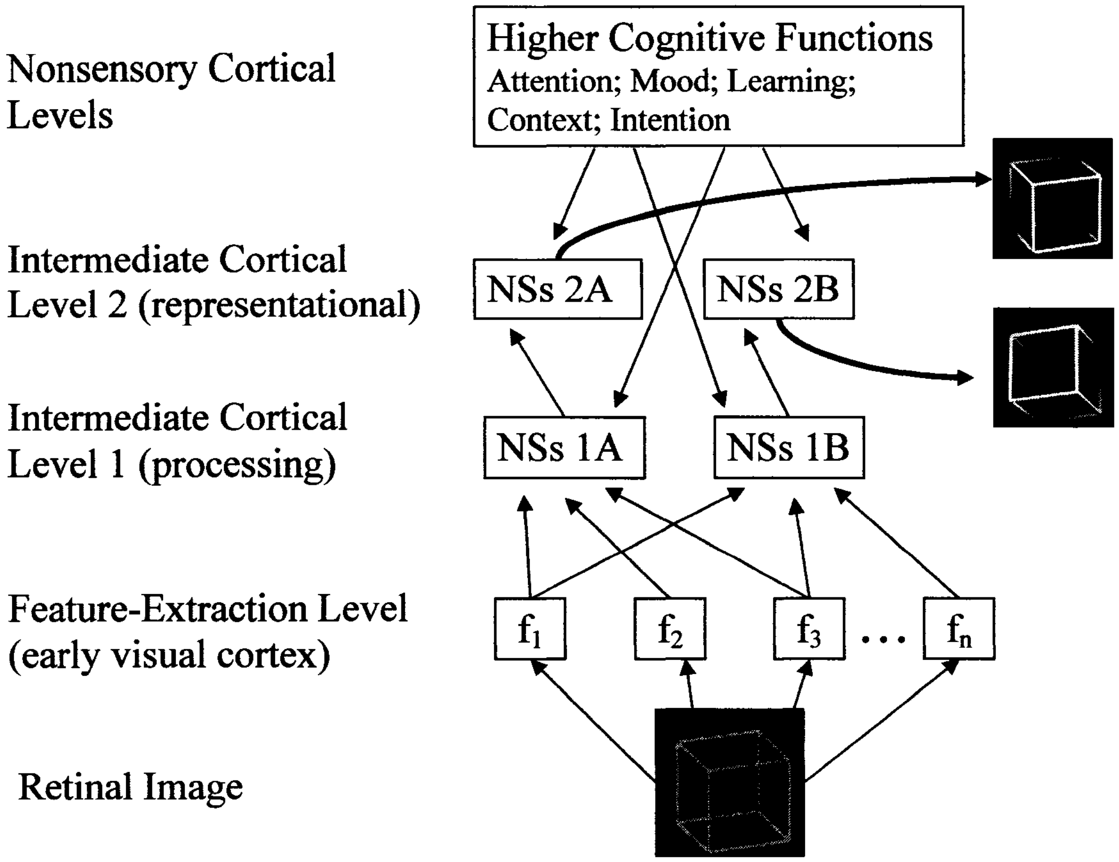


Figure 4.1. Long and Toppino's (2004) tentative hybrid model of bistable perception. In this model, top-down influences such as intention influence perception at intermediate stages of visual processing. NS stands for neural structures, and separate cortical structures (A & B) underlie each of the two possible percepts. Although this model is strictly conceptual, it provides a starting point for further development and refinement toward a neurophysiologically-based model.

Based on the current investigation as well as recent electrophysiological and brain imaging research, modifications to Long and Toppino's hybrid model are proposed in figure 4.2. More precise neuroanatomical locations in which the various processes involved are likely to occur have been added to the model and are listed parenthetically under each processing stage in the left column. The approximate time course (based on ERP studies) of each stage has been estimated and is included parenthetically under each process in the central column. The processing stages of spatial and selective attention (based on ERP findings) have also been added to this updated model. Additional cognitive levels, including memory, goal-direction, and decision-making have been included as well, in order to complete the circuit involved in the current experimental task.

The neural processing loop outlined in figure 4.2 begins with the presentation of an ambiguous visual stimulus to the retina (time = 0), although note that attentional processes in cognitive level 3 are active before and during this initial stimulus presentation. The first visual processing stage (feature extraction level; primary visual cortex) is primarily concerned with the processing of elementary stimulus features, such as edges, orientation of lines, corners, intersections, etc. Intermediate level 1 (extrastriate cortex) is still involved in early visual processing, but is the first potential area affected by feedback from higher-level systems. The dorsal (intermediate level 2) and ventral (intermediate level 3) visual processing pathways are then activated, and attended locations and features are determined respectively. Information gained from intermediate level

