AN INVESTIGATION OF EVENT-RELATED BRAIN POTENTIALS EVOKED BY FEEDBACK DURING PRISM ADAPTATION

by

Stephane MacLean

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ABSTRACT

Prism adaptation (PA) demonstrates how the brain can adapt to a shifted visual field and also serves as a promising rehabilitation approach for treating visuo-spatial neglect (VSN) – a condition marked by deficits in attending and responding to contralesional stimuli. Visuo-motor aiming errors following PA, or *aftereffects*, suggest that adaption is achieved in part by undergoing a basic transformation of spatial maps and egocentric coordinates. This process, referred to as spatial realignment, thus plays a critical role in eliciting improved VSN symptoms following PA. Despite several theoretical accounts of the mechanisms involved in PA, there are limited means to directly measure neural processes engaged during PA that lead to robust aftereffects. The present set of studies investigated event-related brain potentials (ERPs) evoked by different provisions of feedback during blocks of PA performed by young healthy adults. The main purpose of the studies was to identify ERP components that index neural processes during adaptation that lead to robust aftereffects. Previous research has shown that feedback events at the end of reaching movements during PA can evoke an error-sensitive component of the ERP (the error-related negativity, ERN) as well as a component sensitive to phase – i.e. early, middle, late – of adaptation blocks (the P300). Thus the following studies investigated whether the ERN, P300, or any novel ERP components reflect adaptive processes associated with subsequent aftereffects. The different provisions of feedback used here were predicted to evoke either relatively weak, or relatively strong magnitudes of aftereffects. Thus, ERPs were compared between feedback provisions. Feedback events evoked a number of different ERPs across all conditions, thus providing evidence that the brain recruits different systems to support adaptation depending on the feedback condition. The major results from the studies suggest that a purported neural reinforcement learning system, indexed by the ERN, is sufficient to undergo error compensation across adaptation blocks but not sufficient to yield strong aftereffects. Results also suggest, however, that a parieto-occipital component sensitive to phase, resembling the P300, reflects processing associated with spatial realignment as it is consistently evoked by conditions leading to strong aftereffects but absent otherwise. Although further research is necessary, development of PA paradigms can be improved by using feedback conditions that evoke the aforementioned parieto-occipital component response. The use of feedback-evoked brain potentials may also assist clinicians in determining why, or how a person with neglect responds to PA treatment successfully or poorly.

LIST OF ABBREVIATIONS AND SYMBOLS USED

ACC	anterior cingulate cortex
ANOVA	analysis of variance
CI	confidence interval
EEG	electroencephalography
ERN	error-related negativity
ERP	event related potential
LC	locus coeruleus
MT	movement time
NE	norepinephrine
PA	prism adaptation
RL	reinforcement learning
RT	reaction time
SE	standard error
VSN	visuo-spatial neglect
$_p\eta^2$	partial eta squared
d_{rm}	Cohen's d for repeated-measures sample
μV	microvolt

CHAPTER 1: INTRODUCTION

Visuo-motor behaviour is essential to nearly any undertaking. People constantly process visual information from their environment and generate movement based on that information. This helps us taste, touch, communicate, and move our bodies around the world. Importantly, visuo-motor behaviour is supported by a number of systems that function outside the strict domains of vision and movement. Systems devoted to memory, learning, and decision-making, for example, may all support visuo-motor behaviour in some capacity. Therefore, when visuo-motor behaviour is suboptimal, e.g. visuo-motor goals do not match predicted results, several systems in the brain can contribute to improving that behaviour. Prism adaptation (PA) provides a classic example of how the brain can recruit these systems and quickly undergo changes to improve suboptimal visuo-motor behaviour. During prism adaptation, a participant's visual field is shifted laterally by prism goggles; a condition that causes aiming errors when reaching towards targets.

Broadly speaking, the present thesis describes an electroencephalographic (EEG) investigation of PA in order to isolate brain responses (event-related potentials; ERPs) reflecting the contribution of different systems involved in achieving adaptation – i.e. achieving optimal visuo-motor behaviour. Of particular relevance to this thesis is the fact that PA shows promise as a treatment to improve attention-related deficits experienced after stroke – a condition often referred to as visuo-spatial neglect (VSN; "neglect"). Among the many systems that can improve visuo-motor responding during PA, certain systems, or *processes*, are more critical than others to ultimately improving neglect symptoms. For example, systems that support perceptual learning during PA may be more beneficial to persons with neglect than systems supporting online movement corrections (Redding & Wallace, 1993). Therefore, identifying brain responses (ERPs) that reflect critical systems/processes that improve neglect symptoms has potential to enhance the development and use of PA as a clinical treatment. In the broader context, identifying ERPs that reflect different adaptive processes can also contribute to understanding basic neural mechanisms that support optimal perceptual-motor behaviour. Before introducing the experiments, however, more details are provided below regarding the critical elements and questions involved in this thesis.

1.1 Prism Adaptation

Prism adaptation (PA) demonstrates the brain's ability to adapt rapidly to sudden changes in the visually perceived coordinates of objects in space. Prism adaptation paradigms require participants to perform a goal-directed visuo-motor task. This normally requires reaching movements with the dominant hand towards targets along the transverse plane. Furthermore, the task is performed with prism glasses that function to displace the visual field laterally, either left or right by some number of degrees.

Prism adaptation comprises several stages. First, as a result of the laterally displaced visual field, participants experience *direct effects* at the onset of the task: large aiming errors, observed as reaches terminating too far from the target in the direction of the prismatic visual shift. Thus, direct effects are measured according to the size of reaching error from the onset of PA blocks. Direct effects are followed by a stage of rapid *adaptation*, or error correction, usually within 15 trials that results in aiming performance closely approaching baseline levels of accuracy. A slower, unconscious form of adaptation continues to take place after immediate error correction. This latter adaptive process is considered to be critical to producing PA *aftereffects* – abnormal visuo-motor behaviour after prism glasses are removed. Specifically, after PA participants will perform visuo-motor errors by reaching too far from targets in the direction opposite to the preceding prism displacement. Thus, aftereffects are measured by size of reaching error under conditions of normal vision immediately following PA.

The observation of robust aftereffects has led researchers to suggest that the brain compensates for the prismatic visual shift by changing fundamental components of the perceptual-motor system, as opposed to simply engaging deliberate trial-by-trial aiming corrections (Redding and Wallace, 2013). Accordingly, there is evidence that the latter, slower form of adaptation produces larger aftereffects with increased adaptation trials – even well after errors are immediately corrected for (Redding & Wallace, 1996). The different neural systems and processes involved in adaptation, and the role that each plays in producing PA aftereffects have spawned a corpus of research (e.g. Kornheiser, 1976; Redding, et al. 2005; Redding & Wallace, 2006; Newport & Schenk, 2012) and are of major interest to this thesis.

1.2 Visuo-Spatial Neglect

While PA serves as a means to investigate perceptual-motor phenomena, it has garnered significant attention for its promising clinical applications as well. Seminal research by Rossetti et al. (1998) revealed that a session of PA could improve symptoms of visuo-spatial neglect (VSN; neglect) measured by common neuropsychological tests: line bisection, drawing a copy of visible image, drawing an image from memory, reading, and line cancelation. Neglect is viewed primarily as an attention-related disorder and is predominantly caused by right-hemisphere stroke. Indeed, some form of VSN affects a majority of individuals after right-hemisphere stroke (Azouvi et al., 2006; Buxbaum et al., 2004). Although the condition may present a diversity of problems, VSN principally comprises difficulty attending, orienting, and responding to stimuli in contralesional space (Heilman et al., 1993). Neglect can severely impact daily living (Jehkonen et al., 2006; Mutai et al., 2012), and can lead to poorer overall recovery after stroke (Vossel, et al., 2012; Paolucci, et al., 2001). A number of approaches to treating VSN have been investigated, such as visuo-spatial training (Pizzamiglio et al., 2006), continuous theta-burst stimulation (Koch et al., 2012; Cazzoli et al., 2012), repetitive transcranial magnetic stimulation (Brighina et al., 2003; Bjoertomt et al., 2002; Shindo et al., 2006), and limb activation (Eskes & Butler, 2006; Robertson et al., 2002; Luukkainen-Markkula et al., 2009). Among the many approaches (Yang et al., 2013; Luauté et al., 2006; for review), substantial evidence, reported below, suggests prism adaptation is a particularly promising treatment method.

Returning to normal vision after PA improves performance on a number of scanning and reaching tasks among individuals with neglect (Rossetti et al., 1998; Baltitude & Rafal, 2010; Frassinetti et al., 2002; Sarri et al., 2008; Schindler et al., 2009; Serino et al., 2006; Striemer & Danckert, 2007; Nys, et al., 2008a; Keane et al., 2006). More importantly, PA has been shown to improve deficits in daily activities such as reading (Angeli et al., 2004a; Angeli et al., 2004b; Farnè et al., 2002; Serino et al., 2009; Serino et al., 2007), writing (Rode et al., 2006), maintaining postural balance (Tilikete et al., 2001; Shiraishi et al., 2010), and navigating a wheelchair (Jacquin-Courtois et al., 2008; Watanabe & Amimoto, 2010). Finally, PA is reported to also improve daily function as measured through self-report and caregiver observation (Turton et al., 2010; Fortis et al., 2010; Keane et al., 2006; Mizuno et al., 2011; Shiraishi et al., 2010; Vangkilde and Habekost, 2010).

Despite its promise, however, PA continues to generate inconsistent results. Some studies report relatively weak findings in regard to improved daily function (Keane et al., 2006, Pierce and Buxbaum, 2002; Bowen & Lincoln, 2007; Champod et al.), and many cases of improvement are no greater than those observed in control or placebo groups (Rousseaux et al., 2006; Turton et al., 2010; Nys et al., 2008b). Moreover, some studies that do cite functional improvements lack proper control groups and are often limited to single case studies (Angeli et al., 2004a, Angeli et al., 2004b). Finally, in complete contrast to the improvements cited above, PA has also had null effects on reading deficits (Humphreys et al., 2006; McIntosh et al., 2002), visual object recognition, visual object description, (Dijkerman et al., 2003; Datié et al., 2006; Sarri et al., 2011), and visual search tasks (Morris et al., 2004; Nijboer et al., 2008).

Mounting evidence suggests PA's effect on neglect is restricted to mainly motor-intentional behaviours (e.g. goal-directed reaching), and thus yields limited effects on strictly perceptual processes (e.g. Sarri et al., 2006; 2011; Ferber et al., 2003). The lack of improvement on perceptual processes has been illustrated, for example, by the ability of persons with neglect to improve at a line-bisection task, involving both perceptual and motor components, but not a landmark task – the perceptual-only analogue to line-bisection (Striemer & Danckert, 2010).

While PA shows promise as a means to rehabilitate some neglect symptoms, the conflicting results so far suggest further development is required in order to optimize its usefulness in clinical settings. Given VSN's pervasiveness and impact on quality of life, developing treatments is certainly a warranted effort. Further developing PA for persons with neglect could happen in a number of ways. The present thesis aims to contribute to the development of PA for neglect in two ways. First, it can improve knowledge of the basic brain processes involved in adaptation, and thus can improve the design of PA paradigms to recruit the brain processes critical for eliciting robust aftereffects. Second, by identifying brain processes critical to aftereffects, it can improve our means to understand how, or why certain persons with neglect and/or populations respond poorly to PA while others do not. The method is described in further detail below.

1.4 Strategic Recalibration & Spatial Realignment

Current PA theories normally suggest that two brain processes function in parallel to achieve adaptation to the shifted visual field. While a number of authors have described mechanisms responsible for PA (e.g. Welch & Warren, 1980; Bedford, 1993), Redding and Wallace (e.g. Redding & Wallace, 1996; 2002) have undertaken a series of detailed studies concerning basic PA mechanisms and thus they serves as a good benchmark for theories of adaptive visuo-motor behaviour.

Redding and Wallace propose that exposure to prism goggles engages two processes: "strategic recalibration" and "spatial realignment". Both lend to adaptation and subsequent aftereffects in different ways. Recalibration reflects a rapidly implemented and deliberate attempt at correcting consciously perceived aiming errors by adjusting the motor plan. Realignment, on the other hand, reflects an unconscious process by which the brain's spatial map of egocentric coordinates is transformed (i.e. realigned) in such a way to minimize the discrepancies between proprioceptive "felt" hand coordinates and visually perceived hand coordinates during a visuo-motor task performed with prisms. Redding and Wallace note that realignment is a mechanism important for human survival as it enables us to adjust to natural changes in body due to, for example, growth (e.g. lengthening limbs), or accident (e.g. loss of hand) (Redding & Wallace, 1996).

Evidence would suggest that spatial realignment enhances aftereffects beyond the contribution of recalibration. Specifically, it has been shown that the magnitude of aftereffects caused by prism adaptation can increase independent of error correction. For example, Michel et al. (2007) showed that participants experienced larger aftereffects after a session prism exposure without consciously experiencing errors during the course of adaptation compared to adaptation with conscious error correction. This former condition was achieved by exposing participants to prism goggles in small increments. Likewise, Redding and Wallace (1993) probed magnitude of aftereffects across 10 trial increments during a prism adaptation block consisting of 60 trials. Redding and Wallace showed that participants' aftereffects increased across latter phases of the adaptation block despite participants not undergoing any more significant error correction during those phases. Together, the evidence suggests that PA is indeed supported by two separate mechanisms: a faster process engaged to correct consciously perceived errors, i.e. recalibration, and a slower process causing aftereffects that transfer to other tasks post-adaptation, i.e. realignment.

Thus, when considering neural processes that are of importance to persons with neglect, these are normally associated with spatial realignment rather than recalibration. Realignment explains how PA aftereffects can transfer to tasks outside of those trained under PA and thus also explains how persons with neglect may show improvement across a number of domains (Luauté et al., 2006). Indeed, under Redding and Wallace's (2009) model of prism adaptation, persons with neglect primarily undergo realignment during PA and thus are able to benefit from that treatment approach. In summary, recalibration and realignment provide a model of PA involving two distinct processes engaged during adaptation, one of which, realignment, is assumed to enhance aftereffects that can ultimately improve neglect symptoms.

Neural structures involved in recalibration and realignment have been investigated with both neuroimaging and lesion studies. Evidence suggests that adaptation is modulated by a frontal, parietal, and cerebellar network in the brain. Using PET imaging, Clower et al. (1996) revealed the posterior parietal cortex to have enhanced activation during short blocks of prism adaptation primarily involving error correction compared to a similar reaching task performed without prisms. Similarly, using fMRI, Danckert et al. (2008) and Luaute et al. (2009) revealed particular regions of the PPC to have enhanced activation during early error correction trials compared to latter trials of adaptation. The parietal cortex has indeed been implicated as a region involved in error correction of movements (Della-Maggiore et al., 2004; Desmurget et al., 1999; Tunik et al., 2005; Tunik et al., 2007), and would thus be implicated in recalibration processes. Its role in realignment, however, is more questionable given evidence that bilateral parietal lesions have been shown to hinder error correction to prism exposure but maintain aftereffects (Pisella et al., 2004). One fMRI study, however, Chapman et al. (2010), also showed enhanced activation of parietal regions during latter adaptation trials compared to early trials, thus associating the parietal cortex with realignment processes as well. The cerebellum has also been implicated as a region involved in recalibration during prism adaptation. Both Danckert et al. (2008) and Chapman et al. (2010) showed enhanced cerebellar activity during early trials of adaptation compared to later trials. However, evidence suggests cerebellar regions are also critical in realignment processes as well. Cerebellar lesions have been shown to impair not only error correction processes during prism adaptation, but aftereffects as well (Fernandez-Ruiz et al., 2007; Martin et al., 1996). Indeed, Luaute et al. (2009) and Chapman et al. (2010) also reported increased cerebellar activity during latter trials of adaptation, suggesting it plays some role in realignment processes in addition to recalibration. Finally, Danckert et al. (2008) showed increased activity in anterior cingulate cortex during early, error correction trials of adaptation, thus also implicating frontal error monitoring systems in the process of recalibration.