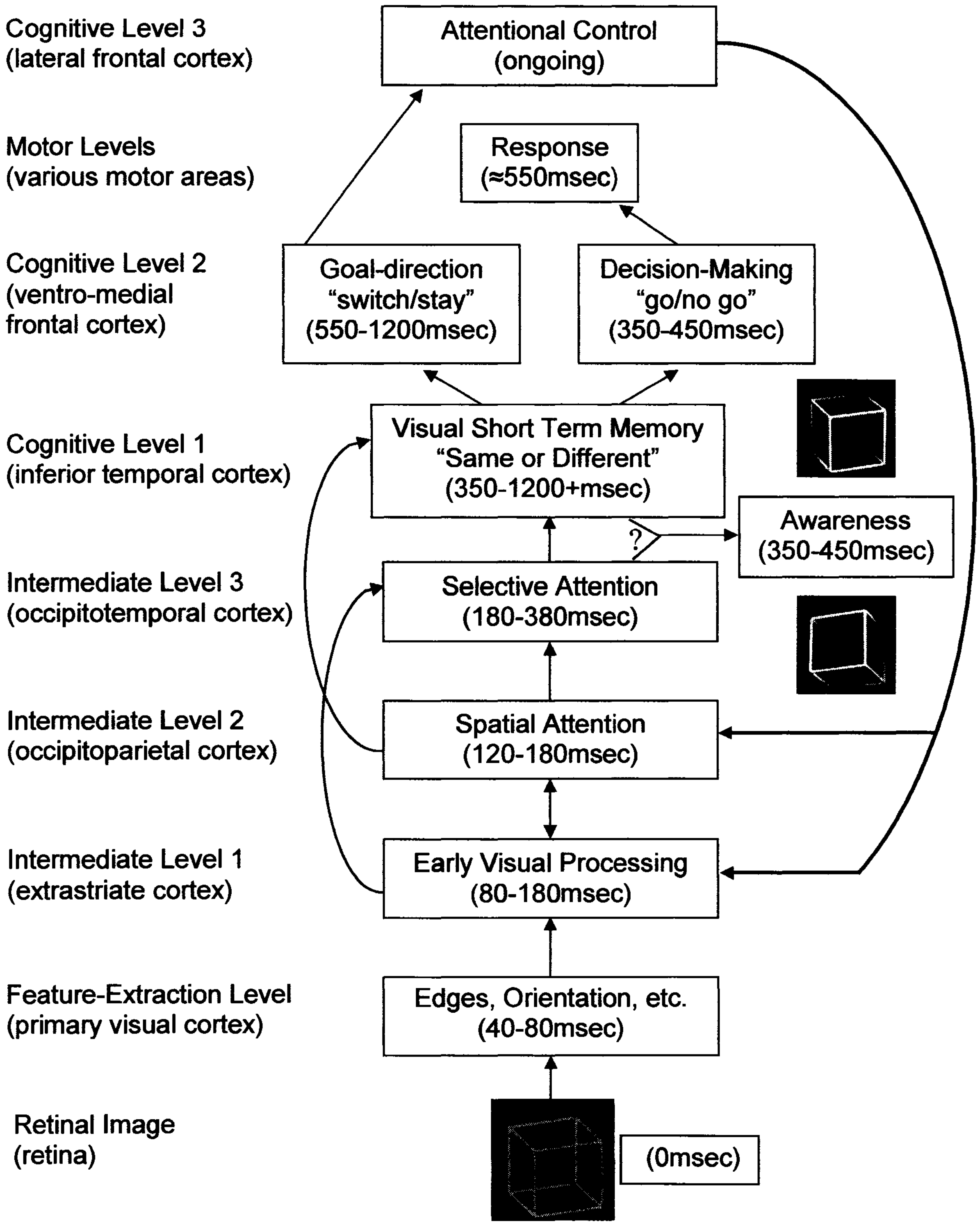


Figure 4.2. Proposed model of top-down control over bistable perception. Levels of processing are listed on the left, along with the probable neuroanatomical location for each process. The various visual and psychological functions involved at each level are shown in the central column, along with estimated time courses.

3 is then compared with existing pattern representations in order to recognize the object. It is unclear whether Long and Toppino's "representational" level is analogous to selective attention (intermediate level 3) or visual short term memory (cognitive level 1) functions. The question of where and when perceptual representation occurs is indeed one of the long-standing, unanswered questions in visual perception research. In the context of the current study, a comparison between the current perception and the previous perception must be made, i.e. in visual short term memory (cognitive level 1), in order to make a response decision (cognitive level 2). At the same time, visual short term memory is utilized to update the current goal-set in order to direct attention to the same or different locations and/or features on the next trial. Finally, note that visual awareness may occur either at intermediate level 3 or cognitive level 1, but is not critical for the function of this processing loop.

The model outlined in figure 4.2 is specific for the task employed in the current experiment, but with a few minor additions, may be applicable to natural viewing conditions. The attentional control centers are most likely influenced by subcortical (possibly limbic system structures), and directed to periodically shift attention in order to 'refresh' perception. This environment exploration mechanism normally works through eye movements, which modify the spatial organization of the retinal image in order to change spatial and subsequently selective attention. In fixation experiments, the exploratory mechanism remains active, but redirects covert attention instead of eye movements. This mechanism also continues to influence attention even when a goal-directed input is present, i.e. resulting in occasional unintentional reversal or unintentional stability. The output of the attention mechanism is therefore dynamic and influenced both by task demands (goal-direction; executive control), as well as more automatic exploratory drives (scan the visual scene in order to disambiguate objects).

The precise neuroanatomical module that is directly influenced by the attention mechanism remains unclear, but is likely to be extrastriate cortex or occipitoparietal cortex (i.e. the split arrow in the model). The timing of each stage in the process has been derived from the current as well as previous ERP studies, and is intended as a general temporal profile. Further research is required to reach more specific conclusions regarding the exact time course of these processes.

It is unclear where and when 'conscious visual awareness' occurs (and what awareness *is*), and which mechanisms have inputs leading to or directly associated with awareness. It is possible that a visual processing stage exists somewhere between the selective attention level (intermediate level 3) and the visual memory level (cognitive level 1), and receives inputs from both. Although, it is equally likely that 'conscious visual awareness' is an unnecessary and misleading concept, and being 'visually aware' is simply what happens when this entire feedforward/feedback circuit is activated. A distributed, multi-stage process involving visual memory, object representation, and an underlying sense of 'self' may eventually replace the elusive concept of 'conscious visual awareness' altogether.

Conclusion

Electrophysiological recordings were made to investigate whether differences in recently identified ERP components (reversal positivity, reversal negativity, late positive component) would be revealed during naturally occurring perceptual reversals of a bistable figure. Additionally, to investigate the role of top-down control over perceptual reversals, observers were instructed to maintain three distinct intentional approaches in separate conditions, and differences in ERP amplitudes across these conditions were evaluated.

The reversal negativity and late positive component were both identified in conditions in which perceptual reversals occurred naturally. The reversal negativity was maximal over the right posterior scalp. When observers attempted to induce perceptual reversals through intention, the reversal negativity was enhanced, and P2 and N2 amplitude differences were found relative to the passive condition. N1 enhancements for the intention-to-reverse condition were also detected, but were not statistically significant. N2 amplitude was enhanced for unintentional reversals compared to passive reversals. When all intention conditions were averaged together, a P1 enhancement for reversals was implicated. The late positive component was largest for passive reversals and smallest for intentional reversals. Taken together, these results suggest a role of spatial attention (indexed by the reversal positivity, P1 and/or N1) and selective attention (indexed by the reversal negativity or selection negativity) in bistable perception. Under natural circumstances, these attention mechanisms are thought to consistently shift on their own, but this research suggests that shifts can be controlled by the intention of the observer as well. Current processing models of bistable perception can be revised based on converging evidence from the current as well as other electrophysiological studies.