1.5 Brain Potentials Evoked during PA Feedback

In an effort to better understand recalibration and realignment, two published studies have used EEG to investigated ERP components evoked by onset of feedback during PA that are sensitive to two particular factors over course of adaptation: (1) accuracy and (2) phase of adaptation. The relationship between these accuracy-sensitive and phase-sensitive ERP components and the processes of recalibration and realignment has yet to be fully elucidated however.

First, Vocat et al. (2011) measured two ERP components evoked by reaching movements during PA that were sensitive to the size of reaching errors during the task: the error-related negativity (ERN), and error-positivity (Pe). Participants reached towards dots on a computer monitor for 10 blocks that each had 12 trials. Blocks alternated between conditions of normal vision and conditions with 10º rightward-displacing prism goggles. Alternating between prism glasses and normal vision enabled participants to adapt and then de-adapt to the prism goggles repeatedly. Vocat et al. (2011) compared ERPs evoked by reaches leading to correct responses against reaches leading to errors of three different magnitudes (large, mild, slight). They reported that a negative-going voltage maximal at fronto-central electrode FCz, and peaking at 76 ms post-response onset, was present on error-trials and increased in negative voltage concomitantly with the size of errors. This component is consistent with the ERN. Vocat also reported a second ERP component, also sensitive to errors, at the same electrode site (FCz) but with a positive-going voltage peaking at 185 ms post-response. Like the former component, this positive voltage deflection also increased in amplitude concomitantly with error size. This latter component is consistent with the Pe.

The ERN has been reported across several experimental conditions by the onset of erroneous responses, typically peaks 50-100 ms post-response onset, is maximal at fronto-central scalp electrodes (e.g. Falkenstein et al., 1991), and has been source-localized to anterior-cingulate cortex (ACC; Van Veen & Carter, 2002). The ERN is observed, for example, during flanker tasks (Gehring et al., 1993; Maier et al., 2012) and during stroop tasks (Hajcak & Simons, 2002) when participants impulsively initiate an incorrect response due to conflicting stimuli. Indeed, a prominent theory holds that the ERN reflects a process of response conflict – thus responses requiring inhibition of alternative choices, or requiring increased cognitive control may evoke an ERN (Yeung et al., 2004; Botvinick et al., 2001). A theory proposed by Holroyd and Coles (2002) suggests the ERN, or *response*-ERN, may index activity from a neural reinforcement learning (RL) system. The "RL-ERN" theory would suggest the ERN is evoked by a response-outcome prediction-error, and is thus sensitive to the first indication that the outcome of a selected action is worse than predicted. Although theoretical accounts of the ERN may differ, the timing of the ERN and its sensitivity to errors would suggest that it is evoked by some internal evaluation of responses, e.g. evaluation of an efference copy of the motor command, rather than evaluation of external feedback indicating error. Relevant to PA, the ERN has previously been reported during tasks requiring visuo-motor learning (e.g. Bediou et al., 2012; Anguera et al., 2009).

The second component reported by Vocat et al. (2011), the Pe, has garnered slightly less attention than the ERN and possesses a less-defined role in error processing. When present, the Pe is typically observed as a positive-going voltage peaking ~150ms after the ERN at centro-parietal electrode sites. Several studies have suggested the Pe relates to conscious awareness of errors, as it is absent or significantly attenuated on trials in which participants report not being aware they made an error (e.g. Nieuwenhuis et al., 2001; but see Overbeek et al., 2005). The ERN, however, is still observed on trials in which participants are reportedly unaware they made an error (Endrass et al., 2005; O'Connell et al., 2007). Typically, the manipulation of error awareness is achieved by having participants perform speeded response tasks that sometimes require response inhibition (failure to inhibit causes an error). A subsequent manual rating (i.e. button press) indicating whether or not they subjectively experienced an error on the previous trial is required. Therefore, observation of the ERN when the later Pe is absent, and when participants do not report awareness of errors, lends support to the theory that the response ERN is modulated by internal evaluation mechanisms that may not always come into full awareness (Van Veen & Carter, 2002). The Pe is also reportedly sensitive to certainty, or valence of errors – the Pe increases when participants are more certain an error occurred than less certain (Boldt & Yeung, 2015). In addition to error awareness, the Pe amplitude has also been positively correlated with post-error slowing (Hajcak et al., 2003), thus leading to the possibility that it reflects additional post-error compensatory processing. Finally, source localization studies have suggested the Pe component may originate in rostral ACC, anterior ACC, posterior cingulate cortex, and the precuneus (Herrmann et al., 2004; O'Connell et al., 2007; Vocat et al., 2008).

In addition to Vocat et al. (2011), MacLean et al. (2015) also studied ERPs evoked during PA. Similar to Vocat et al., (2011), participants performed several blocks of goal directed reaching towards targets on a monitor. Blocks also alternated between conditions of normal vision and prism exposure. MacLean et al. (2015) ensured participants were unable to see their reaching arm until the very end of the movement. Thus, feedback-evoked potentials, rather than response-evoked potentials, were measured at the termination of the reaching movement when the participant made contact with the screen. Furthermore, participants were subjected to longer blocks of adaptation (45 trials) than in Vocat's study in order to measure ERP components that were sensitive to different phase of adaptation blocks (early, middle and late trials). MacLean et al. (2015) found that screen-touch evoked an early ERN-like component sensitive to errors, peaking ~75ms post-screen-touch. In addition to the ERN, screen-touch also evoked a P300 component sensitive to phase of adaptation independent of accuracy. Here, phase reflected the early (1-15), middle (16-30), and late (31-45) trials of adaptation blocks. The P300 component manifested as an increased positive-going voltage during the early phase of adaptation compared to the latter phases. The observation that the P300 was evoked independent of accuracy (i.e. hit or miss) but that it also diminished in amplitude across trials suggests the possibility that the component reflects neural activity associated with engaging realignment.

The observation of an early ERN component evoked by screen-touch in MacLean et al. (2015) was rather interesting. The result suggests that the brain can rapidly use external feedback information (e.g. vision of miss-positioned hand during reach) to evoke internal error evaluation mechanisms. This result was indeed novel, seeing as provisions of external error feedback normally evoke a different error-sensitive component: the feedback-related negativity (FRN). It was hypothesized in MacLean et al. (2015) that the onset of seeing the hand next to the target would be processed similarly to external feedback stimuli, thus would evoke an FRN rather than an ERN.

The FRN is evoked by the onset of external stimuli (e.g. auditory tone or visual symbol) indicating failure at achieving a desired outcome. Such instances are observed, for example, during time-estimation tasks when participants receive feedback (in the form of a visual stimuli) indicating their response was not approximate to one second (Miltner et al., 1997; Holroyd & Krigolson, 2007). More classically, however, the FRN is commonly reported during gambling tasks at the onset of feedback (in the form of a visual stimuli) indicating participants lost based on their selected response (e.g. Krigolson et al., 2013; Yu & Zhou, 2006; San Martin et al., 2010; Dunning et al., 2007). The FRN commonly peaks ~250ms after onset of error feedback and is normally maximal at fronto-central scalp electrodes. While the FRN and ERN are not identical in timing and evoking event, the RL-ERN theory proposed by Holroyd & Coles (2002) suggests they originate from the same neural learning system, although this theory has been disputed.

Both, nonetheless, have been source localized to medial-frontal cortex, specifically anterior cingulate cortex (ACC) (Dehaene et al., 1994; Herrmann et al., 2004; Ullsperger & von Cramon, 2001; Gehring & Willoughby, 2002; Van Veen & Carter, 2002; Debener et al., 2005).

Relevant to PA, the FRN has also been evoked by error trials in a number of visuo-motor tasks similar to those used during PA, such as manual tracking tasks (Krigolson & Holroyd, 2006, 2007a, 2007b; Krigolson et al., 2008) and postural control tasks (Hassall et al., 2014). Prism adaptation, nonetheless, presents a very novel paradigm from which the FRN, and ERN, have been investigated and raises important question about their evoking stimuli (further discussed following Experiment 1). For the purposes of the following experiments, instances of fronto-central negative-going voltage deflections sensitive to errors peaking 50-100ms post-evoking-event will be labeled as ERNs, whereas fronto-central negative-going voltage deflections sensitive to errors peaking ~250ms post-evoking-event will be labeled as FRNs.

The P300 component, also reported in MacLean et al. (2015), has been studied extensively and evoked by a number of experimental conditions. It is reportedly sensitive to an evoking-stimulus' probability (Duncan-Johnson & Donchin, 1977), task-relevance (Donchin & Cohen, 1967), novelty (Friedman et al., 2001), as well as participants' allocation of attention (Becker and Shapiro, 1980; Heinze et al., 1990), and memory (Polich et al., 1983; Johnson et al., 1985). The accumulation of data has led to some overarching theories regarding the underlying processes that govern the P300. Two predominant theories are the context-updating hypothesis (Donchin & Coles 1988) and the locus-coeruleus norepinephrine (LC-NE) theory (Nieuwenhuis et al., 2005).

According to the context-updating hypothesis, the P300 reflects an updating of participants working model of the environment. Thus, stimuli that require participants to integrate information and update their model of the environment evoke a P300 response. The LC-NE theory, however, stems from both P300 research as well as neurophysiological observations in animal research. Here, the P300 is suggested to reflect a phasic increase in firing from the LC-NE system. Studies with non-human primates suggest that phasic increase in LC-NE firing promotes exploratory behaviour by increasing the gain of its target neurons (in hippocampus and higher cortical regions), thus decreasing the "threshold" for action selection (Aston- Jones et al., 1994, 1997; Usher et al., 1999). The theory thus purports that the P300 reflects a neural response that improves decision-making, or action selection, in response to its evoking stimuli.

P300 components reported in the literature are evidently not all identical. The classic P300 has thus also been conceived of as having different subcomponents, possibly reflecting different processes, referred to as the P3a and P3b. The P3a is normally associated with a more narrow voltage deflection at central electrode sites (e.g. Cz) while the P3b is normally associated with a later, broader voltage deflection at parietal electrode sites (e.g. POz). A review by Polich (2007) suggests these components may reflect, respectively, allocation of attention mechanisms to the evoking stimuli, and subsequent information integration (i.e. memory storage, context-updating). The P3a and P3b can therefore be viewed as distinct, but connected neural processes.

1.6 Summary & Current Experiments

Vocat et al (2012) and MacLean et al. (2015) showed that responses and feedback during PA can elicit brain potentials sensitive to (1) accuracy, and (2) phase of adaptation. The experiments presented below further investigate these brain potentials by measuring how they are evoked across different types of feedback-events over the course of prism adaptation. To this end, participants' electroencephalography (EEG) is measured in a number of PA blocks, each with different feedback provisions. Some of these feedback provisions are predicted to yield strong aftereffects, while others are predicted to yield weak aftereffects. Specifically, some of the PA blocks reported below will appeal to (1) conditions of delayed visual feedback, and (2) conditions of symbolic hand representation. Based on previous studies, these conditions are predicted to yield weaker aftereffects than control conditions using (1) immediate visual feedback (Kitazawa et al., 1995), or (2) direct vision of hand (Wilms and Hala, 2002). Thus, according to the model of prism adaptation proposed by Redding and Wallace (2002), conditions yielding weaker aftereffects may do so as a result of limited spatial realignment taking place over the course of adaptation.

Post-experiment, the event-related potential (ERP) technique is used to specifically compare averaged EEG responses at the scalp to the onset of these different discrete feedback events. Varying the provision of feedback in different PA blocks enables the comparison of feedback-evoked brain potentials in conditions yielding different magnitudes of aftereffects and thus potentially different magnitudes of realignment.

The following experiments specifically investigate accuracy-sensitive (ERN, FRN, and Pe) and phase-sensitive (P300) ERP components. Sensitivity to accuracy is measured by comparing ERPs evoked by hit trials and error trials. Sensitivity to phase is measured by comparing ERPs evoked by different bins of trials corresponding to early, middle and late phases of adaptation blocks. This proposed criteria thus enables these ERP components to be associated to error-specific adaptation processes (i.e. recalibration) and error-independent adaptation processes (i.e. realignment).

Broadly speaking, it is hypothesized that feedback provisions yielding larger aftereffects will evoke a phase-sensitive ERP component, the P300, that is not evoked by feedback conditions yielding weaker aftereffects. The P300 is a strong candidate for a neural event indexing realignment because it has been previously evoked independent of aiming errors, but also appears sensitive to the course of learning (i.e. phase) across PA blocks (MacLean et al., 2015). It is hypothesized that accuracy-sensitive ERP components, e.g. the ERN, FRN, and Pe, will be evoked by all feedback events that reveal an aiming error has occurred, thus providing some evidence they index a neural event associated with engaging the process of recalibration. Implications for understanding the basic mechanisms of PA, developing PA paradigms for persons with neglect, and improving our understanding of their responsiveness to PA are all addressed in the general discussion.

CHAPTER 2: EXPERIMENT 1

2.1 Introduction

Prism adaptation aftereffects are normally measured by the size of errors in the opposite direction to the prism shift after returning to normal vision. Previous research has shown that aftereffects are modulated by different provisions of visual feedback during the preceding PA block. Kitazawa et al. (1995) presents such an instance where visual feedback provisions affect adaptation and aftereffects. In Kitazawa's study, healthy participants were exposed to conditions of goal-directed open-loop reaching with prism glasses - participants' vision was thus fully occluded at the onset of the reaching movement. Full visual feedback, which enabled participants to see the target and their pointing hand against a monitor, was returned to the participants either immediately upon completing the reach or following various periods of delay (0-10 seconds). The authors showed that delaying visual feedback for as little as 50 ms after reach completion produced decrements in adaptation and subsequent aftereffects compared to conditions with 0 ms feedback delay. Similarly, prior research by Held & Durlach (1966) showed that delaying ongoing visual feedback of participants' continuous arm movement by 300ms or more, with the visual field displaced by prisms, also greatly reduced the subsequent aftereffects compared to condition of 0ms feedback delay.

Indeed, the availability of visual information is an important factor in any instance of goal-directed reaching as it may improve one's ability to correct errors and learn through feedback (Goodale & Milner, 1992; Elliot et al., 2001). When visual information is removed or limited, movement performance tends to deteriorate in respect to accuracy and variable error (e.g. Proteau et al., 1987; Carlton, 1981). Under conditions such as those described in Kitazawa et al. (1995) for example, participants may recruit additional systems to support movement accuracy in lieu of visual feedback-guided control. They may, for example, rely on stored memory of the spatial environment as well as available allocentric cues relevant to the target (Krigolson & Heath, 2004, Elliott & Madalena, 1987, Westwood et al., 2003), or rely more so on a feed-forward model of control (e.g. Heath et al., 2004) to maintain accurate movements.

In Kitazawa et al. (1995), adaptive processes (e.g. recalibration or realignment) that lead to strong aftereffects were not engaged by delayed visual feedback to the same degree as they were with immediate visual feedback. Although speculative, delays in visual feedback may specifically fail to engage spatial realignment processes to the same degree as immediate visual feedback upon completing reaching movements.

Electroencephalography (EEG) data provide a means to elucidate differences in neural processes engages specifically by immediate visual feedback and delayed visual feedback after reaching movements during PA. Comparing how the brain responds to visual feedback evoked immediately at the termination of reach versus after a period of delay may to isolate brain processes that, based on Kitazawa et al. (1995), increase subsequent aftereffects. The present study collected electroencephalography (EEG) to compare brain potentials evoked by immediate and delayed visual feedback. Here, participants performed memory-guided reaches toward targets on a touchscreen monitor. The target was occluded (disappeared from screen), then participants experienced a brief delay before they were cued to reach. Participants also reached below an occlusion board for most of the movement that prevented vision of limb until the very end of the reach. Importantly, this experimental design meant that participants would experience visual feedback of limb (their pointing finger, more specifically) immediately upon terminating reach in both the immediate and delayed feedback condition, although the target would only be available immediately in the former condition. The PA blocks in the present experiment were 60 trials long. This is slightly longer than MacLean et al. (2015). The reason for extending the length of blocks was to acquire a better measurement of differences across adaptation phases. MacLean et al. (2015) only found a difference between trials 1-15 (early phase) and trials 16-45 (middle and late phase). In the current study, however, phase will be measured in bins of 10 trials thereby enabling comparison across a total of 6 phases of adaptation, and thus providing better resolution with which to measure difference from early to late adaptation. This analysis approach nonetheless preserved the ERP technique of investigation used in MacLean et al. (2015), and thus enables comparison of ERP components (e.g. P300) across different experiments.

Each participant was exposed to two PA blocks with immediate target-feedback (reappearance of the target), and two PA blocks with delayed target-feedback (reappearance of the target after 800 ms) after terminating reach (making contact with touchscreen). One block for each set of feedback conditions was performed with rightward displacing prism goggles, while the other was performed with leftward displacing prism goggles (this helped prevent gradual adaptation to prism exposure across numerous blocks). The order of PA blocks was randomized for each participant at the onset of the task, thus effects of learning across the entire experiment were counterbalanced across conditions. All PA blocks were immediately followed by a 10 trial block performed with clear glasses and reaching limb fully occluded from vision. These blocks, referred to as a proprioceptive-visual straight ahead (PVSA) test, measure size of errors in the opposite direction of the preceding prism shift and thus provide a magnitude of aftereffects following each PA block. Furthermore, each PVSA block was followed by a 60 trial “sham” block with clear glasses in order to de-adapt to the prisms for the next PA block. Importantly, sham blocks were only used to achieve de-adaptation and are thus not a major part of the results analysis.

As normally the case during PA paradigms, participants were expected to show large errors at the onset of PA blocks (direct-effects) that eventually reduced in magnitude towards baseline levels of accuracy. Based on the results from Kitazawa et al. (1995), it was predicted that participants would fail to reduce aiming errors in the delayed feedback blocks to the same degree as the immediate feedback block. No difference in aiming errors was predicted to result between leftward-shifted and rightward-shifted PA blocks. Also based on Kitazawa et al.’s (1995) results, it was predicted that participants would show larger errors during PVSA blocks (i.e. aftereffects) following immediate feedback PA blocks compared to delayed feedback PA blocks.

Using the event-related potential technique, EEG data were averaged according to three separate events: screen-touch with immediate target-feedback, screen-touch with delayed target-feedback, and target-feedback following a 800ms delay. These events are only reported for PA blocks. Event-related potentials are not reported for sham blocks. Based on the results from MacLean et al. (2015), the ERP analysis was designed to see if error-sensitive ERP components (ERN, Pe, FRN), and phase-sensitive components (e.g. P300) would be evoked differently in response to onset of immediate and delayed feedback. It was specifically hypothesized that both screen-touch with immediate target-feedback and target-feedback following a delay would evoke a FRN component, seeing as both conditions eventually provide equally clear reach-accuracy information based on an external stimuli (target). Thus, these results were hypothesized to differ from MacLean et al. (2015) where it was shown that an ERN component, reflecting internal error evaluation, was evoked at termination of reaching movement when the target was visible during the entire trial. The result from MacLean et al. (2015), showing that P300 amplitude reduced after the early phase of adaptation, irrespective of accuracy, raised the possibility that the P300 signals a neural process associated with engaging spatial realignment. Thus, it was hypothesized that if the immediate feedback condition does indeed produce larger aftereffects compared to the delayed feedback condition, then screen-touch with immediate target-feedback would evoke a P300 component more sensitive to phase (greater voltage change between phases) compared to the target-feedback after delay. Although no particular hypotheses were made regarding screen-touch with delayed target-feedback, we acknowledged the possibility that it could also evoke accuracy-sensitive and phase-sensitive components. If that were the case, it would reveal the value of visually perceiving the hand location irrespective of target presence during PA blocks. Finally, because the Pe response was only reported in Vocat et al. (2011), not MacLean et al (2015), it was predicted that this component would not be evoked in the present experiment seeing as the conditions more closely resembled MacLean et al (2015). In Vocat et al. (2011), ERPs were measured from onset of reaching movement (i.e. response-locked ERPs), whereas ERPs in MacLean et al. (2015), like the present study, were locked to screen-touch (termination of response). The observed Pe response in Vocat et al. (2011) might thus be specific to error processing that is triggered by erroneous *responses*, rather than error *feedback*.

2.2 Methods

2.2.1 Participants

The study recruited 20 young adult participants. Two participants were excluded from data analysis because of poor EEG data quality resulting in high artifact rejection (> 50%). Thus the results below reflect data from 18 participants (mean age = 19.5, SD = 1.7, 16 females, 3 left handed). All participants were students at Dalhousie University who voluntarily participated in the study for extra credit points going towards Psychology & Neuroscience classes. Participants provided informed consent consistent with the Nova Scotia Health Authority Research Ethics Board. All participants reported having normal or corrected-to-normal vision, no neurological illness, not being under any medications affecting cognitive performance, and not having any upper body impairment preventing reaching movements with their dominant arm.

2.2.2 Materials

Every participant was seated at an adjustable chair in front of a desk. A 28" touchscreen monitor (Intellitouch, USA) was located 48 cm from the edge of the desk and raised by 7 cm. A chinrest was locked to the edge of the desk to maintain participants' distance from the screen. The height of the chinrest was consistent across participants to keep their gaze in line with the centre of the monitor. Consequently, height of the chair was adjusted for each participant to achieve optimal comfort on the chinrest. A keyboard, used to record response onset, was placed 10 cm in front of the chinrest with the spacebar in line with the centre of the monitor. Speakers, used to emit a go-cue, were positioned directly to the left and right of the monitor. A black horizontal occlusion board (a flat piece of ¼ inch cardboard) extended from the chinrest (at chin height) to the monitor. The occlusion board blocked vision of the bottom third of the monitor and prevented vision of the reaching movement until the last 3 cm immediately before the monitor. For certain blocks of the experiment (see below), an extension was placed at the end of the occlusion board near the monitor to prevent any vision of limb during the reaching movement. For every block, participants wore a set of glasses. Glasses varied depending on the condition, but either had clear lenses, Fresnel prism lenses deviating towards the right, or Fresnel prism lenses deviating towards the left (Insight Optometry Group, Halifax NS). Both prism glasses induced a 30 diopter, or 17.7° visual shift.

2.2.3 Procedure and Design

The experiment was designed to compare the effects of immediate and delayed feedback during memory guided reaching on feedback-evoked brain potentials and subsequent aftereffects. Thus the experiment employed a within-subject design with feedback timing (immediate, delayed) as the main factor. Every participant underwent 4 blocks of prism adaptation. Two blocks provided immediate feedback on each trial, while the other 2 blocks provided delayed feedback on each trial. Furthermore, within each feedback condition, one of the two blocks was performed with leftward displacing prism glasses, and the other with rightward displacing prism glasses. Prism adaptation blocks consisted of 60 trials.

Participants were required to reach towards vertical line targets on a touchscreen monitor. Every PA trial was initiated when the participants pressed the spacebar with their dominant hand. They were instructed to hold the spacebar until cued to reach. A fixation-cross appeared for 400-600 ms at the centre of the screen after the spacebar was held of 500 ms. Immediately after offset of the fixation cross, a target appeared on the screen for 700-900 ms. The target consisted of a vertical black line that spanned the entire height of the monitor and was approximately 1.3 cm wide. On each trial during PA blocks, the target appeared randomly in 1 of 4 possible locations along the screen's horizontal axis. These locations were: (1) 5 cm to the left of the screen's centre, (2) 2.5 cm left of the screen's centre, (3) 2.5 cm right of the screen's centre, and (4) 5 cm right of the screen's centre. After target offset, the screen remained blank for 1000-1200 ms before the participants heard an auditory cue (1000 Hz, .05 ms, 30dB). Upon hearing the auditory cue, they were instructed to release the spacebar and, with the same arm, reach quickly and accurately to the remembered location of the target on the touchscreen. Participants reached below the occlusion board and were only able to see the tip of their finger at the very end of their reaching movement. Participants were instructed to maintain their movement velocity during the entire reach (i.e. not slow down in anticipation of seeing their finger), and to not make corrective movements at the end of their reach upon seeing their finger. Finally, they were also instructed to reach high enough to see their finger make contact with the screen when it passed the occlusion board (participants could have reached low enough to not get a sufficient visual angle to see their finger at all). When participants made contact with the screen, they were instructed to hold their finger where it landed until they saw the target reappear, then disappear again. After the target disappeared, the trial was complete and participants returned to the spacebar to initiate the next trial. During the immediate feedback condition, the target reappeared immediately upon contact being made with the screen. During the delayed feedback condition, the target reappeared 750-850 ms after contact was made with the screen. In both conditions, the target remained visible for 1000 ms before disappearing. It is noteworthy that "immediate" and "delayed" feedback are defined according to when the target becomes visible after the reach. As discussed in the introduction, other forms of feedback are available during/after the reach – particularly proprioceptive feedback and visual feedback of finger upon passing the occlusion board. Thus the feedback being manipulated in this experiment is referred to as "target-feedback". See Figure 2.1 for an illustration of a typical trial. The timing of events across each trial was chosen to provide ample gaps between onsets of each event (e.g. from target offset, to memory delay, to auditory cue). This timing would ensure ERPs did not significantly overlap between events. Although not reported in this thesis, the timing of events enables proper measurement of ERPs locked to any event of the trial (between fixation cross and target-feedback). Furthermore, variable timing of delayed target-feedback (750-850 ms) reduces the impact of anticipatory-related EEG activity leading up to onset of target-feedback. Finally, latencies that could vary between two values (e.g. 750-850 ms) were determined by random number generation between the two latencies in Matlab on a trial-by-trial basis.

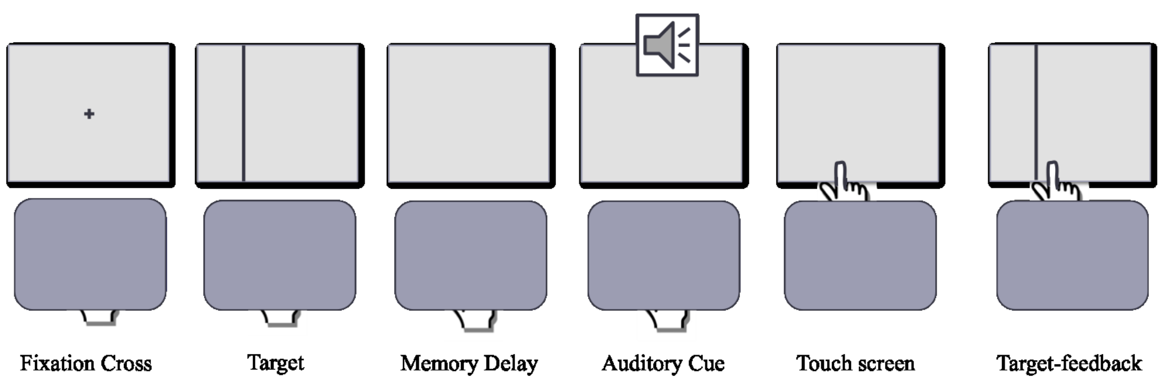

Figure 2.1 A typical PA trial (from left to right) with delayed target-feedback after touching the screen.

Every PA block was immediately followed by a block measuring the strength of aftereffect produced by the adaptation. These short blocks consisted of what is commonly referred to as a Proprioceptive Visual Straight Ahead (PVSA) test, or Total Straight Ahead (TSA) test. These blocks required participants to reach quickly and accurately to a vertical-line target on the touchscreen. The PVSA blocks, however, differed from the PA blocks in a few ways. First, PVSA blocks only had 10 trials and the vertical-line target always appeared at the centre of the screen. Second, the reaching movement was not memory guided – the participants could see the target during the entire reach. The auditory cue therefore sounded 700-900 ms after the target appeared (i.e. no additional 1000 ms delay period before reach). Third, an extension was added to the occlusion board to prevent any vision of arm/hand/finger during the entire reaching movement. This meant that participant had no visual feedback of how accurate their finger was to the target at the end of the reach. Finally, PVSA blocks were always completed with clear lenses. Mean error during PVSA blocks provided a measure of post-adaptation aftereffects.

After every PVSA block, participants performed a sham block in order to de-adapt to the prism exposure they just experienced. Sham blocks were always performed with clear lenses. ERP data collected during sham blocks are not reported in the thesis. Participants were again required to reach as quickly and accurately as possible to vertical-line targets that appeared randomly in one of four locations on a touchscreen. Every sham block had 60 trials and was performed with memory-guided reaching. An occlusion board allowed participants to see their finger at the very end of the reach. Unlike the PA blocks, however, the sham condition presented both immediate and delayed target feedback together in each block – randomized across trials. This randomization between immediate and delayed feedback ensured that the de-adaptation process was identical following both types of PA blocks (immediate, and delayed). Thus, as the experiment went on, any effect observed from different feedback conditions during PA could not be explained by differences in how the preceding de-adaptation occurred.

In addition to the four PA blocks followed by PVSA and sham blocks, participants also began every experiment with a baseline PVSA and a baseline sham block. Both of these blocks were identical to the PVSA and sham blocks described above, however they were not preceded by any prism adaptation. Thus, both baseline blocks provide a measure of participants' accuracy excluding any prism adaptation aftereffects. The entire experiment consisted of a total of 14 blocks (See Table 2.1). The order of PA blocks (right/delay, right/immediate, left/delay, left/immediate) was randomized for each participant.

Table 2.1 Sequence of blocks in Experiment 1.

Block	**Condition**	**Trials**
1	PVSA (BL)	10
2	Sham (BL)	60
3	Prism	60
4	PVSA	10
5	Sham	60
6	Prism	60
7	PVSA	10
8	Sham	60
9	Prism	60
10	PVSA	10
11	Sham	60
12	Prism	60
13	PVSA	10
14	Sham	60

2.2.4 Behavioural Data Collection and Analysis

On each trial, participants' reaction time (RT), movement time (MT), and error were recorded. RT was measured as the time (ms) between the auditory cue and participants' response onset (spacebar release). MT was measured as the time (ms) between response onset and contact with the touchscreen. Errors were measured in pixels and then converted to visual degrees. On each trial, error was recorded as the horizontal distance between the location of contact made on the screen and the location of the target. Distances to the left of the target were recorded as negative values; distances to the right of the target were recorded as positive values. To examine for the presence of outliers in the behavioural data, all data were converted to standardized scores within their respective conditions (e.g. prism-right, prism-left, baseline PVSA, etc.). Any absolute standardized score exceeding 2.5 was removed from further behavioural data analysis. Table A1 shows percentage of each participant's behavioural data that were removed prior to final analyses.

2.2.5 Measuring Adaptation and De-Adaptation

To determine the direction and magnitude of errors across trials in the prism, sham, and baseline sham conditions, we calculated the error-by-trial linear regression slope and intercept for each participant in the following conditions: prism-right, prism-left, sham(right), sham(left), and baseline sham. Sham(right) indicates a sham block that was preceded by a prism-right block, while sham(left) indicates a sham block that was preceded by a prism-left block. Here, immediate and delayed feedback conditions were collapsed together. Errors to the left of the target were plotted as negative value on the Y-axis, while errors to the right of the target were plotted as positive values on the Y-axis. Trial numbers (1-60) were plotted on the X-axis. These slopes and intercepts were separately submitted to a one-way repeated-measures ANOVA with “exposure” as the only factor: prism-right, prism-left, sham(right), sham(left), and baseline. This analysis would determine if prism blocks resulted in larger aiming errors at the onset of blocks (intercepts) and greater decreases in error size across trials (slope) compared to sham blocks and baseline. Furthermore, it would ensure that intercepts and slopes reflect the predicted direction of errors based on prism glasses (left, right) and their respective aftereffects. Thus, prism-right and sham-left conditions were predicted to show positive value intercepts and negative slopes, while prism-left and sham(right) conditions were expected to show negative value intercepts and positive slopes. Finally, slopes and intercepts in both prism and sham conditions were predicted to differ from the baseline condition.