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APPENDIX A

Table A.1. RP mean amplitudes (98-138msec)

Subject	PassRev Central	PassStab Central	PassRev Left	PassStab Left	PassRev Right	PassStab Right
3	6.952	6.317	4.750	3.856	5.859	5.759
4	6.813	6.187	4.157	2.659	6.138	6.216
6	6.914	7.323	4.256	4.116	4.377	5.132
13	5.275	4.894	5.361	2.550	4.841	5.352
14	14.452	11.408	7.930	5.834	9.764	6.763
15	4.352	3.480	1.089	0.419	5.165	4.356
20	2.809	1.317	1.730	1.300	1.966	0.797
22	3.893	3.556	2.466	1.434	5.612	4.981
24	3.028	2.319	3.416	2.322	4.301	2.819
25	0.384	1.997	-0.478	0.263	-0.836	2.836
26	4.213	3.938	2.746	1.046	3.935	4.744
28	5.191	5.606	1.420	3.613	6.654	4.412
30	8.898	9.041	4.405	5.159	5.962	6.216
32	7.276	6.354	3.524	3.059	9.178	7.510
33	10.549	11.018	8.180	8.595	9.892	10.207
35	3.707	5.670	1.504	4.170	2.768	5.506
37	9.247	10.108	5.322	6.173	9.282	9.626
38	4.871	4.115	4.564	2.470	3.039	3.951
41	2.808	2.741	6.343	5.167	3.808	4.426
42	5.352	4.743	3.948	3.886	4.026	2.697
46	3.457	4.003	2.982	3.396	3.665	4.425
47	2.244	5.971	1.453	3.988	1.775	4.203
49	4.843	4.845	4.493	4.173	4.222	4.473
50	5.253	5.633	2.368	2.690	6.147	6.257
51	7.788	5.510	6.046	5.125	4.516	3.811
52	7.983	8.159	5.212	6.063	7.619	7.054
53	4.673	4.979	4.722	5.010	3.403	3.730

Table A.2. RN mean amplitudes (170-370msec)

Subject	PassRev Central	PassStab Central	PassRev Left	PassStab Left	PassRev Right	PassStab Right
3	0.584	1.620	0.943	0.270	-0.567	1.769
4	2.030	2.395	1.511	0.633	1.947	3.211
6	-0.511	1.136	-0.046	0.230	-2.662	-0.292
13	1.273	-0.337	0.885	-2.589	0.681	1.793
14	4.931	2.154	3.864	1.468	5.055	1.802
15	-3.406	-3.947	-3.671	-5.137	-3.313	-3.257
20	1.628	0.456	0.362	-0.012	1.071	0.604
22	-2.415	-1.627	-1.956	-1.924	-2.277	-1.254
24	-1.052	-1.308	-0.312	-1.809	-1.041	-0.930
25	-1.807	0.394	-2.291	0.063	-1.728	1.503
26	-1.566	-0.292	-2.646	-1.808	-1.517	0.708
28	1.187	1.197	-1.143	1.181	2.379	0.264
30	2.745	2.807	1.425	2.322	1.002	1.200
32	4.826	4.676	1.100	1.693	5.589	4.518
33	-0.109	0.144	-0.947	-0.939	-1.695	-0.870
35	1.911	1.265	-1.806	-1.012	-0.698	1.338
37	-0.923	0.432	-1.402	-0.343	-1.024	0.340
38	-1.115	-0.639	0.394	-0.085	-2.036	-1.395
41	0.601	-0.984	-0.199	-1.381	0.814	-0.136
42	-0.610	1.332	-0.362	1.110	-1.377	-0.699
46	1.919	1.947	1.453	1.442	0.820	1.186
47	4.220	3.842	0.875	0.623	4.475	4.004
49	0.283	0.018	0.061	-0.206	0.072	0.333
50	0.315	1.124	-0.128	0.578	0.566	1.315
51	-2.461	-3.984	-2.952	-3.592	-1.046	-1.831
52	1.145	1.523	-0.733	-0.560	0.208	1.726
53	-0.060	1.760	0.443	0.604	-1.624	1.121

Table A.3. LPC mean amplitudes (300-500msec) Central Parietal

Subject	PassRev	PassStab
3	2.544	1.141
4	2.358	0.055
6	2.805	0.542
13	3.412	-2.259
14	4.108	0.587
15	3.450	3.116
20	3.316	0.501
22	0.244	1.624
24	2.774	-0.356
25	-1.103	-0.317
26	2.597	1.405
28	2.402	-0.765
30	2.404	0.089
32	6.962	3.460
33	1.982	0.978
35	5.123	2.006
37	2.638	2.057
38	1.128	1.106
41	5.825	1.605
42	2.143	1.260
46	3.535	1.913
47	4.159	0.904
49	3.875	-0.109
50	0.983	-0.093
51	1.150	-3.024
52	1.519	0.462
53	1.026	0.401

Table A.4. P1 peak amplitudes Occipital

Subject	PassRev	PassStab	TRevRev	TRevStab	TStabRev	TStabStab
3	8.255	7.635	8.673	10.691	9.985	10.369
4	7.996	7.335	7.943	7.777	9.128	8.261
6	8.200	8.414	10.066	9.467	10.222	8.348
13	5.900	5.956	5.444	2.964	5.244	5.236
14	18.506	14.974	16.884	15.613	16.872	17.824
15	8.507	5.859	8.825	8.925	8.845	7.864
20	4.006	2.694	2.869	2.039	2.534	2.576
22	4.770	4.266	1.847	3.357	3.245	3.569
24	3.638	3.199	2.308	4.220	4.742	2.835
25	2.343	2.902	5.373	4.514	2.167	4.500
26	5.832	4.111	5.964	5.818	3.209	3.349
28	6.292	7.101	9.125	6.377	7.065	5.532
30	11.915	11.959	9.991	11.923	10.735	10.413
32	8.161	6.946	10.000	7.869	7.342	7.707
33	11.416	11.436	10.757	13.888	12.292	12.460
35	4.802	6.543	4.291	5.994	5.314	5.296
37	10.472	11.342	11.320	10.041	11.442	12.743
38	5.622	4.811	7.371	5.765	6.208	6.001
41	2.571	3.133	2.918	3.386	3.531	3.070
42	6.161	5.190	4.417	3.950	4.313	5.104
46	6.115	6.492	6.850	7.035	6.531	5.732
47	3.472	6.614	7.633	5.679	5.020	4.207
49	6.343	6.059	5.715	4.717	7.297	6.616
50	7.322	7.111	6.581	7.114	8.808	7.627
51	9.492	7.310	8.591	7.110	8.989	9.307
52	9.734	9.624	9.737	8.787	11.670	10.199
53	5.964	6.828	6.992	6.343	7.255	6.403

Table A.5. P1 peak amplitudes Parietal-Occipital

Subject	PassRev	PassStab	TRevRev	TRevStab	TStabRev	TStabStab
3	6.695	5.970	6.381	9.179	7.488	6.701
4	4.801	4.309	4.543	4.743	6.033	4.778
6	6.920	7.196	8.691	8.102	8.552	6.534
13	4.918	3.791	3.054	0.989	3.373	2.650
14	13.654	10.291	12.318	11.551	11.415	12.358
15	5.229	4.316	5.286	7.376	5.868	4.596
20	4.418	2.676	3.067	1.566	2.676	2.412
22	5.160	4.773	2.552	3.721	4.272	4.245
24	4.031	1.794	2.370	2.308	4.286	2.203
25	2.325	1.404	4.296	2.961	0.656	3.059
26	1.442	5.260	4.977	4.696	1.780	2.484
28	4.732	5.562	7.724	4.654	5.521	4.158
30	7.154	7.013	6.153	7.348	6.992	5.992
32	6.165	5.797	7.536	6.363	6.558	6.694
33	5.035	4.516	4.606	6.020	4.774	5.489
35	4.459	6.336	3.757	6.189	4.301	4.406
37	5.898	7.147	5.247	5.995	6.293	7.759
38	4.343	3.273	5.604	3.412	5.305	3.422
41	1.642	0.469	0.749	1.850	1.557	1.250
42	4.906	3.801	3.801	4.122	3.953	3.681
46	4.887	5.300	5.243	5.471	5.300	4.624
47	2.948	5.131	7.119	5.536	4.095	2.422
49	6.104	5.476	4.757	4.386	6.847	6.035
50	4.843	4.611	4.292	5.048	5.816	5.365
51	7.008	4.690	6.384	4.751	7.553	6.264
52	8.788	8.649	8.647	7.342	10.268	9.041
53	4.402	3.476	5.493	4.254	4.247	2.666

Table A.6. N1 peak amplitudes Occipital

Subject	PassRev	PassStab	TRevRev	TRevStab	TStabRev	TStabStab
3	0.958	2.017	0.468	2.078	4.010	4.206
4	2.995	3.002	2.638	3.197	2.389	3.633
6	-4.637	-1.310	-0.994	-1.169	-1.448	-0.373
13	-0.340	-0.525	-1.915	-1.776	-4.292	-0.917
14	3.038	-0.413	0.991	0.390	-0.656	0.837
15	-5.415	-5.640	-5.196	-4.275	-5.250	-4.638
20	0.535	-0.545	-0.184	0.305	-0.406	-0.470
22	-0.990	-1.047	-3.245	-1.200	-2.349	-1.317
24	-0.602	-1.427	-2.346	-0.541	-0.178	-2.061
25	-2.413	-1.324	0.654	-1.303	-3.081	-0.244
26	-0.829	-0.145	-1.563	0.331	-2.251	-1.604
28	0.630	1.420	2.091	-0.530	0.268	-0.325
30	3.257	4.466	1.963	3.221	3.651	4.780
32	3.360	3.680	4.609	5.299	3.135	3.444
33	3.160	1.523	-0.085	1.498	1.187	2.590
35	1.657	1.280	-1.445	0.771	-0.168	0.243
37	-3.073	-2.030	-3.229	-2.139	-1.663	-0.102
38	-4.539	-5.028	-3.723	-3.864	-3.654	-3.987
41	-4.330	-5.477	-5.786	-5.593	-4.513	-5.598
42	0.383	0.671	-0.801	2.199	-0.900	1.818
46	-0.273	0.671	-1.385	0.569	1.696	2.036
47	3.005	2.725	1.095	-0.957	0.031	1.473
49	1.034	0.887	0.356	0.212	1.854	1.331
50	0.485	2.171	1.470	2.371	2.835	2.704
51	-3.970	-3.898	-5.970	-5.178	-3.701	-2.961
52	2.385	2.587	1.628	0.995	2.047	2.171
53	2.337	3.683	2.439	2.839	2.775	2.224

Table A.7. N1 peak amplitudes Parietal-Occipital

Subject	PassRev	PassStab	TRevRev	TRevStab	TStabRev	TStabStab
3	0.773	2.004	0.416	2.447	4.262	3.042
4	2.455	2.204	2.552	2.442	1.632	2.374
6	-3.451	-0.201	0.017	0.056	0.104	0.541
13	0.581	-0.494	-1.139	-1.372	-3.467	-0.946
14	3.372	0.515	2.904	2.109	0.588	2.567
15	-2.134	-1.295	-2.023	-0.503	-2.261	-1.300
20	1.415	-0.460	-0.129	-0.023	-0.152	-0.253
22	0.579	0.471	-2.558	-0.136	-1.407	-0.442
24	-0.156	-2.100	-1.337	-1.695	0.300	-2.122
25	-1.618	-1.049	-0.107	-0.792	-1.322	0.440
26	-2.590	1.819	0.690	2.552	-0.131	1.518
28	0.953	1.770	2.439	-0.644	0.283	0.067
30	2.061	2.967	1.022	3.035	3.970	2.646
32	3.213	3.594	3.165	4.537	3.813	3.660
33	1.245	0.774	1.193	1.394	0.250	2.119
35	1.726	1.199	-1.636	1.524	-0.413	0.364
37	-3.276	-1.860	-3.538	-1.850	-2.427	-0.483
38	-3.051	-3.497	-2.372	-2.623	-1.306	-3.636
41	-0.560	-3.016	-2.196	-2.426	-1.880	-2.611
42	0.893	0.626	0.559	3.547	-0.134	1.486
46	-0.563	0.252	-1.623	0.249	1.268	1.621
47	3.548	2.491	1.293	0.628	0.418	1.307
49	2.031	1.932	1.397	0.916	3.009	1.878
50	-1.745	0.310	0.622	1.093	0.133	1.283
51	-3.850	-4.374	-6.853	-5.266	-2.844	-3.644
52	2.948	2.700	1.794	1.421	2.717	2.741
53	2.145	1.831	2.452	1.683	1.690	0.205