2.2.6 Immediate vs. Delayed PA Feedback: Error, RT, MT

To determine if there were differences in aiming errors between immediate and delayed feedback conditions during prism exposure, we submitted absolute error-by-trial slopes and intercepts to paired sample *t*-tests comparing immediate target-feedback and delayed target-feedback. Here, prism-right and prism-left were collapsed together.

In addition to this, prism exposure blocks were divided into 6 phases of adaptation: trial 1-10, 11-20, 21-30, 31-40, 41-50, 51-60. Differences across these bins could thus be contrasted to difference between bins of phases used to measure ERPs (described below). Absolute errors were then submitted to a 2 x 6 repeated-measure ANOVA with the following factors: feedback (immediate, delayed) and phase (1-6). MT and RT were also separately submitted to a 2 x 6 repeated-measure ANOVA with the following factors: feedback (immediate, delayed) and phase (1-6).

2.2.7 Immediate vs. Delayed PA Feedback: Aftereffects

Finally, in order to compare magnitude of aftereffects produced by both feedback conditions, absolute PVSA errors for each participant were submitted to a 2x2 repeated-measures ANOVA with the following factors: feedback (immediate, delayed) and direction of preceding PA displacement (prism-right, prism-left). Prior to running the ANOVA, however, PVSA error scores were "corrected" by subtracting each participant's mean baseline PVSA error. It was thus predicted that the "direction" factor would yield no effect on mean PVSA error, as any baseline bias towards right or left would be eliminated.

2.2.8 Electroencephalography Data Collection

EEG data were collected from 64 electrodes in a standard 10-20 layout, using Brain Vision PyCorder (Brain Products, Germany). The EEG was recorded with an average reference, sampled at 500 Hz, amplified (ActiCHamp, Brain Products, Germany), and filtered online through an 8 kHz anti-aliasing filter. Impedance at each electrode was kept below 20KΩ. The experiment was designed in Matlab (Mathworks, 2014) using the Psychophysics toolbox extension (Brainard, 1997).

2.2.9 Electroencephalography Data Analysis

Each participant's EEG data were processed offline in several steps using the EEGLAB toolbox (Delorme & Makeig, 2004) and its extension ERPLAB (Lopez-Calderon & Luck, 2014). First, raw EEG data were visually inspected and channels showing abnormal activity (e.g. dead, noisy, frequent large artifacts) were removed. Next, data were filtered (IIR Butterworth) using a high-pass of 0.1 Hz, a low-pass of 30 Hz, and a 24 dB/oct roll-off. All data were then re-referenced to the average of the two mastoid channels, after which the mastoid channels were removed from the data. The EEG data were then segmented into 1100 ms epochs surrounding the experiment event markers (300 ms pre, 800 ms post). While a number of events were marked in each trial (e.g. auditory cue, response onset, etc.) only those pertaining to feedback are reported here. Following segmentation, any channel that had a mean voltage 5 or more standard deviations from the joint probability of all channels was removed. Furthermore, any epoch showing mean voltage 6 or more standard deviation from either the within-channel mean, or across-channel mean for that epoch was also removed. The remaining data were submitted to an Independent Component Analysis using the runica function in EEGLAB. Components reflecting ocular artifacts (e.g. blinks, saccades) were removed from the data. Then, an artifact rejection was performed on the data such that any epoch involving a change in voltage that exceeded 100μV, or any sample-to-sample voltage change exceeding 10μV was removed from the data. Finally, removed channels were interpolated and segments were averaged together based on events of interest. Table A1 shows percentage of each participant's ERP data that were removed prior to final analyses.

2.2.10 Comparing Feedback-Evoked Brain Potentials

An ERP analysis was conducted separately on the 3 feedback events that participants experienced during prism exposure blocks: (1) screen-touch with immediate target-feedback, (2) screen-touch with delayed target-feedback, and (3) target-feedback following delay. The latter two feedback events occur within the same trial, one before the other. The ERP analysis does not compare grand average differences between each event. Each event is inherently different, thus some differences are naturally expected due to, for example, the appearance of a target that causes a visual-evoked potential in one condition, but not in another condition when the target is absent. Rather, the analysis focuses on differences within each event that are evoked by two factors: phase (1-6) and accuracy (hit, small miss, big miss). Differences in respect to those two factors *between* feedback events are addressed in the discussion section.

Each feedback event was analyzed separately per accuracy and phase. Differences between levels of accuracy would determine whether participants evoked an FRN component, whereas differences between levels of phase would determine if participants evoked a parietal P300 component. All analyses began with visual inspection of waveforms. Specifically, ERPs were first averaged according to the three levels of accuracy: hit, small miss, and big miss. Hits encompassed any trial in which the participant's screen-touch was within the target's 1.3cm width. Small misses encompassed any screen-touch recorded within 2.6cm of the target's edge on either side. Finally, big misses encompass any trial in which screen-touch was recorded beyond 2.6cm of the target's edge on either side. Thus, accuracy levels were determined by doubling the size of the target width. Percentage of hits, small misses, and big misses across each phase of both feedback conditions is shown in Figure A19. Grouping accuracy according to three levels (hits, small misses, big misses) enables measurement of the FRN, typically measures by comparing hit-waveforms to miss-waveforms, but additionally enables us to determine if error-sensitive components during PA scale to size or error. A difference-waveform was calculated by subtracting hit-data from all miss-data. Voltage was plotted on the Y-axis, while time was plotted on the X-axis. This difference waveform was also displayed in a series of panels corresponding to each electrode. At each time-point of the difference wave, 95% CIs were calculated to reveal if any time-points significantly differed from zero. Specifically, any 95% CI that did not cross zero on the Y-axis would be considered significantly different than zero. This technique would thus reveal a significant difference between levels of accuracy at time ranges corresponding to the 95% CIs that did not cross the zero on the Y-axis. Visual inspection of these panels yielded (1) electrode sites displaying maximal differences between levels of accuracy and (2) time-windows corresponding to the maximal differences between levels of accuracy. Particular attention was paid to electrode FCz in time range of 50-100 ms post-feedback, and 250-300 ms post-feedback, as these latencies and electrode site are respectively consistent with the ERN and FRN components. Nevertheless, all difference waves were inspected for differences revealed by 95% CIs. The differences between levels of accuracy identified by 95% CIs with difference waveforms were further tested by measuring the mean voltage +/- 50ms surrounding the peak of the identified difference (at respective electrode sites) for each level of accuracy for each participant. These averages were submitted to a one-way repeated measures ANOVA with accuracy as the only factor: hit, small miss, big miss.

A similar procedure was conducted for the analysis of phase. Here, however, ERPs were averaged according to the six levels of phase (trials 1-10, 11-20, 21-30, 31-40, 41-50, 51-60). Thus, six waveforms belonging to each phase were displayed in a series of panels corresponding to each electrode. A difference-waveform was calculated by subtracting P6-data from P1-data. This difference-waveform was also displayed in a series of panels corresponding to each electrode, and was surmised to show the maximal difference between early trials and late trials of PA. At each time-point of the difference wave, 95% CIs were also calculated to reveal if any time-points significantly differed from zero. Specifically, any 95% CI that did not cross zero on the Y-axis would be considered significantly different than zero. This technique would thus reveal a significant difference between levels of phase at time ranges corresponding to the 95% CIs that did not cross the zero on the Y-axis. Visual inspection of these panels yielded (1) electrodes displaying maximal differences between levels of phase and (2) latencies corresponding to maximal differences between phases. Particular attention was paid to electrode Pz in time range of 250-400 ms post-feedback, as this latency and electrode site is consistent with the P300 component. As with accuracy, the mean voltage +/- 50ms surrounding the peak difference identified with 95% CIs (at respective electrodes) was calculated for each level of phase for each participant. These averages were submitted to a one-way repeated measures ANOVA with phase as the only factor: P1-P6.

There are some rare exceptions to the +/- 50ms mean that are made apparent in the results section (i.e. some time windows are more narrow/wide). When a repeated-measures ANOVA revealed a significant effect of either accuracy or phase, pairwise comparison between each level were completed using the Bonferroni adjustment. The ERP component means submitted to the ANOVAs for accuracy and phase were also submitted to a contrast analysis to determine if mean voltage showed a linear trend in respect to either factor. This would help determine if voltage decreases/increases with improvement in accuracy, and if voltage decreases/increases from early to late phases. Finally, Greenhouse-Geisser corrected degrees of freedom were used in reporting all statistical test that did not meet the assumption of sphericity using Mauchly's test ($p < .001$). Difference waves with 95% CIs used to determine differences between levels of accuracy and phase are shown in the Appendix section.

2.3 Results

2.3.1 Adaptation and De-Adaptation: Slopes and Intercepts

The analysis revealed a significant effect of exposure condition on slope, $F(2.1, 36.5) = 107.9$, $p < .001$, ${}_{p}\eta^2 = .86$. Figure 2.2 illustrates the relationship between trial number and error for each exposure condition. Table 2.2 shows mean slope scores, SE, and 95% CI for each condition. Bonferroni-adjusted pairwise comparisons revealed that the slopes of all conditions significantly differed from each other ($p < .05$). The analysis also revealed a significant effect of exposure on intercepts, $F(1.8, 31.1) = 178.4$, $p < .001$, ${}_{p}\eta^2 = .91$. Table 2.3 shows the mean intercept, SE, and 95% CI for each exposure condition. Bonferroni-adjusted pairwise comparisons revealed that intercepts in all conditions also significantly differed from each other ($p < .05$).

A two-way ANOVA comparing absolute slope scores between prism-right, prism-left, sham(right), and sham(left) revealed an effect of exposure (prism vs. sham) on absolute slope, $F(1, 17) = 56.9$, $p < .001$, ${}_{p}\eta^2 = .77$, such that prism slopes were larger than sham slopes. The analysis revealed no effect of direction (left vs. right) on absolute slopes, $F(1, 17) = 1.15$, $p = .3$, ${}_{p}\eta^2 = .06$, and no interaction effect, $F(1, 17) = 1.12$, $p = .3$, ${}_{p}\eta^2 = .06$. A two-way ANOVA comparing absolute intercept scores between prism-right, prism-left, sham(right), and sham(left) revealed an effect of exposure (prism vs. sham) on absolute intercepts, $F(1, 17) = 106.9$, $p < .001$, ${}_{p}\eta^2 = .86$, such that prism intercepts were larger than sham intercepts. The analysis revealed no effect of direction (left vs. right) on absolute intercepts, $F(1, 17) = 1.82$, $p = .2$, ${}_{p}\eta^2 = .09$, and no interaction effect, $F(1, 17) = 0.23$, $p = .6$, ${}_{p}\eta^2 = .01$..

In summary, the prism-right condition resulted in a negative slope, reflecting the reduction of large positive-value (right) errors across trials. The prism-left condition resulted in a positive slope, reflecting the reduction of large negative-value (left) errors across trials. The sham(right) condition produced a positive slope, reflecting reduction in negative-value (left) errors across trial due to the aftereffect produced by the prism-right block. Similarly, the sham(left) condition produced a negative slope, reflecting the reduction of positive-value (right) errors across trial due to the aftereffect produced by the prism-left block. The Sham conditions produced smaller slopes and intercepts compared to prism conditions, reflecting the reduction of smaller errors across trials in the Sham block. Baseline slope and intercept were smaller than both prism and sham conditions.

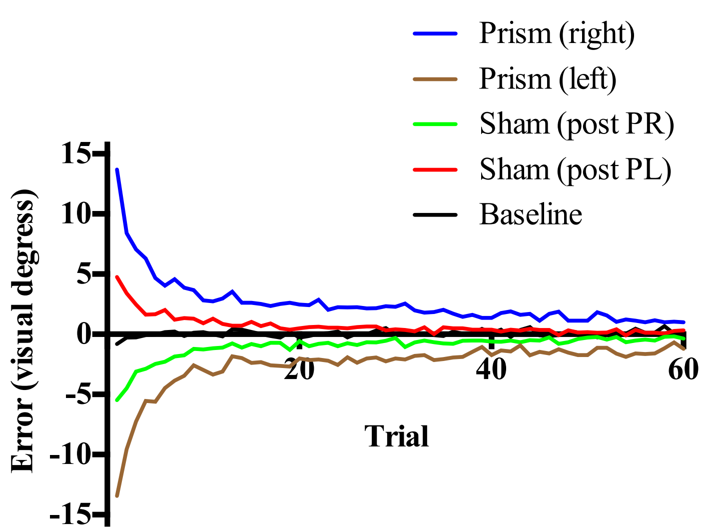

Figure 2.2 Mean error size in visual degrees across all trials, averaged according to Prism (left, right), Sham (left, right), and Baseline sham conditions.

Table 2.2 Error-by-trial linear regression slopes for prism, sham, and baseline exposure conditions.

Condition	**Slope**	**SE**	**95% CI**
Baseline	.004	0.002	0.0003, 0.008

Prism right	-.083	0.007	-0.098, -0.067
Prism left	.082	0.008	0.065, 0.099
Sham (right)	.043	0.006	0.03, 0.056
Sham (left)	-.033	0.003	-0.039, -0.026

Table 2.3 Error-by-trial linear regression intercepts for prism, sham, and baseline exposure conditions.

Condition	**Intercept**	**SE**	**95% CI**
Baseline	-0.07	0.09	-0.27, 0.13
Prism right	5.09	0.39	4.27, 5.90
Prism left	-4.88	0.42	-5.77, -3.98
Sham (right)	-2.15	0.13	-2.43, -1.87
Sham (left)	1.70	0.14	1.41, 1.99

2.3.2 Immediate vs. Delayed PA Feedback: Error

The analysis of absolute error-by-trial linear regression slopes revealed a difference between immediate and delayed feedback conditions (mean difference: .023, SE = .007), $t(17) = 4.07$, $p < .005$, Cohen's $d_{rm} = .84$. Specifically, the immediate feedback condition had a larger slope (mean = -.087, SE = .007) than the delayed feedback conditions (mean = -.064, SE = .006). The relationship between trial and absolute error for both conditions is illustrated in Figure 2.3. The analysis of absolute error-by-trial linear regression intercepts also revealed a difference between immediate and delayed feedback conditions (mean difference: 1.41, SE = 0.23), $t(17) = 6.08$, $p < .001$, Cohen's $d_{rm} = 1.02$. Specifically, the immediate feedback condition had a larger intercept (mean = 5.84, SE = 0.34) than the delayed feedback conditions (mean = 4.43, SE = 0.3).

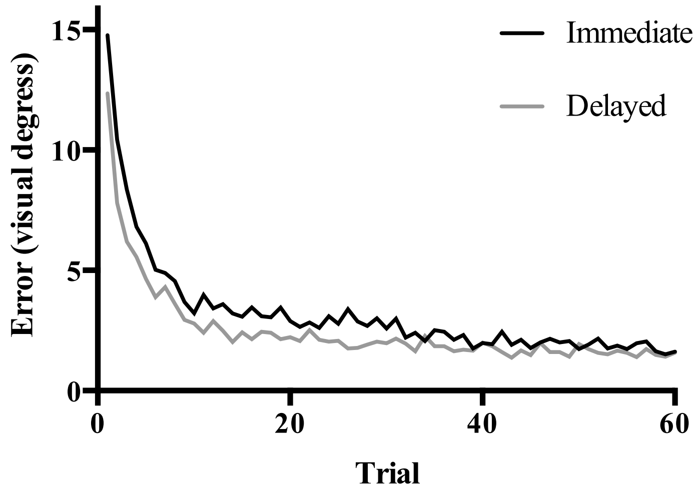

Figure 2.3 Mean error across trials for the immediate and delayed feedback conditions.