Table A.8. P2 peak amplitudes Occipital

Subject	PassRev	PassStab	TRevRev	TRevStab	TStabRev	TStabStab
3	2.555	4.240	2.474	4.478	4.868	6.139
4	4.379	4.991	3.200	4.180	3.661	4.461
6	2.366	4.903	4.321	4.919	5.978	3.580
13	4.509	4.822	1.964	2.227	0.181	3.266
14	9.433	5.412	4.816	4.423	5.781	5.035
15	-0.519	-0.052	-0.544	1.173	-0.802	-0.813
20	2.811	1.472	1.287	1.567	0.651	1.137
22	-0.458	-0.337	-1.270	-0.015	-1.140	-0.186
24	1.636	1.619	0.033	0.967	1.598	0.057
25	0.749	1.464	3.198	2.526	1.160	2.424
26	-0.108	0.397	-2.488	0.107	-1.542	-0.748
28	1.563	2.596	2.689	-0.011	1.912	0.666
30	4.171	5.029	3.055	6.039	4.698	5.104
32	7.542	6.803	7.558	7.605	7.457	6.507
33	3.287	0.986	0.513	2.999	1.721	2.858
35	2.599	2.316	-0.418	3.746	0.426	1.935
37	0.433	2.445	1.557	2.417	2.190	3.575
38	2.565	2.413	1.693	3.775	1.817	2.410
41	2.821	1.238	0.732	1.952	3.211	2.630
42	-0.676	1.542	0.205	2.690	1.310	2.143
46	4.956	3.979	4.906	3.724	5.077	4.429
47	5.210	5.712	6.739	5.306	4.297	3.844
49	5.375	5.421	4.905	4.776	6.326	6.230
50	3.105	3.432	2.940	3.712	4.497	4.774
51	-0.340	-1.443	-1.216	-0.869	-1.127	-0.704
52	3.729	3.941	3.715	2.699	4.291	4.047
53	2.444	4.963	3.081	4.309	3.864	4.013

Table A.9. P2 peak amplitudes Parietal-Occipital

Subject	PassRev	PassStab	TRevRev	TRevStab	TStabRev	TStabStab
3	2.917	4.246	3.075	5.010	5.170	5.195
4	3.904	4.129	2.890	3.527	2.943	3.631
6	3.005	5.405	4.893	5.360	6.581	3.637
13	4.101	3.227	1.029	0.996	-0.041	1.871
14	10.092	5.737	6.205	5.653	6.845	5.900
15	3.793	4.309	3.324	5.556	3.491	3.339
20	4.070	2.075	1.844	1.437	1.091	1.730
22	2.140	2.196	0.804	1.844	0.926	1.659
24	3.948	2.935	1.940	1.818	4.311	0.986
25	1.591	1.756	3.591	3.445	2.711	3.413
26	-0.941	2.373	-1.488	2.716	0.649	2.046
28	2.150	2.415	3.166	-0.381	1.684	0.529
30	3.854	3.727	2.417	4.369	4.511	3.864
32	7.341	6.905	6.194	6.950	8.307	6.721
33	3.837	1.664	2.641	2.779	2.397	3.679
35	2.814	2.140	-0.348	4.523	0.414	2.112
37	1.691	3.883	3.304	4.027	3.592	4.594
38	4.353	3.755	2.655	4.081	3.592	2.680
41	4.734	3.465	2.477	3.583	4.730	4.175
42	0.004	1.250	1.108	4.218	2.262	1.938
46	4.500	3.524	4.368	3.295	4.936	4.219
47	6.480	5.722	6.738	6.066	5.399	3.269
49	5.688	5.353	5.000	4.635	6.896	6.500
50	0.825	1.160	1.481	1.764	2.437	2.322
51	0.168	-1.662	-1.310	-1.062	0.074	-0.988
52	3.775	3.947	3.510	2.414	4.363	4.199
53	2.181	2.536	2.892	2.788	2.695	1.395

Table A.10. N2 peak amplitudes Occipital

Subject	PassRev	PassStab	TRevRev	TRevStab	TStabRev	TStabStab
3	-0.147	0.175	-0.467	0.424	0.588	1.397
4	-1.429	-0.639	-3.009	-1.804	-1.570	-1.432
6	-1.333	0.340	-0.751	1.677	0.239	-0.267
13	-1.126	-3.730	-3.897	-2.798	-5.894	-2.119
14	1.844	-0.728	-1.053	-0.384	-1.357	0.419
15	-5.918	-6.317	-5.595	-5.161	-5.850	-4.944
20	0.096	-0.372	-0.438	-1.253	-1.674	-0.786
22	-4.819	-4.105	-5.863	-3.359	-4.962	-3.988
24	-0.467	-2.613	-3.570	-1.702	-1.942	-3.425
25	-3.673	-0.283	0.976	0.719	-2.345	0.094
26	-0.700	-1.364	-3.626	-0.862	-2.965	-1.898
28	-1.302	-0.164	-1.812	-2.262	-0.758	-1.375
30	2.304	2.265	0.691	2.457	1.343	1.532
32	2.061	2.316	-0.407	0.795	1.613	2.416
33	-1.303	-1.083	-2.096	1.142	-2.088	0.769
35	-0.762	-0.119	-2.993	-0.301	-2.581	-0.609
37	-2.686	-0.816	-4.529	-1.822	-3.297	-1.102
38	-2.168	-1.291	-1.903	-0.708	-3.593	-1.976
41	-0.357	-1.827	-2.063	-1.981	-1.199	-0.111
42	-2.458	0.497	-2.248	0.159	-1.490	1.257
46	1.103	0.662	-0.485	-0.087	0.285	0.274
47	3.665	2.545	2.189	0.885	1.468	1.348
49	-1.342	-2.258	-2.284	-2.964	-2.030	-1.189
50	-1.342	-0.730	-1.412	-1.214	-1.338	-0.630
51	-3.986	-6.446	-5.979	-5.441	-8.204	-5.124
52	0.347	-0.309	-0.423	-0.630	0.088	-1.871
53	-1.249	0.174	-0.617	-0.173	-0.077	-0.294

Table A.11. N2 peak amplitudes Parietal-Occipital

Subject	PassRev	PassStab	TRevRev	TRevStab	TStabRev	TStabStab
3	0.045	0.481	0.468	0.829	1.071	0.078
4	-0.887	-0.903	-2.231	-1.879	-1.011	-1.796
6	-1.508	0.575	0.150	1.346	0.473	-0.550
13	-0.078	-3.329	-3.055	-2.381	-3.932	-2.493
14	0.885	-1.439	-1.667	-0.683	-2.007	0.764
15	-1.832	-2.170	-1.685	-1.118	-1.247	-0.852
20	0.853	-0.340	-0.030	-1.993	-1.491	-0.749
22	-3.494	-1.574	-4.991	-2.637	-3.933	-2.974
24	2.679	-0.870	-0.686	-0.802	0.466	-1.897
25	-4.209	-0.798	-0.491	0.586	-2.101	-0.132
26	-1.983	-0.739	-2.694	1.143	-1.526	1.259
28	-0.327	-0.006	-1.496	-2.770	-0.632	-1.132
30	1.724	1.076	0.229	1.876	0.638	0.660
32	2.052	2.692	-0.460	0.830	2.675	2.915
33	0.225	-0.002	-0.552	1.299	-0.768	1.819
35	0.246	0.465	-2.294	0.881	-2.070	-0.115
37	-2.388	-0.320	-3.749	-1.014	-2.581	-0.938
38	-0.498	-0.125	-1.340	0.149	-1.867	-1.892
41	3.500	0.826	0.817	0.685	1.729	1.765
42	-1.587	0.382	-1.079	0.550	-0.062	0.886
46	1.513	0.820	-0.040	0.145	0.879	0.644
47	4.748	2.326	1.475	1.466	1.211	0.598
49	1.114	0.367	0.205	-0.972	0.924	0.593
50	-2.207	-1.581	-1.442	-1.462	-2.219	-1.518
51	-2.690	-6.365	-5.346	-5.343	-6.693	-4.991
52	0.992	0.082	0.105	0.085	0.742	-1.639
53	-0.321	-0.738	0.477	-0.360	-0.917	-1.779

Table A.12. RN mean amplitudes (170-370msec) Occipital

Subject	PassRev	PassStab	TRevRev	TRevStab	TStabRev	TStabStab
3	0.846	2.002	0.927	1.927	2.909	3.560
4	2.085	2.372	0.709	1.789	1.666	1.874
6	-0.378	1.318	0.611	1.456	1.987	0.690
13	1.175	-0.566	-1.644	-1.232	-3.734	-0.020
14	5.264	2.322	2.450	2.211	1.794	2.985
15	-2.876	-3.740	-2.679	-2.453	-3.360	-2.520
20	1.716	0.468	0.815	-0.058	-0.403	0.050
22	-2.437	-1.637	-3.648	-1.472	-2.926	-1.745
24	-0.848	-1.004	-2.327	-0.567	-0.936	-1.926
25	-1.472	0.476	2.378	1.707	-0.606	1.628
26	0.074	-0.424	-2.084	0.014	-1.252	-1.119
28	0.870	1.200	0.712	-0.934	1.111	-0.225
30	3.100	3.268	1.897	3.710	3.292	3.443
32	5.293	4.865	2.778	3.897	5.054	5.221
33	0.144	0.392	-0.645	1.990	0.318	1.783
35	1.582	1.497	-0.679	2.397	-0.647	0.712
37	-0.694	0.704	-1.354	0.363	-0.534	1.346
38	-0.804	-0.458	-0.654	0.378	-1.830	-0.605
41	0.982	-0.913	-0.642	-0.682	0.891	0.448
42	-0.577	1.139	-0.701	1.240	0.165	1.743
46	2.136	2.144	1.537	1.369	2.741	2.258
47	4.678	3.930	3.163	2.441	2.901	2.568
49	0.850	0.212	0.219	-0.669	0.772	0.788
50	0.321	1.189	0.520	1.006	1.628	1.653
51	-2.577	-4.119	-3.995	-3.925	-4.685	-3.156
52	1.245	1.620	1.523	0.807	1.739	0.871
53	0.418	2.372	1.369	1.917	1.940	1.603

Table A.13. RN mean amplitudes (170-370msec) Parietal-Occipital

Subject	PassRev	PassStab	TRevRev	TRevStab	TStabRev	TStabStab
3	1.248	1.964	1.666	2.336	3.369	2.162
4	2.228	1.859	0.888	1.364	1.492	1.165
6	0.216	1.692	1.236	1.931	2.520	0.609
13	2.043	-0.865	-1.278	-1.155	-2.474	-0.575
14	5.236	2.146	2.905	2.703	1.892	3.631
15	1.505	0.787	1.699	2.348	1.335	1.860
20	2.707	0.714	1.266	-0.579	-0.140	0.266
22	-0.376	0.563	-2.425	-0.413	-1.597	-0.587
24	1.932	-0.089	0.030	-0.171	1.117	-0.675
25	-1.053	0.254	1.776	1.879	0.253	1.926
26	-0.773	0.760	-1.154	2.298	0.833	2.160
28	1.566	1.150	1.026	-1.434	1.097	-0.165
30	2.631	2.100	1.534	3.153	2.923	2.426
32	5.052	4.845	2.124	3.477	5.809	5.462
33	1.364	1.021	0.913	2.322	0.907	2.593
35	2.173	1.586	-0.491	3.121	-0.553	0.794
37	0.349	1.480	-0.318	1.431	0.272	1.742
38	0.894	0.834	0.513	1.247	0.087	-0.508
41	3.943	1.252	1.583	1.339	3.004	2.349
42	0.181	1.182	0.602	1.881	1.215	1.499
46	2.345	2.057	1.604	1.386	2.893	2.304
47	6.032	3.682	2.591	3.093	2.946	2.057
49	3.009	1.652	2.332	0.533	3.050	2.254
50	-0.833	-0.246	0.037	0.094	0.364	0.117
51	-1.430	-4.171	-3.548	-3.630	-3.406	-3.261
52	1.822	1.609	1.837	1.140	1.994	1.097
53	1.073	0.863	2.081	1.279	1.066	-0.178

Table A.14. LPC mean amplitudes (300-500msec) Occipital

Subject	PassRev	PassStab	TRevRev	TRevStab	TStabRev	TStabStab
3	1.019	1.001	0.013	0.757	2.781	2.423
4	1.187	0.594	-0.372	0.434	-0.096	-0.073
6	1.397	0.058	0.388	0.078	2.359	-0.734
13	1.092	-2.860	-2.023	-1.528	-4.147	-0.499
14	5.278	1.635	1.858	1.866	1.718	2.884
15	-1.331	-2.739	-1.790	-2.224	-2.300	-1.858
20	2.706	0.395	1.247	-0.811	-0.301	0.023
22	-2.086	-0.027	-3.756	-0.029	-2.115	-0.620
24	-2.436	-1.790	-3.494	-0.813	-2.220	-2.563
25	-1.881	1.009	2.933	1.989	0.058	1.451
26	1.296	0.144	-1.749	-0.381	-0.218	-0.831
28	3.930	0.870	0.806	-0.011	3.586	0.634
30	2.341	1.048	1.388	3.060	1.104	1.726
32	7.858	4.063	1.258	2.315	6.750	4.558
33	-1.517	-0.887	-2.403	0.821	-1.541	0.768
35	4.704	2.582	2.840	3.990	1.250	1.057
37	0.806	1.744	-0.346	1.417	0.146	2.070
38	-1.149	-0.376	-1.177	0.536	-2.913	-0.693
41	1.944	-0.423	-0.005	-1.034	1.305	-0.423
42	0.456	1.011	-0.587	0.492	1.660	2.106
46	3.005	2.002	3.000	0.148	3.588	1.301
47	3.478	2.205	2.165	1.595	3.335	2.021
49	-0.860	-2.614	-1.869	-3.547	-1.032	-1.409
50	-0.208	0.332	0.302	0.173	1.722	0.416
51	-0.727	-3.438	-2.923	-3.732	-3.378	-2.488
52	0.624	0.912	0.869	0.454	1.606	-0.011
53	-0.401	0.371	1.251	0.323	0.742	-0.100