Absolute errors submitted to a 2x6 repeated-measures ANOVA with feedback (immediate, delayed) and phase (1-6) as factors revealed a significant effect of phase on error size, $F(1.6, 27.9) = 154.2$, $p < .001$, ${}_p\eta^2 = .9$, such that error size decreased from early to late phase. Post-hoc comparisons revealed that mean error was different across all phases except between P5 and P6 ($p < .05$). The analysis also revealed a significant effect of feedback condition on error size, $F(1, 17) = 46.1$, $p < .001$, ${}_p\eta^2 = .73$, such that mean error across phases was larger in the Immediate feedback condition compared to the Delayed feedback condition. Finally, the analysis also revealed an interaction between phase and feedback condition, $F(2.6, 44.4) = 6.7$, $p = .001$, ${}_p\eta^2 = .28$. Table 2.4 shows means, SEs, and 95% CIs for errors across each phase and feedback condition. Figure 2.4 illustrates the interaction effect in a bar graph and indicates pairwise differences.

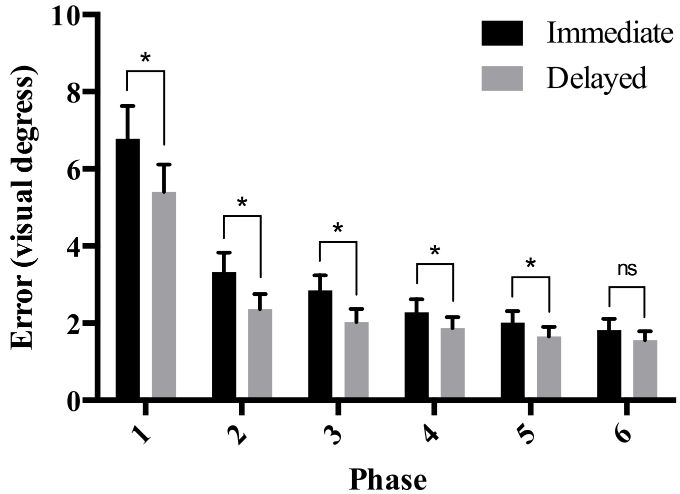

Figure 2.4 Mean error size across phases for immediate and delayed target-feedback PA blocks. Error bars indicate standard error. Asterisks (*) indicates a significant pairwise difference ($p < .05$), "ns" indicates no significant pairwise difference ($p > .05$).

Table 2.4 Absolute errors in each phase of both PA feedback conditions.

Feedback	Phase	Mean	SE	95% CI
Immediate	1	6.78	0.40	5.94, 7.63
	2	3.32	0.24	2.81, 3.83
	3	2.85	0.19	2.46, 3.20
	4	2.28	0.16	1.93, 2.62
	5	2.01	0.14	1.71, 2.31
	6	1.82	0.13	1.53, 2.11
Delayed	1	5.41	0.34	4.70, 6.12
	2	2.36	0.19	1.96, 2.76
	3	2.02	0.16	1.68, 2.37
	4	1.87	0.13	1.59, 2.15
	5	1.65	0.12	1.40, 1.91
	6	1.56	0.11	1.34, 1.78

2.3.3 Immediate vs. Delayed PA Feedback: RT

A 2x6 repeated-measures ANOVA with feedback (immediate, delayed) and phase (1-6) as factors revealed no effect of phase on RT, $F(5, 85) = 1.2$, $p = .32$, ${}_p\eta^2 = .06$, no effect of feedback on RT, $F(1, 17) = 0.2$, $p = .91$, ${}_p\eta^2 = .001$, and no interaction between the two factors, F(5, 85) = 1.5, p = .24, $_p\eta^2$ = .08. Table 2.5 shows RT means, standard errors, and 95% confidence intervals across phase and feedback conditions.

Table 2.5 Reaction time in each phase of both PA feedback conditions.

Feedback	Phase	Mean (ms)	SE (ms)	95% CI (ms)
Immediate	1	666	008	650, 682
	2	659	004	652, 667
	3	675	017	640, 711
	4	654	003	649, 660
	5	668	010	648, 689
	6	655	002	650, 660
Delayed	1	658	003	650, 665
	2	660	005	649, 672
	3	662	006	650, 674
	4	695	033	624, 765
	5	665	007	651, 678
	6	653	002	649, 658

2.3.4 Immediate vs. Delayed PA Feedback: MT

A 2x6 repeated-measures ANOVA with feedback (immediate, delayed) and phase (1-6) as factors revealed a main effect of feedback on MT, F(1, 17) = 4.7, $p < .05$, $_p\eta^2$ = .22. The delayed feedback condition produced longer MTs (mean = 205ms, SE = .016ms) compared to the immediate feedback condition (mean = 181 ms, SE = .018ms). There was no effect of phase on MT, F(5, 85) = 1.5, p = .18, $_p\eta^2$ = .08, nor any interaction between factors F(5, 85) = 1.6, p = .16, $_p\eta^2$ = .09. Table 2.6 shows mean MTs, standard errors, and 95% confidence intervals across phase and feedback conditions.

Table 2.6 Movement time in each phase of both PA feedback conditions.

Feedback	Phase	Mean (ms)	SE (ms)	95% CI (ms)
Immediate	1	175ms	020ms	132ms, 218ms
	2	195ms	020ms	153ms, 237ms

	3	188ms	017ms	153ms, 223ms
	4	176ms	021ms	131ms, 221ms
	5	183ms	020ms	140ms, 226ms
	6	168ms	019ms	128ms, 208ms
Delayed	1	187ms	017ms	151ms, 223ms
	2	206ms	018ms	169ms, 244ms
	3	206ms	016ms	173ms, 239ms
	4	207ms	017ms	171ms, 244ms
	5	207ms	017ms	171ms, 244ms
	6	213ms	017ms	178ms, 249ms

2.3.5 Immediate vs. Delayed PA Feedback: Aftereffects

A 2x2 repeated-measures ANOVA with preceding prism direction (prism-left, prism-right) and preceding prism feedback (immediate, delayed) as factors revealed no effect of prism direction, $F(1, 17) = 1.2$, $p = .3$, ${}_{p}\eta^2 = .06$, no effect of feedback, $F(1, 17) = 2.7$, $p = .11$, ${}_{p}\eta^2 = .14$, and no interaction effect, $F(1, 17) = 1.5$, = $p = .27$, ${}_{p}\eta^2 = .08$, on size of aftereffects. Means, standard errors, and 95% confidence intervals are presented in Table 2.7.

Table 2.7 PVSA errors produce by both PA feedback conditions and their respective direction of prism shift

Feedback	**Prism Direction**	**Mean**	**SE**	**95% CI**
Immediate	Right	5.52	0.40	4.68 , 6.35
	Left	5.23	0.48	4.22 , 6.24
Delayed	Right	5.34	0.35	4.60 , 6.08
	Left	6.22	0.30	5.59 , 6.85

2.3.6 PA ERPs: Screen-Touch with Immediate Target-Feedback

The event of touching the screen with immediate target feedback yielded one ERP component sensitive to accuracy (Figure 2.5), and two ERP components sensitive to phase (Figure 2.6).

2.3.6.1 Accuracy-Sensitive ERP component

Mean voltage 270-370 ms post-touch at electrode FCz was sensitive to accuracy, $F(2,34) = 16.56$, $p < .001$, $\eta p2 = .49$ (Figure 2.5). Means, SE, and 95% CI corresponding to each level of accuracy are presented in Table 2.8. Bonferroni-adjusted post hoc comparisons revealed that Small Misses and Big Misses both had more negative amplitudes than Hits ($p < .05$). Furthermore, a contrasts analysis revealed a linear trend across levels of accuracy $F(1,17) = 14.72$, $p = .001$, ${}_{p}\eta^2 = .46$. This effect, however, was likely mainly driven by the difference between hit and both small/big misses, seeing as small misses actually has a more negative voltage than big misses. These results suggest an FRN was evoked on miss trials during the immediate feedback condition.

Table 2.8 Accuracy-sensitive negative-going ERP component. Evoked by screen-touch with immediate target-feedback. Amplitude measured at FCz, 270-370ms post-touch for each level of accuracy

Feedback	**Error**	**Mean** (μV)	**SE** (μV)	**95% CI** (μV)
	Hit	11.1	1.7	7.6, 14.7
Immediate	Small Miss	6.7	1.6	3.4, 10.1
	Big Miss	7.1	1.4	4.1, 10.1

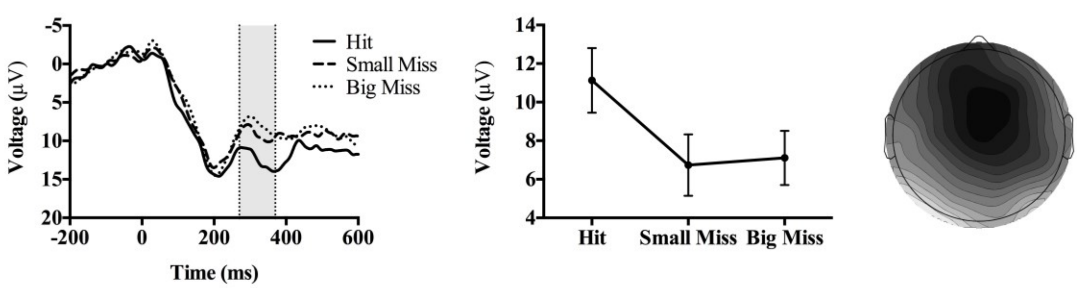

Figure 2.5 **Left**: average waveforms at FCz corresponding to each level of accuracy evoked by screen-touch with immediate feedback. The gray window corresponds to the time-window used to calculate mean difference between levels of accuracy. **Centre**: mean voltage 270-370ms at FCz corresponding to each level of accuracy. Error bars represent standard error of the mean. **Right**: scalp topography derived by subtracting hits

from all misses and corresponding to maximal difference. Darker tone indicates negative-going voltage.

2.3.6.2 Phase-Sensitive ERP component (1)

Mean voltage 180-280 ms post-touch at electrode Cz was sensitive to phase, $F(5,85) = 3.67$, $p = .005$, $\eta p2 = .18$. Means, SE, and 95% CI corresponding to each level of phase are presented in Table 2.9. Bonferroni-adjusted post hoc comparisons revealed that P1 had a more positive amplitude than P3 and P4 ($p < .05$). A contrast analysis revealed a significant linear trend across levels of phase, suggesting that positive voltage decreased from P1 to P6, $F(1,17) = 6.54$, $p < .05$, ${}_p\eta^2 = .28$. These results suggest that an early, centro-maximal component was largest during early trials and diminished in voltage during subsequent trials. The timing and scalp distribution of the component may be suggestive of a P3a component, but the timing would also suggest that it is a P2 component that is sensitive to phase in this condition. The top panel in Figure 2.6 corresponds to these results.

Table 2.9 First phase-sensitive positive-going ERP component. Evoked by screen-touch with immediate target-feedback. Amplitude measured at Cz, 180-280ms post-touch for each phase of adaptation

Feedback	**Phase**	**Mean (μV)**	**SE (μV)**	**95% CI (μV)**
Immediate	1	15.5	1.7	12, 19
	2	13.3	1.6	10, 16.6
	3	12.5	1.5	9.4, 15.7
	4	12.8	1.8	9.1, 16.6
	5	12.8	1.5	9.6, 16
	6	12.2	1.7	8.6, 15.7

2.3.6.3 Phase-Sensitive ERP component (2)

Mean voltage 270-370 ms post-touch at electrode Oz was sensitive to phase as well, $F(5,85) = 2.90$, $p = .05$, $\eta p2 = .15$. Means, SE, and 95% CI corresponding to each level of phase are presented in Table 2.10. Bonferroni-adjusted post hoc comparisons did not reveal any significant differences between phases. A contrasts analysis between each level of phase approached significance, $F(1,17) = 4.10$, $p = .06$, $\eta p2 = .19$, providing some evidence of a linear trend across each level of phase such that positive amplitude decreased from P1 to P6. The bottom panel in Figure 2.6 corresponds to these results. While the effect only approached significance, the result is suggestive that a occipital component is sensitive to phase. While the component appears too parietal to be a traditional P300, it does indeed share similar latency to a typical parietal P300.

Table 2.10 Second phase-sensitive positive-going ERP component. Evoked by screen-touch with immediate target-feedback. Amplitude measured at Oz, 270-370ms post-touch for each phase of adaptation

Feedback	**Phase**	**Mean (μV)**	**SE (μV)**	**95% CI (μV)**
Immediate	1	10.0	1.1	7.7, 12.3
	2	7.9	0.8	6.3, 9.6
	3	8.0	0.9	6.1, 9.9
	4	7.4	1.2	4.9, 9.8
	5	6.7	1.1	4.5, 9
	6	7.4	1.4	4.5, 10.3

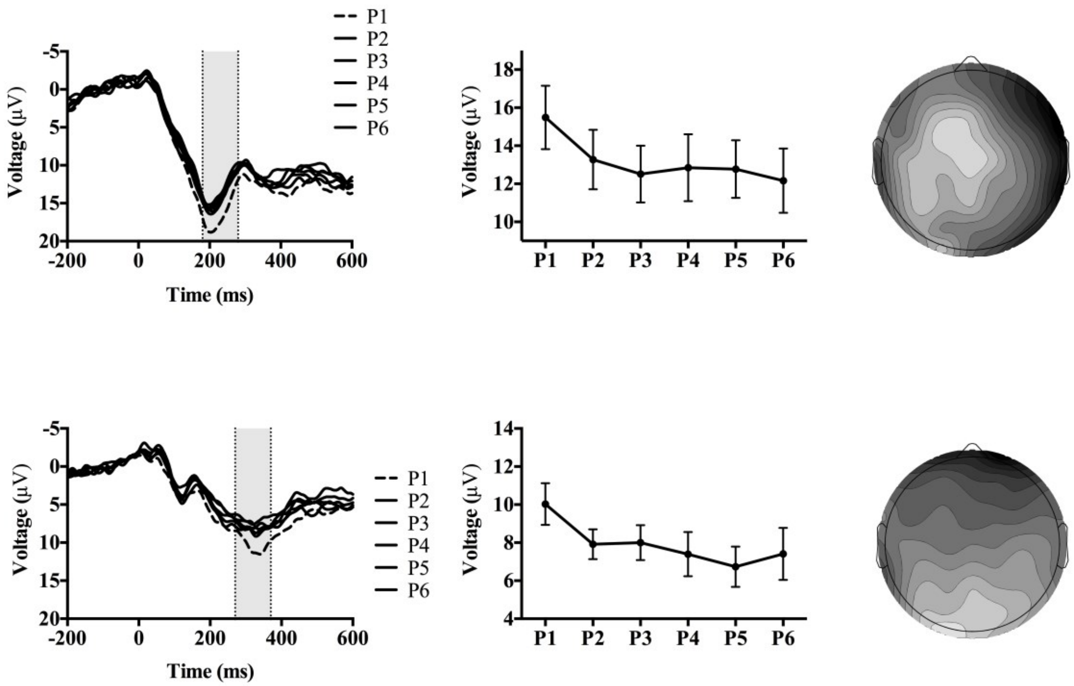

Figure 2.6 **Top Left**: average waveforms at Cz corresponding to each level of phase evoked by screen-touch with immediate feedback. The gray window corresponds to the time-window used to calculate mean difference between levels of phase. **Top Centre**: mean voltage 180-280ms at Cz corresponding to each levels of phase. Error bars represent standard error of the mean. **Top Right**: scalp topography derived by subtracting P6 data from P1 data and corresponding to maximal difference 180-280ms. Lighter tone indicates positive-going voltage. **Bottom Left**: average waveforms at Oz corresponding to each level of phase evoked by screen-touch with immediate feedback. The gray window corresponds to the time-window used to calculate mean difference between levels of phase. **Bottom Centre**: mean voltage 270-370ms at Oz corresponding to each levels of phase. Error bars represent standard error of the mean. **Bottom Right**: scalp topography derived by subtracting P6 data from P1 data and corresponding to maximal difference 270-370ms. Lighter tone indicates positive-going voltage.