Table A.15. LPC mean amplitudes (300-500msec) Parietal-Occipital

Subject	PassRev	PassStab	TRevRev	TRevStab	TStabRev	TStabStab
3	2.037	0.953	1.602	1.366	3.966	0.923
4	2.010	0.138	0.198	0.040	0.459	-0.399
6	2.348	0.420	1.297	0.523	3.040	-0.841
13	2.621	-2.631	-0.881	-1.302	-1.983	-0.875
14	5.142	1.072	1.598	1.521	0.968	2.849
15	2.233	1.452	2.227	3.282	2.081	1.754
20	3.461	0.312	1.422	-1.668	-0.259	-0.094
22	-0.837	1.411	-2.113	0.380	-0.567	0.099
24	1.661	-0.422	-0.205	-0.258	0.752	-0.763
25	-1.645	0.587	1.742	1.984	0.917	1.142
26	1.676	0.768	-1.628	1.437	2.336	1.939
28	4.416	0.380	0.723	-0.764	3.525	0.430
30	2.362	-0.081	1.348	2.705	0.920	1.073
32	7.871	3.848	1.132	1.864	7.638	4.676
33	1.087	0.362	-0.217	1.757	0.149	1.916
35	5.349	2.353	2.987	4.365	0.827	0.540
37	2.090	2.285	0.673	2.116	1.056	2.040
38	0.616	0.805	-0.085	1.247	-1.157	-0.938
41	5.511	1.643	2.947	1.184	3.804	1.607
42	1.498	1.208	1.260	0.620	2.821	1.879
46	3.362	2.045	3.024	0.049	3.794	1.383
47	5.143	1.234	1.126	2.246	2.520	1.549
49	1.851	-1.402	1.082	-1.996	1.885	0.083
50	-0.029	-0.465	1.185	-0.200	1.906	-0.659
51	0.959	-3.824	-1.640	-2.866	-1.702	-2.581
52	1.505	0.693	1.338	0.955	1.719	-0.085
53	0.582	-0.525	2.713	0.190	0.102	-0.755

APPENDIX B

Table B.1. Reversal Positivity 2x3 ANOVA

	F	p	η^2	power	MSerror
Perception	.115	.738	.004	.062	2.063
Location	19.256	.000	.425	1.0	2.656
Perception x Location	.534	.589	.020	.133	.372

Table B.2. Reversal Negativity 2x3 ANOVA

	F	p	η^2	power	MSerror
Perception	1.035	.318	.038	.165	1.858
Location	9.344	.000	.264	.972	1.213
Perception x Location	3.890	.027	.130	.678	.401

Table B.3. Late Positive Component 1x3 ANOVA

	F	p	η^2	power	MSerror
Perception	40.070	.000	.606	1.0	1.402

Table B.4. P1 3x2x2 ANOVA

	F	p	η^2	power	MSerror
Intention	.413	.664	.016	.113	2.194
Perception	5.083	.033	.164	.584	1.581
Location	39.172	.000	.601	1.0	8.327
Intention x Perception	.145	.866	.006	.071	1.485
Intention x Location	3.014	.058	.104	.560	.140
Perception x Location	.450	.508	.017	.099	.350
Int x Perc x Loc	1.113	.336	.041	.235	.211

Table B.5. N1 3x2x2 ANOVA

	F	p	η^2	power	MSerror
Intention	1.122	.333	.041	.237	2.380
Perception	5.748	.024	.181	.636	2.071
Location	3.412	.076	.116	.428	3.959
Intention x Perception	1.106	.369	.038	.218	1.473
Intention x Location	1.636	.205	.059	.330	.236
Perception x Location	1.646	.211	.060	.235	.257
Int x Perc x Loc	1.436	.247	.052	.294	.175

Table B.6. P2 3x2x2 ANOVA

	F	p	η^2	power	MSerror
Intention	1.171	.318	.043	.246	1.980
Perception	1.423	.244	.052	.210	2.843
Location	3.843	.061	.129	.471	4.627
Intention x Perception	3.236	.047	.111	.592	1.533
Intention x Location	.057	.945	.002	.058	.149
Perception x Location	9.204	.005	.261	.832	.274
Int x Perc x Loc	2.739	.074	.095	.518	.086

Table B.7. N2 3x2x2 ANOVA

	F	p	η^2	power	MSerror
Intention	4.802	.012	.156	.774	1.622
Perception	5.863	.023	.184	.645	3.103
Location	10.529	.003	.288	.878	3.651
Intention x Perception	5.146	.009	.165	.803	1.446
Intention x Location	.126	.882	.005	.068	.192
Perception x Location	9.731	.004	.272	.851	.305
Int x Perc x Loc	1.695	.194	.061	.341	.099

Table B.8. Reversal Negativity 3x2x2 ANOVA

	F	p	η^2	power	MSerror
Intention	2.748	.073	.096	.519	1.598
Perception	1.355	.255	.050	.202	2.090
Location	8.625	.007	.249	.807	3.631
Intention x Perception	3.875	.027	.130	.676	1.181
Intention x Location	.315	.731	.012	.098	.159
Perception x Location	14.289	.001	.355	.953	.260
Int x Perc x Loc	2.842	.067	.099	.534	.074

Table B.9. Late Positive Component 3x2x2 ANOVA

	F	p	η^2	power	MSerror
Intention	3.726	.031	.125	.658	2.793
Perception	6.245	.019	.194	.672	4.504
Location	12.366	.002	.322	.923	3.501
Intention x Perception	7.839	.001	.232	.941	1.846
Intention x Location	.955	.391	.035	.207	.159
Perception x Location	35.329	.000	.576	1.000	.319
Int x Perc x Loc	3.248	.047	.111	.594	.142

Table B.10. Reversal Positivity t-tests

	Left	Central	Right
Mean Difference (reversal-stability)	0.199	0.074	-0.044
MSerror	2.063	2.063	2.063
t value	0.720	0.267	-0.158
Significant?	NO	NO	NO

Table B.11. Reversal Negativity t-tests

	Left	Central	Right
Mean Difference (reversal-stability)	0.070	-0.131	-0.593
MSerror	1.858	1.858	1.858
t value	0.268	-0.500	-2.259
Significant?	NO	NO	**YES (p<.05)**