2.3.7 PA ERPs: Screen-Touch with Delayed Target-Feedback

The event of touching the screen with delayed target-feedback yielded three ERP components sensitive to accuracy (Figure 2.7), and one ERP component sensitive to phase (Figure 2.8).

2.3.7.1 Accuracy-Sensitive ERP component (1)

Resembling results from Maclean et al. (2015), mean voltage 30-130 ms post-touch at electrode FCz was sensitive to accuracy, $F(2,34) = 12.84$, $p < .001$, $\eta p2 = .43$ (top panel of Figure 2.7). Means, SE, and 95% CI corresponding to each level of accuracy are presented in Table 2.11. Bonferroni-adjusted post hoc comparisons revealed that hits differed from both small and big misses ($p < .05$), but that small and big misses only differed from each other at $p < .06$. Furthermore, a contrasts analysis revealed a linear trend across levels of accuracy, $F(1,17) = 18.95$, $p < .001$, $\eta p2 = .53$. Together, the results lend some evidence that amplitude became more negative as error size increased. These results suggest that an early ERN component was evoked by screen-touch without immediate target-feedback when participants missed the target.

Table 2.11 First accuracy-sensitive negative-going ERP component. Evoked by screen- touch with delayed target-feedback. Amplitude measured at FCz, 30-130ms post-touch for each level of accuracy.

Feedback	**Error**	**Mean (μV)**	**SE (μV)**	**95% CI (μV)**
Delayed	Hit	3.3	1.2	0.8, 5.8
	Small Miss	1.5	1.1	-0.8, 3.9
	Big Miss	0.5	0.9	-1.4, 2.3

2.3.7.2 Accuracy-Sensitive ERP component (2)

Mean voltage 150-250 ms post-touch at electrode Cz was also sensitive to accuracy, $F(2,34) = 3.54$, $p < .05$, $\eta p2 = .17$ (middle panel of Figure 2.7). Means, SE, and 95% CI corresponding to each level of accuracy are presented in Table 2.12. Bonferroni-adjusted post hoc comparisons did not reveal any significant differences between levels of accuracy. However, a contrasts analysis revealed a linear trend across each level of accuracy, suggesting amplitude became more positive as error size increased, $F(1,17) = 5.10$, $p < .05$, $\eta p2 = .23$. Although the results were only moderately significant, they lend some evidence that a centro-maximal component, subsequent to the ERN, was evoked on large miss trials by screen-touch without immediate target-feedback. The effect may thus reflect a Pe component, or, similar to that reported above, a component in the P2 time-range.

Table 2.12 Second accuracy-sensitive positive-going ERP component. Evoked by screen- touch with delayed target-feedback. Amplitude measured at Cz, 150-250ms post-touch for each level of accuracy.

Feedback	**Error**	**Mean (μV)**	**SE (μV)**	**95% CI (μV)**
Delayed	Hit	8.8	1.2	6.1, 11.4
	Small Miss	8.9	1.3	6.1, 11.7
	Big Miss	10.3	1.4	7.4, 13.3

2.3.7.3 Accuracy-Sensitive ERP component (3)

Finally, mean voltage 240-340 ms post-touch at electrode POz was also sensitive to accuracy, $F(2,34) = 15.13$, $p < .001$, $\eta p2 = .47$ (bottom panel of Figure 2.7). Means, SE, and 95% CI corresponding to each level of accuracy are presented in Table 2.13. Bonferroni-adjusted post hoc comparisons revealed a significant difference between big misses and both hits and small misses ($p < .05$). A contrasts analysis revealed a linear trend across levels of accuracy, $F(1,17) = 19.95$, $p < .001$, $\eta p2 = .54$, providing some evidence that amplitude became more positive as error size increased, although the effect might be primarily driven by the difference between big misses and both hits/small misses. Together, the results suggest a later parieto-occipital component was also evoked on large miss trials by screen-touch without immediate target-feedback. The component may thus reflect a second Pe-like component sensitive to errors, but may also reflect a P300-, or P3a-like component given its timing – albeit slightly more occipital than normally reported.

Table 2.13 Third accuracy-sensitive, positive-going ERP component. Evoked by screen- touch with delayed target-feedback. Amplitude measured at POz, 240-340ms post-touch for each level of accuracy.

Feedback	Error	Mean (μV)	SE (μV)	95% CI (μV)
	Hit	4.1	1.3	1.2, 6.9
Delayed	Small Miss	4.9	1.1	2.5, 7.3
	Big Miss	7.7	1.1	5.3, 10.1

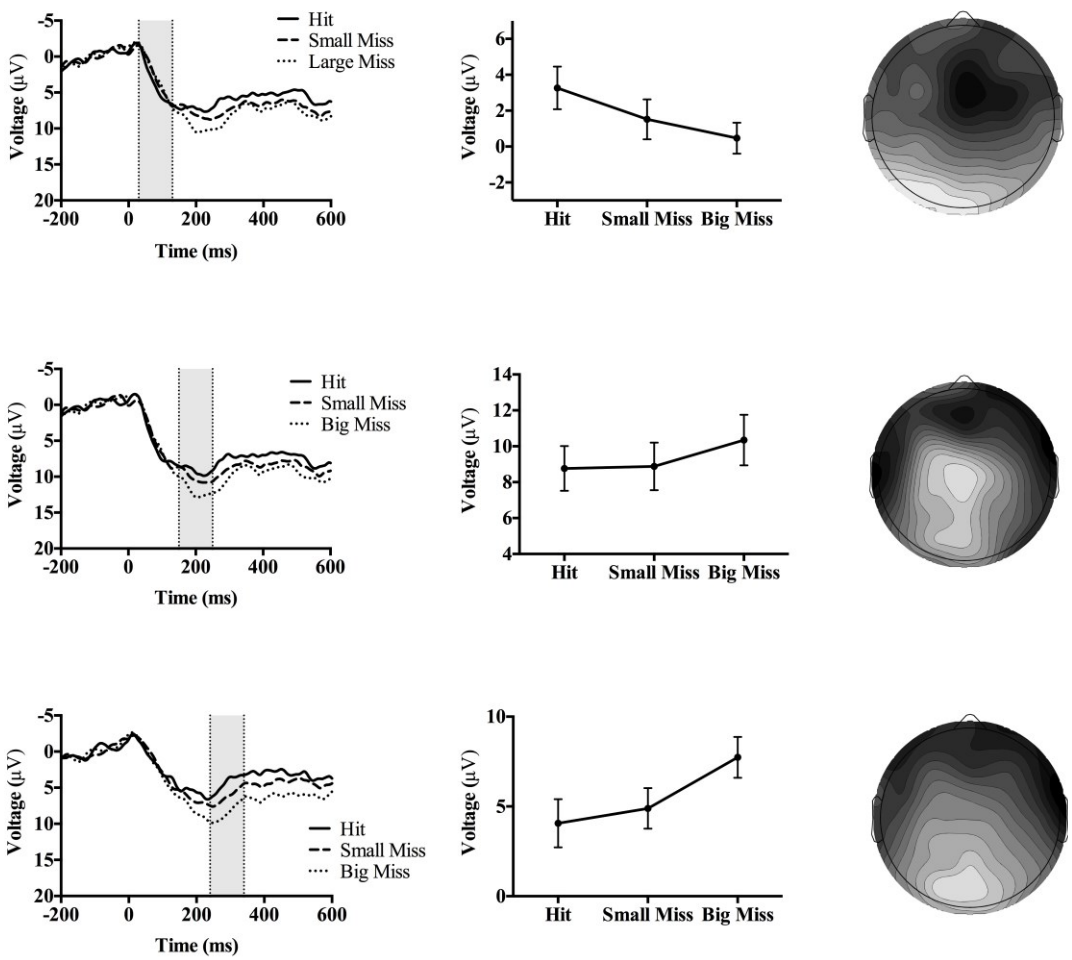

Figure 2.7 **Top Left**: average waveforms at FCz corresponding to each level of accuracy evoked by screen-touch with delayed feedback. The gray window corresponds to the time-window used to calculate mean difference between levels of accuracy. **Top Centre**: mean voltage 30-130ms at FCz corresponding to each levels of accuracy. Error bars represent standard error of the mean. **Top Right**: scalp topography

derived by subtracting hit data from all miss data and corresponding to maximal difference 30-130ms. Darker tone indicates negative-going voltage. **Middle Left**: average waveforms at Cz corresponding to each level of accuracy evoked by screen-touch with delayed feedback. The gray window corresponds to the time-window used to calculate mean difference between levels of accuracy. **Middle Centre**: mean voltage 150-250ms at Cz corresponding to each levels of accuracy. Error bars represent standard error of the mean. **Middle Right**: scalp topography derived by subtracting hit data from all miss data and corresponding to maximal difference 150-250ms. Lighter tone indicates positive-going voltage. **Bottom Left**: average waveforms at POz corresponding to each level of accuracy evoked by screen-touch with delayed feedback. The gray window corresponds to the time-window used to calculate mean difference between levels of accuracy. **Bottom Centre**: mean voltage 240-340ms at POz corresponding to each levels of accuracy. Error bars represent standard error of the mean. **Bottom Right**: scalp topography derived by subtracting hit data from all miss data and corresponding to maximal difference 240-340ms. Lighter tone indicates positive-going voltage.

2.3.7.4 Phase-Sensitive ERP component

In addition to sensitivity to accuracy, mean voltage 200-300 ms post-touch at electrode POz was sensitive to phase, $F(5,85) = 5.98$, $p = .001$, $\eta p2 = .26$ (Figure 2.8). Means, SE, and 95% CI corresponding to each level of accuracy are presented in Table 2.14. Bonferroni-adjusted post hoc comparisons revealed P1 differed from P3-P6 ($p < .05$), however there was no difference between P1 and P2. A contrasts analysis revealed a linear trend across levels of phase, suggesting voltage became less positive from P1 to P6, 12.71, $p = .002$, $\eta p2 = .43$. These results suggest an occipital component that diminished in voltage from early to late trials was evoked by screen-touch without immediate feedback. The timing of the component may suggest it reflects a P300, albeit far more occipital than normally reported.

Table 2.14 Phase-sensitive positive-going ERP component. Evoked by screen-touch with delayed target-feedback. Amplitude measured at POz, 200-300ms post-touch for each phase of adaptation.

Feedback	Phase	Mean (μV)	SE (μV)	95% CI (μV)
Delayed	1	9.8	1.3	7.2, 12.5
	2	7.1	1.2	4.6, 9.7
	3	6.1	1.3	3.5, 8.8
	4	6.1	1.0	3.9, 8.2
	5	5.6	1.0	3.4, 7.7
	6	5.7	1.2	3.2, 8.2

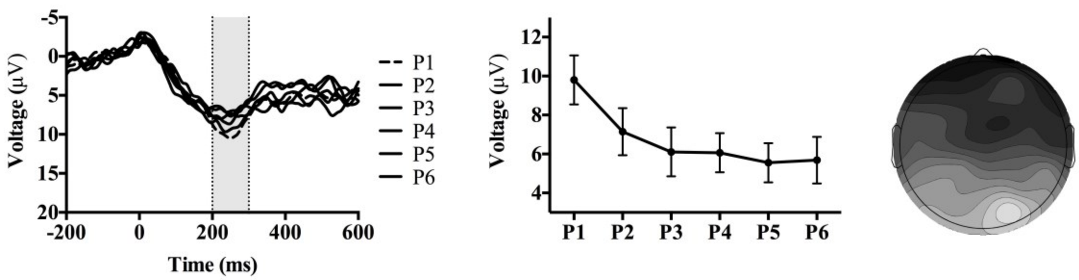

Figure 2.8 **Left**: average waveforms at POz corresponding to each level of phase evoked by screen-touch with delayed feedback. The gray window corresponds to the time-window used to calculate mean difference between levels of phase. **Centre**: mean voltage 200-300ms at POz corresponding to each levels of phase. Error bars represent standard error of the mean. **Right**: scalp topography derived by subtracting P6 data from P1 data and corresponding to maximal difference 200-300ms. Lighter tone indicates positive-going voltage.

2.3.8 PA ERPs: Target-Feedback Onset

The onset of target feedback after a period of delay yielded one ERP component sensitive to accuracy (Figure 2.9). Visual inspection of waveforms did not reveal a component that decreased in amplitude across phase. In contrast, however, it appears that a P300-like component was sensitive to phase in the opposite direction to what has been previously reported – thus positive amplitude was largest during late trials a opposed to early trials (Figure 2.10).

2.3.8.1 Accuracy-Sensitive ERP component

Mean voltage 230-330 ms post-target-onset at electrode FCz was sensitive to accuracy, $F(2,34) = 8.45$, $p = .001$, ηp2 = .33 (Figure 2.9). Means, SE, and 95% CI corresponding to each level of accuracy are presented in Table 2.15. Bonferroni-adjusted post hoc comparisons revealed a significant difference between Hits and both Big and Small misses ($p < .05$). A contrasts analysis also revealed a linear trend across each level of accuracy, such that amplitude became more negative as error size increased, $F(1,17) = 11.12$, $p = .004$, ηp2 = .40. These results suggest an FRN component was also evoked on miss trials by onset of target-feedback.

Table 2.15 Accuracy-sensitive negative-going ERP component. Evoked by target-onset after delay. Amplitude measured at FCz, 230-330ms post-target-onset for each level of accuracy.

Feedback	Error	Mean (μV)	SE (μV)	95% CI (μV)
	Hit	8.8	0.9	7, 10.7
Target Delayed	Small Miss	6.0	1.0	3.9, 8.2
	Big Miss	5.3	0.9	3.3, 7.3

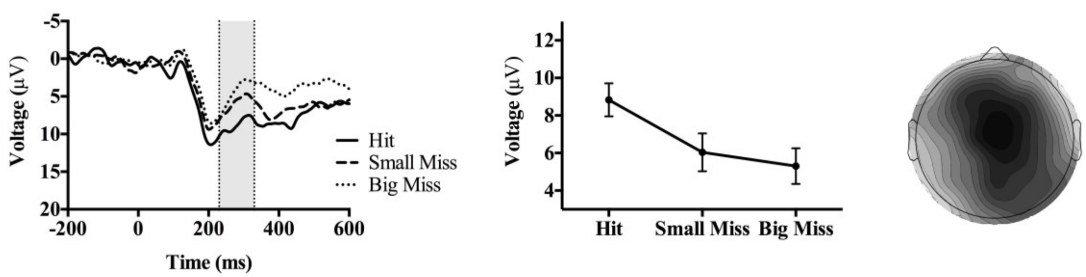

Figure 2.9 **Left**: average waveforms at FCz corresponding to each level of accuracy evoked by target-feedback after delay. The gray window corresponds to the time-window used to calculate mean difference between levels of accuracy. **Centre**: mean voltage 230-330ms at FCz corresponding to each levels of accuracy. Error bars represent

standard error of the mean. **Right**: Scalp topography derived by subtracting hit data from all miss data and corresponding to maximal difference 230-330ms. Darker tone indicates negative-going voltage.

2.3.8.2 Phase-Sensitive ERP component

Mean voltage 200-350 ms post-target-onset at electrode POz was sensitive to phase, $F(5,85) = 5.01$, $p = .001$, $\eta p2 = .23$ (Figure 2.10). Means, SE, and 95% CI corresponding to each level of accuracy are presented in Table 2.16. Bonferroni-adjusted post hoc comparisons only revealed differences between P5 and both P1 and P4 ($p < .05$). A contrasts analysis revealed a linear trend across levels of phase, suggesting amplitude became more positive from P1 to P6, $F(1,17) = 9.43$, $p = .007$, $\eta p2 = .36$. These results suggest that target-onset following a delay evoked a parieto-occipital component sensitive to phase, particularly during late trials.

Table 2.16 Phase-sensitive negative-going ERP component. Evoked by target-onset after delay. Amplitude measured at POz, 200-350ms post-target-onset for each level of accuracy.

Feedback	**Phase**	**Mean** (µV)	**SE** (µV)	**95% CI** (µV)
Target Delayed	1	3.512	1.010	1.382, 5.643
	2	3.916	1.217	1.349, 6.483
	3	5.033	1.077	2.761, 7.305
	4	4.248	1.088	1.953, 6.543
	5	7.257	1.120	4.894, 9.621
	6	5.941	1.243	3.318, 8.564

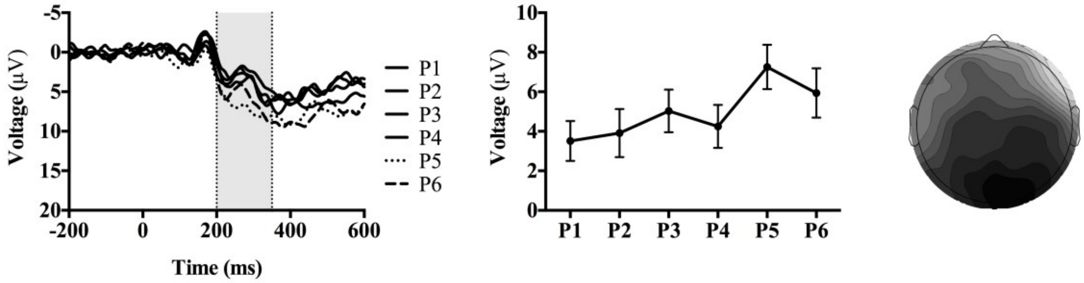

Figure 2.10 **Left**: average waveforms at Oz corresponding to each level of phase evoked by target-feedback after delay. The gray window corresponds to the time-window used to calculate mean difference between levels of phase. **Centre**: mean voltage 200-350ms at Oz corresponding to each levels of phase. Error bars represent standard error of the mean. **Right**: Scalp topography derived by subtracting P6 data from P1 data and corresponding to maximal difference 200-350ms. Darker tone indicates negative-going voltage.

2.4 Discussion

Participants underwent memory-guided prism adaptation (PA) with blocks of immediate target-feedback and blocks of delayed target-feedback Aiming accuracy, RT, and MT were recorded, and ERPs were measured at screen touch and at the onset of target feedback following a delay. Each prism exposure block was followed by a PVSA block to measure size of aftereffects, and then a block of sham exposure to de-adapt to the preceding prism exposure block. The purpose of the study was to compare the effects of immediate and delayed feedback on ERP components sensitive to accuracy (e.g. ERN, Pe, FRN) and phase (e.g. P300).

It was hypothesized that prism exposure blocks would show large aiming errors at the onset of blocks. Blocks of delayed target-feedback, however, were predicted to result in less error correction following those large errors compared to immediate target-feedback. Prism exposure blocks with delayed target-feedback were also hypothesized to produce smaller aftereffects than immediate-feedback blocks. Consequently, PVSA blocks following delayed target-feedback PA were hypothesized to show smaller mean error than PVSA blocks following immediate target-feedback PA. Furthermore, target-feedback was predicted to evoke an ERN-like response, sensitive to errors, in both immediate and delayed target-feedback conditions. A P300-like component was predicted to be evoked by target-feedback, but show greater sensitivity to phase in the immediate feedback condition compared to target-feedback following a delay – under the assumption the latter condition would produce smaller aftereffects. Finally, the question remained as to whether or not screen-touch with delayed target-feedback would evoke any accuracy- or phase-sensitive ERPs.

Analysis of error-by-trial slopes and intercepts confirmed that the paradigm resulted in typical effects of prism exposure. Prism-right and prism-left blocks each produced, respectively, large rightward and large leftward errors at the onset of blocks, but also gradually approached baseline-levels of accuracy as the trials went on. Sham(right) and sham(left) blocks, respectively, produced leftward and rightward errors (after-effect of preceding prism blocks) at onset and also approached baseline-levels of accuracy across trials. The paradigm thus successfully produced direct effects of prism exposure, error correction during continued reaching, aftereffects in the opposite direction, and de-adaptation.

Comparison of immediate and delayed target-feedback conditions revealed a number of behavioural results that deviate from our hypotheses. First, reaching errors during prism exposure blocks were larger in the immediate condition than the delayed conditions in all except the very last phase of prism adaptation. These results are contrary to those in Kitazawa et al. (1995). It is noteworthy, however, that the immediate feedback condition had a larger intercept, and, based on visual inspection of the error-by-trial figures (Figure 2.2), appeared to also have a larger mean error on Trial 1. Thus, while errors were unexpectedly larger in the immediate feedback condition, the effect might stem mainly from participants producing larger errors at the onset of the immediate feedback blocks. Accordingly, the immediate feedback condition actually had a larger slope than the delayed feedback condition, suggesting participants underwent more error correction in the former condition. There is no plainly obvious explanation for errors being larger at the onset of immediate feedback blocks, seeing as the feedback manipulation did not take effect until participants completed their first reach (at which point the error was already made).

While no differences in reaction time were observed, the delayed feedback condition did yield longer movement times than the immediate feedback condition across all phases – a result that was not reported in Kitazawa et al. (1995). Finally, contrary to our expectations, there was no difference in magnitude of aftereffect produced by the immediate and delayed feedback PA conditions.

The result that participants have longer MTs in the delayed condition suggests there were factors impacting their movements that were not present in Kitazawa et al. (1995) where MTs did not differ between feedback conditions. The present study, unlike Kitazawa's, had participants perform memory-guided, reaches with only the target occluded, as opposed to open-loop reaches with no view of limb or target. It is not surprising then that different systems supporting movement were engaged between the two studies. Importantly, the present conditions likely engaged retrieval of visual-memory and also dependence on allocentric cues more-so than was the case in

Kitazawa's study. The ERP results discussed below may present an explanation as to why participants had longer MTs in the delayed feedback condition and also smaller errors across most phases.

Analysis of the ERP components evoked by the three feedback events yielded interesting results, some of which also deviated from our hypotheses. Screen-touch with immediate target-feedback indeed produced a component sensitive to accuracy resembling the FRN. Thus, when participants missed the target, screen-touch and simultaneous target-feedback information together evoked error-processing activity in the brain, or activity of a purported reinforcement learning system (Holroyd & Coles, 2002; 2008). This neural activity is not similarly evoked when participants hit the target – i.e. it is specific to errors. This finding, in respect to PA, is novel. In MacLean et al. (2015) for example, screen-touch with the target visible during the entire reach evoked an earlier ERN-like component rather than an FRN. Thus, when the target is removed from vision, but available immediately at screen touch, the brain appears to utilizes error-evaluation mechanisms differently than when the target is always visible (i.e. FRN-generating neural process vs. ERN-generating neural process)

Screen-touch with immediate target-feedback also produced two positive-going ERP components sensitive to phase of adaptation: one with a central scalp distribution, followed by one with a parietal scalp distribution. While the hypothesis that immediate target-feedback would evoke a phase-sensitive component was supported, the timing and scalp distribution the reported components may not reflect the same P300 observed in MacLean et al. (2015). Rather, the present results perhaps match reports of the P3a and P3b components reviewed by Polich (2007). The first positive-going component, at Cz, may thus reflect frontal attention-mechanisms engaged in response to the visual-information provided by the onset of immediate target-feedback. The second positive-going component, at Oz, may then reflect the integration of that visual information into participants' model of the environment and task parameters, akin to "context-updating" described by Donchin & Coles (1988). Importantly, both the purported attention process (P3a) and information integration (P3b) appear to diminish with increased adaptation – particularly following the first phase of adaptation blocks. Alternatively, the components measured at Cz and Oz may simply reflect, first, increased neural activity in the P2 time range during early phases of adaptation, and second, increased parieto-occipital activity also during early phases of adaptation. Indeed, the component at Cz appears to be modulated by phase at a time-window very close to the P2 component. Furthermore, the maximal activation of the second component at Oz may suggest it is located in a region too occipital to reflect a typical P300 response. It must also be considered, however, that the Cz and Oz maximal components do not actually reflect distinct components. The evoking stimulus, timing, and polarity are all similar. Furthermore, it is not unusual for a component's topography to drifts slightly across time. As a result, it is possible that the two positive-going deflections in the waveform actually consist of a single component that drifts in in maximal amplitude from central to occipital scalp electrodes.

Screen-touch with delayed target-feedback yielded several unexpected components sensitive to accuracy. An early ERN component similar to that reported in MacLean et al (2015) was evoked, and peaked ~75ms post-touch. As it was suggested in MacLean et al. (2015), the early ERN might reflect error-processing specifically evoked by vision of the reaching hand immediately prior to touching the screen (here, referred to as "hand-feedback"). That we replicated this result without any target-feedback at screen-touch supports the idea that participants can use hand-feedback as an error signal, and thus undergo internal error evaluations based on that signal to produce an ERN response. Based on the RL-ERN hypothesis, hand-feedback would in fact serve as the earliest indication that participants will not achieve accuracy.

Interestingly, the present result suggests that participants need not see the target simultaneously with the hand in order to attribute error information to hand-feedback. As it has been previously suggested (Heath, 2005; Krigolson & Heath, 2004), our results might thus provide evidence that participants are actually retrieving accurate target information from memory and thus use vision of limb and allocentric cues to make reliable judgments of movement errors. Thus, although participants did not explicitly see the target, a memory representation of the target may have contributed to calculating movement error based on visible hand location. While participants did not fully correct errors on the trials where screen-touch with delayed feedback evoked an early ERN, it is noteworthy that they were (1) instructed to refrain from making major corrective movement upon seeing their hand, (2) the ERN did not actually peak until after screen touch – suggesting hand-feedback can provide error information but that it is not fully processed till the reach is complete, and (3) the error-related components observed during other visuo-motor tasks would suggest the ERN is only evoked by *imminent* error – i.e. too late to be corrected (Krigolson & Holroyd, 2006; 2007a; 2007b).

Considering these ERP results, it is important to revisit the finding that participants had longer MTs in the delayed target-feedback condition. This effect might stem from the fact that participants experienced an error signal from hand-feedback immediately prior to touching the screen with delayed target-feedback. Although the ERN component peaked after screen-touch, processing hand-feedback might have fed into other systems that rapidly evoked some form of mild movement compensation – thus prolonging MT. Indeed, participants did show slightly smaller errors across most phases in the delayed feedback condition as well, which would also support that theory.

The results from the delayed feedback condition also help inform results from the immediate feedback condition. In addition to faster MTs and larger errors, the immediate feedback condition did not evoke an early ERN (potentially evoked by hand-feedback) ~75ms post-touch. Thus, it appears that when participants anticipate receiving reliable error information (target-feedback) without delay, they withhold attributing error information to hand-feedback. However, when reliable error-information from target-feedback will be delayed (e.g. by 800ms), hand-feedback acquires predictive error information.

Screen-touch with delayed target-feedback also produced two positive-going components sensitive to large errors: one with a central scalp distribution, followed by one with a parieto-occipital scalp distribution. Both appeared after the ERN. The behavioural results in the conditions of delayed target-feedback may support the notion that these ERP components reflect the previously reported Pe component (Vocat et al., 2011). If the positive-going component, particularly at Cz, is indeed a Pe response, it may reflect further error-processing leading to post-error adjustments (Hajcak et al., 2003), rather than conscious awareness of errors (Nieuwenhuis et al., 2001). First, although we did not demonstrate a correlation between Pe amplitude and post-error slowing on the following trial, the fact that MTs were longer in the delayed feedback condition might suggest that the Pe-like components evoked here did in fact reflect some process resulting in post-error slowing on subsequent trials. This interpretation is suspect, however, seeing as (1) the positive-going components appeared mainly sensitive to large errors that were far less frequent in later phases of adaptation, whereas the difference in MT was consistent across all phases, and (2) this would likely conflict with our interpretation of increased MT resulting from minor error compensations due to the hand-feedback signal. Nevertheless, the fact that MTs were longer and that errors were smaller in the delayed feedback condition suggests that the error-sensitive positive-going components at Cz and POz may reflect some form of post-error processing that led to additional adaptive processes not present in the immediate feedback condition. Whether this specifically reflects increased "awareness" of errors cannot be confirmed. It does, however, further support the idea that participants are able to undergo error-processing before explicit visual target information is available.

It is also worth noting how closely the two positive-going components, at Cz and POz, evoked by screen-touch with delayed target-feedback resemble the components at Cz and Oz evoked by screen-touch with immediate target-feedback. These latter components, however, were sensitive to phase rather than errors. If both pairs of components in fact reflect the same central to parieto-occipital neural signal, then it would be interesting that one instance was sensitive to phase while the other was sensitive to error. It was hypothesized that the phase-sensitive Cz-to-Oz signal in the immediate feedback condition might reflect a P3a-P3b response. It is possible that this is also the case in the delayed feedback condition, such that large errors would evoke the type of processing purportedly reflecting the P3a and P3b components. Indeed, large errors observed at screen touch may recruit increased attention-related processes due to their significance and thus subsequently require integration into participants working model of the task.

Screen-touch with delayed target-feedback also evoked a parieto-occipital component sensitive to phase of adaptation. Specifically, it showed a larger positive voltage during early trials and diminished across subsequent phases. Although this component is in a time-range consistent with the P300, it is more occipital than normally reported. Furthermore, although it shows sensitivity to phase, the P300 reported in MacLean et al. (2015) was measured at a parietal electrode – Pz. The differences between these components brings into questions whether the current component at POz, evoked by screen-touch with delayed target-feedback, reflects context-updating processes. Although labeling the component may be difficult, it certainly lends some evidence that participants undergo increased parieto-occipital processing during early phases of adaptation.

When evaluating this phase-sensitive component at POz, it is important to note the relationship between phase and error. Errors are evidently larger in early phases of adaptation compared to late, thus any difference across phase could be attributed to more, or larger errors early on. Thus, taking into account the positive-going components (Cz-POz) evoked by large errors, it is possible that the phase-sensitive parietal component is just an artifact of error-sensitive parietal activity. This is an ongoing question, discussed in MacLean et al. (2015) as well, and will be considered further in Experiments 2 and 3.

Nevertheless, the fact that these central to parieto-occipital components were evoked by error, and not phase in the delayed feedback condition might come as a result of the differences in early error processing. The delayed feedback condition evoked an ERN, ~peaking 75ms post-touch, where as immediate feedback did not. The early ERN component, perhaps evoked by hand-feedback, in the delayed condition may have allowed more capacity for participants to undergo further error processing at screen-touch with the central to parieto-occipital system. In the immediate feedback condition however, participants did not undergo any error processing until target-feedback (i.e. did not process hand-feedback as an error), where they eventually showed an FRN. Although it may be a crude interpretation, the FRN-evoking system may simply override the central to parieto-occipital system. Thus, the central to parieto-occipital components, sensitive to errors, are only observed if the FRN is absent in that same time-range (for example, if an ERN is present beforehand).

The final feedback event, target-feedback following 800ms delay, evoked an FRN, sensitive to errors, similar to that evoked by screen-touch with immediate target-feedback. Their resemblance lends support to the idea that under condition of immediate target-feedback at screen-touch, the error-information pertains to target-information rather than hand-feedback. The identification of an FRN component evoked by target-feedback after delay also has major implications for the preceding ERN component identified by screen-touch without immediate target-feedback. Indeed, the results suggest that during the delayed feedback condition participants undergo two instances of error-processing: (1) evoked by hand-feedback, and (2) evoked by target-feedback. This result would thus fail to coincide with Holroyd & Coles' (2002) RL-ERN hypothesis that suggests the prediction-error, which may produce either the ERN or FRN, is evoked by the earliest indication that the outcome of an action is worse than predicted. Such as the case, either the ERN of FRN should only be evoked once for any given erroneous actions – not one after the other.