Table B.12. Late Positive Component t-test

	Central-Parietal
Mean Difference (reversal-stability)	2.040
MSerror	1.402
t value	8.951
Significant?	**YES (p<.001)**

Table B.13. P1 Perceptual Reversal t-tests

Location:	Occipital	Occipital	Occipital	Occ-Par	Occ-Par	Occ-Par
Conditions compared:	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab
Mean Difference	-0.173	-0.230	-0.056	-0.064	-0.106	-0.042
MSerror	2.194	2.194	2.194	2.194	2.194	2.194
t value	-0.608	-0.805	-0.198	-0.226	-0.373	-0.147
Significant?	NO	NO	NO	NO	NO	NO

Table B.14. P1 Perceptual Stability t-tests

Location:	Occipital	Occipital	Occipital	Occ-Par	Occ-Par	Occ-Par
Conditions compared:	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab
Mean Difference	-0.204	-0.270	-0.066	-0.256	0.064	0.320
MSerror	2.194	2.194	2.194	2.194	2.194	2.194
t value	-0.717	-0.949	-0.232	-0.897	0.226	1.124
Significant?	NO	NO	NO	NO	NO	NO

Table B.15. N1 Perceptual Reversal t-tests

Location:	Occipital	Occipital	Occipital	Occ-Par	Occ-Par	Occ-Par
Conditions compared:	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab
Mean Difference	0.566	0.238	-0.327	0.368	0.009	-0.359
MSerror	2.380	2.380	2.380	2.380	2.380	2.380
t value	1.905	0.803	-1.102	1.240	0.031	-1.209
Significant?	**NO, but (p<.10)**	NO	NO	NO	NO	NO

Table B.16. N1 Perceptual Stability t-tests

Location:	Occipital	Occipital	Occipital	Occ-Par	Occ-Par	Occ-Par
Conditions compared:	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab
Mean Difference	0.156	-0.256	-0.413	-0.118	-0.196	-0.078
MSerror	2.380	2.380	2.380	2.380	2.380	2.380
t value	0.527	-0.863	-1.390	-0.398	-0.662	-0.264
Significant?	NO	NO	NO	NO	NO	NO

Table B.17. P2 Perceptual Reversal t-tests

Location:	Occipital	Occipital	Occipital	Occ-Par	Occ-Par	Occ-Par
Conditions compared:	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab
Mean Difference	0.611	0.140	-0.471	0.689	0.002	-0.688
MSerror	1.980	1.980	1.980	1.980	1.980	1.980
t value	2.256	0.516	-1.740	2.546	0.007	-2.539
Significant?	**YES (p<.05)**	NO	**NO, but (p<.10)**	**YES (p<.05)**	NO	**YES (p<.05)**

Table B.18. P2 Perceptual Stability t-tests

Location:	Occipital	Occipital	Occipital	Occ-Par	Occ-Par	Occ-Par
Conditions compared:	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab
Mean Difference	-0.041	0.055	0.097	-0.120	0.132	0.252
MSerror	1.980	1.980	1.980	1.980	1.980	1.980
t value	-0.152	0.204	0.356	-0.443	0.487	0.930
Significant?	NO	NO	NO	NO	NO	NO

Table B.19. N2 Perceptual Reversal t-tests

Location:	Occipital	Occipital	Occipital	Occ-Par	Occ-Par	Occ-Par
Conditions compared:	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab
Mean Difference	0.982	0.831	-0.151	1.036	0.771	-0.265
MSerror	1.622	1.622	1.622	1.622	1.622	1.622
t value	4.007	3.391	-0.615	4.227	3.146	-1.081
Significant?	**YES (p<.001)**	**YES (p<.01)**	NO	**YES (p<.001)**	**YES (p<.01)**	NO

Table B.20. N2 Perceptual Stability t-tests

Location:	Occipital	Occipital	Occipital	Occ-Par	Occ-Par	Occ-Par
Conditions compared:	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab
Mean Difference	0.016	-0.096	-0.111	0.013	0.084	0.071
MSerror	1.622	1.622	1.622	1.622	1.622	1.622
t value	0.064	-0.391	-0.455	0.051	0.342	0.290
Significant?	NO	NO	NO	NO	NO	NO

Table B.21. Reversal Negativity Perceptual Reversal t-tests

Location:	Occipital	Occipital	Occipital	Occ-Par	Occ-Par	Occ-Par
Conditions compared:	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab
Mean Difference	0.724	0.375	-0.350	0.891	0.475	-0.416
MSerror	1.598	1.598	1.598	1.598	1.598	1.598
t value	2.977	1.541	-1.437	3.663	1.951	-1.711
Significant?	**YES (p<.001)**	NO	NO	**YES (p<.001)**	**NO, but (p<.10)**	**NO, but (p<.10)**

Table B.22. Reversal Negativity Perceptual Stability t-tests

Location:	Occipital	Occipital	Occipital	Occ-Par	Occ-Par	Occ-Par
Conditions compared:	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab
Mean Difference	0.074	-0.121	-0.196	-0.085	-0.068	0.017
MSerror	1.598	1.598	1.598	1.598	1.598	1.598
t value	0.305	-0.499	-0.804	-0.349	-0.280	0.069
Significant?	NO	NO	NO	NO	NO	NO

Table B.23 Late Positive Component Perceptual Reversal t-tests

Location:	Occipital	Occipital	Occipital	Occ-Par	Occ-Par	Occ-Par
Conditions compared:	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab
Mean Difference	1.211	0.632	-0.578	1.482	0.865	-0.617
MSerror	2.793	2.793	2.793	2.793	2.793	2.793
t value	3.765	1.96	-1.799	4.609	2.690	-1.918
Significant?	**YES (p<.001)**	**NO, but (p<.10)**	**NO, but (p<.10)**	**YES (p<.001)**	**YES (p<.05)**	**NO, but (p<.10)**

Table B.24 Late Positive Component Perceptual Stability t-tests

Location:	Occipital	Occipital	Occipital	Occ-Par	Occ-Par	Occ-Par
Conditions compared:	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab	Pass – Int Rev	Pass – Int Stab	Int Rev – Int Stab
Mean Difference	0.017	-0.159	-0.177	-0.228	-0.121	0.106
MSerror	2.793	2.793	2.793	2.793	2.793	2.793
t value	0.055	-0.496	-0.552	-0.709	-0.377	0.332
Significant?	NO	NO	NO	NO	NO	NO