While the present ERN/FRN results perhaps stray from that theory, they may also present evidence that, during this reaching task, the brain monitors ongoing components of the reach separately rather than as a single unitary action. The brain may specifically monitor two ongoing predictions separately: (1) a prediction of where the reaching limb/hand is located based on proprioceptive feedback and/or a feed-forward movement plan, and (2) a prediction of success pertaining to the movement's end-goal, i.e. to hit the target. This would thus explain how, during conditions of delayed feedback, hand-feedback evokes error-processing pertaining to prediction #1, and later target-feedback evokes error-processing pertaining to prediction #2. Thus, hand-feedback evokes a form of rapid internal error evaluation, whereas target-feedback evokes a slower form of error evaluation requiring more extensive processing of external feedback information.

Interestingly, however, when the target-feedback is provided immediately at screen touch, the brain would appear to forgo error processing related to hand-feedback – thus forgo evaluation of prediction #1 described above. As speculated earlier, this might be related to limited attention capacity when target- and hand-feedback are nearly simultaneous. When they are separated by a delay, the brain can process each separately.

Importantly, target-feedback did not produce a phase sensitive P300-like response consistent with that observed in MacLean et al. (2015), nor consistent with the parieto-occipital component evoked by screen-touch in the preceding conditions.. Rather, a positive voltage in the P300 time-range was actually largest during the latter phases of adaptation, particularly P5. While this result will be considered in the next Experiments, the voltage trend suggests target-feedback after a delay evokes different neural events sensitive to phase compared to when target-feedback is delivered immediately at screen-touch.

The most interesting result from this experiment was that both feedback conditions produced similar strengths of aftereffect. Thus, contrary to our expectations, ERP components in either condition cannot be explicitly associated with producing strong aftereffects. Nevertheless, the ERP results can be discussed in terms of similarities, rather than differences, between feedback conditions. While numerous differences were reported above, the most striking similarity between feedback conditions was a late parieto-occipital (Oz, POz) positive-going component evoked by screen-touch that decreased in voltage across phase (see bottom panel of Figure 2.6, and Figure 2.8). These components were evoked both with and without explicit target-feedback available, and their respective conditions both ultimately produced equally robust aftereffects. That result, in combination with their sensitivity to phase independent of error, suggests they warrant close attention as a potential component reflecting adaptive perceptual processes.

The FRN components evoked by both instances of target-feedback were also very similar – albeit they appeared at different stages of the trial. Thus, they also warrant close attention as an important neural event in producing aftereffects. However, the fact that MacLean et al. (2015) only reported an early ERN (i.e. the one evoked by hand-, not target-feedback) but still observed fairly strong aftereffect suggests the error-sensitive component specifically evoked by target-feedback (the FRN) need not be present to produce strong aftereffects. Similarly, the immediate feedback condition did not evoke an early ERN purportedly sensitive to hand-feedback, but did produce strong aftereffects. Thus, the early, hand-feedback-sensitive ERN need not necessarily be present either to produce strong aftereffects. This does not, however, preclude the possibility that at least either one of the two (ERN, or FRN) components reported so far must be present to generate strong aftereffects. Experiment 2 presents conditions that will further elucidate the role of these ERPs.

CHAPTER 3: EXPERIMENT 2

3.1 Introduction

Experiment 1 showed that blocks of memory-guided PA with either delayed or immediate target-feedback at the end of discrete reaches produced similar magnitude of aftereffects. The results did not correspond to the original hypothesis, based on Kitazawa et al. (1995), that delayed feedback would produce decrements in aftereffects. Also out of line with Kitazawa et al. (1995), the delayed target-feedback condition actually had less error across most trials and also resulted in longer MTs. While both feedback conditions evoked a number of accuracy-sensitive and phase-sensitive ERP components – some which might explain the difference in error and MTs, it was difficult to determine if any reflected processes that increased aftereffects seeing as both feedback conditions did not differ in that respect. Both feedback conditions did however yield two fairly similar ERP components worth further investigation. First, both instances of target-feedback evoked a fronto-central FRN component sensitive to errors. Second, both instances of screen-touch evoked a parieto-occipital component sensitive to phase of adaptation. Notably, however, we also reported an early ERN component as well as positive-going central to parieto-occipital components sensitive to errors at the onset of hand-feedback under conditions of delayed target-feedback. These latter components were not reported in the immediate feedback condition, thus are presently considered less critical to producing aftereffects. The goal of Experiment 2 is to further investigate the role that feedback-evoked brain response might play in generating robust PA aftereffects.

The phase sensitive parieto-occipital component evoked by screen-touch in both the immediate and delayed target-feedback condition may have actually been a response to hand-feedback immediately before touching the screen – seeing as the component was present both with and without target onset at screen touch. Unlike Kitazawa et al. (1995), where vision was fully occluded at reach onset, Experiment 1 only occluded the target from sight. In Experiment 1, participants reached below an occlusion board terminating just before the monitor, and were always able to see the tip of their finger (i.e. hand-feedback) at termination of reach in both immediate and delayed conditions.

The behavioural results obtained in Experiment 1, in contrast to those reported in Kitazawa et al. (1995), certainly also suggest that direct visual information of the reaching limb is an important factor in how adaptation takes place and how aftereffects develop. In Kitazawa et al. (1995), delaying visual information of limb position caused decrements in adaptation and aftereffects. In Experiment 1, hand-feedback was not delayed in either feedback condition, and coincidently no differences in aftereffects were observed despite target-feedback being delayed in one condition.

While the result that hand-feedback evokes a phase-sensitive parieto-occipital component – perhaps indexing adaptive realignment processes – would be novel, evidence that hand-feedback is critical to generating aftereffects is not new. Several studies that completely eliminate direct hand-feedback in exchange for a “symbolic” hand position during PA have shown that this can decrease aftereffects. For example, Wilms and Mala (2010) elicited weaker after effects during PA using a computer monitor that showed hand position via small icons compared to traditional PA reaching at a board with direct view of hand at the end of the reach. Clower and Boussaoud (2000) showed the same effect when comparing feedback with a light positioned on the tip of participants’ finger versus a similar sized spot of light appearing against a monitor in place of the finger. While both conditions resulted in similar adaptation, only the former condition yielded typical aftereffects. Most recently, Veilleux and Proteau (2015) also compared PA involving actual vision of hand versus a computer-generated representation of hand location. The provision of "virtual" hand-feedback resulted in weaker aftereffects compared to direct hand-feedback.

Veilleux and Proteau (2015), and Redding and Wallace (2006) both drew attention to the "assumption of unity" described by Welch and Warren (1980) to explain the observation that direct hand-feedback is critical to producing robust aftereffects. Welch and Warren (1980) proposed that participants only experience true discord between perceptual systems (e.g. proprioceptive and visual) if feedback information meets the assumption of unity. For the assumption of unity to be met, provisions of feedback must make it obvious that proprioceptive information originates from the same body that is perceived by the visual system. Otherwise, if the assumption of unity is not met, the error information provided by feedback will not be attributed to a discord between perceptual systems and thus perceptual learning (e.g. realignment) does not take place. Instead, other learning mechanisms (e.g. recalibration) may be recruited to correct the error.

Accordingly, research so far suggests that error information is not sufficient to engage adaptive realignment processes that lead to strong aftereffects. An assumption of unity between discordant perceptual information must also be present. An icon on a monitor, or a virtual image representing hand location does not make it obvious enough that felt hand position and the symbolic hand position originate from the same body. There, the assumption of unity is not met and aftereffects do not develop.

The assumption of unity may be an important factor regarding the phase-sensitive P300-like components evoked in MacLean et al. (2015) and the phase-sensitive parieto-occipital components observed in Experiment 1. While the components could indeed be associated with adaptive realignment processes, given their attenuation across phase independent of error, they rather may simply reflect the brain's response to discordant perceptual information. If that were the case, it is hypothesized that the assumption of unity would have to be met in order for the reported parieto-occipital, or P300 component to be evoked. PA conditions where the assumption of unity is not met would thus not evoke a parieto-occipital component sensitive to phase, nor would robust aftereffects be produced. Adaptation, however, could still be observed as long as error information is provided – regardless of the unity assumption. Likewise, it would also be hypothesized that a PA paradigm could evoke an FRN component sensitive to error information, thus leading to successful adaptation, but ultimately show weak aftereffects. An ERN would not be predicted to occur, seeing as MacLean et al. (2015) and Experiment 1 would suggest that, during PA, the ERN is evoked only when direct vision of the reaching hand indicates error.

Experiment 2 investigates these hypotheses. Here, participants performed memory-guided reaching with prism glasses over the course of 4 blocks, each followed by a PVSA block to measure aftereffects and a sham block to de-adapt. The experimental conditions were nearly identical to Experiment 1. Most importantly, participants in Experiment 2 performed reaches below a *fully* extended occlusion board – thus they were completely unable to acquire hand-feedback at any point during the reach. It should be noted that "hand-feedback" refers to any direct vision of the real hand, in contrast to indirect information regarding hand position. In lieu of hand-feedback, participants' touch-location on the monitor was indicated by a light-gray vertical line that resembled the target. Thus, in Experiment 2, "target-feedback" involved the simultaneous appearance of the original target line as well as a line indicating hand position along the horizontal axis of the monitor. For sake of comparison with Experiment 1, target-feedback for PA was blocked according to immediate and delayed conditions. Seeing as direct-hand feedback was not available at all, we predicted that behavioural results between immediate and delayed feedback would more closely resemble Kitazawa et al (1995) than did Experiment 1. As noted above, the major hypotheses were that any instance of target-feedback here would (1) not produce a phase-sensitive parieto-occipital response, and (2) lead to smaller aftereffects compared to Experiment 1. It was also hypothesized, however, that an FRN component sensitive to accuracy (errors) would still be evoked by target-feedback. Finally, it was hypothesized that ERN and Pe-like components would not be evoked by target-feedback here, because those components reported in Experiment 1 were only evoked when hand-feedback was available and never evoked specifically by the onset of target-feedback (e.g. target-feedback following delay).

3.2 Methods

3.2.1 Participants

The study recruited 25 participants. Three participants were excluded from data analysis because of poor EEG data quality resulting in high artifact rejection (> 50%). Additionally, one participant's behavioural data were lost due to a recording error, although their EEG data were still available. Anecdotally, this participant was observed performing the experiment consistent with expectations (e.g. adapted, de-adapted) and showed no markedly abnormal behaviour. Their EEG data were thus included in the ERP analysis to help increase power. The behavioural results below therefore reflect data from 21 participants (mean age = 19.3, SD = 1.3, 17 females, 1 left hander), while the ERP results reflect data from 22 participants (mean age = 19.7, SD = 1.4, 18 females, 1 left hander). All participants were students at Dalhousie University who voluntarily participated in the study for extra credit points going towards Psychology & Neuroscience classes. Participants provided informed consent consistent with the Nova Scotia Health Authority Research Ethics Board. All participants reported having corrected or corrected-to-normal vision, no neurological illness, not being under any medications affecting cognitive performance, and not having any upper body impairment preventing reaching movements with their dominant arm.

3.2.2 Materials

The present materials were almost identical to Experiment 1. Unlike Experiment 1, however, all PA blocks in the present experiment were performed with a fully extended occlusion board preventing any vision of the reaching limb (see procedure below). EEG data collection was done with the same equipment as in Experiment 1.

3.2.3 Procedure and Design

The design was identical to Experiment 1. Every participant underwent 4 blocks of prism adaptation. Two blocks provided immediate target-feedback on each trial, while the other 2 blocks provided delayed target-feedback on each trial. Furthermore, within each feedback condition, one of the two blocks was performed with leftward displacing prism glasses, and the other with rightward displacing prism glasses. In contrast to

Experiment 1, the participants would receive no vision of their hand upon completing a reach during the PA blocks. Instead, the touch-location on the monitor would be indicated on the screen by a light-gray line (similar in shape to the target) that also extended the entire height of the monitor. Therefore, the provision of "target-feedback" in the present study included simultaneous onset of two vertical lines indicating (1) the original target position, and (2) location of screen-touch along the monitor's horizontal axis.

See Figure 3.1 for an illustration of a typical trial. The trial procedure was nearly identical to Experiment 1. When participants made contact with the screen, they were instructed to hold their finger where it landed until they saw the target reappear simultaneously with a second line indicating where their finger landed, then saw both lines disappear. After both lines disappeared, the trial was complete and participants returned to the spacebar to initiate the next trial.

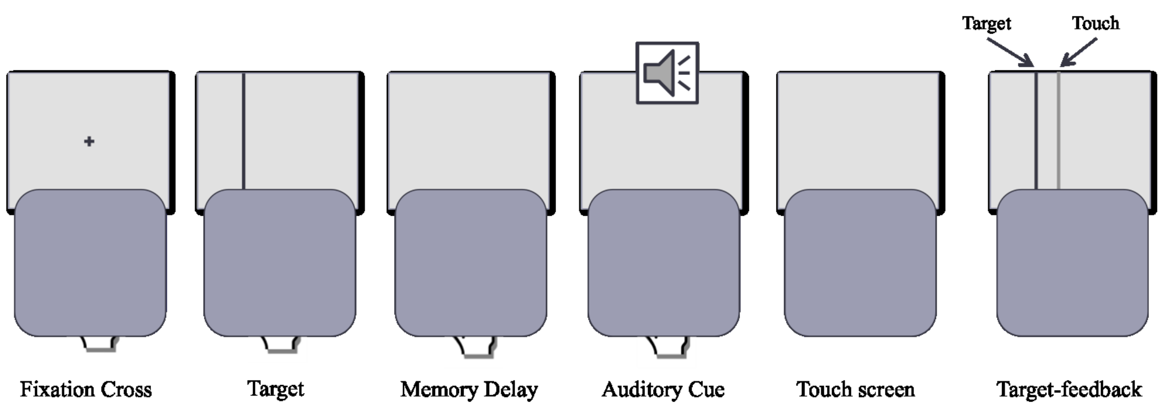

Figure 3.1 A typical PA trial (from left to right) with delayed target-feedback after touching the screen.

As in Experiment 1, every PA block was followed by a PVSA block measuring strength of aftereffects. The PVSA blocks were identical to those described in Experiment 1.

After every PVSA block, participants performed a sham block identical to those in Experiment 1, in order to de-adapt to the prism exposure they just experienced. Thus, in addition to vision of hand being available at the end of the reaching movement, a second line did not appear simultaneously with the target to indicate hand position. As before, immediate and delayed target-feedback were randomized within sham blocks. This provision of feedback during the sham condition ensured any differences between Experiment 1 and Experiment 2 would not be caused by differences in how participants de-adapted.

Participants also began every experiment with a baseline PVSA and a baseline sham block – identical to those described above. The entire experiment thus consisted of a total of 14 blocks (See Table 3.1).

Table 3.1 Sequence of blocks in Experiment 2.

Block	**Condition**	**Trials**
1	PVSA (BL)	10
2	Sham (BL)	60
3	Prism	60
4	PVSA	10
5	Sham	60
6	Prism	60
7	PVSA	10
8	Sham	60
9	Prism	60
10	PVSA	10
11	Sham	60
12	Prism	60
13	PVSA	10

3.2.4 Behavioural Data Collection and Analysis

Same as Experiment 1. Table A2 shows percentage of each participant's behavioural data that were removed prior to final analyses.

3.2.5 Measuring Adaptation and De-Adaptation

Same as Experiment 1.

3.2.6 Immediate vs. Delayed PA Feedback: Error, RT, MT

Same as Experiment 1.

3.2.7 Immediate vs. Delayed PA Feedback: Aftereffects

Same as Experiment 1.

3.2.8 Electroencephalography Data Collection

Same as Experiment 1.

3.2.9 Electroencephalography Data Analysis

Same as Experiment 1. Table A2 shows percentage of each participant's ERP data that were removed prior to final analyses.

3.2.10 Comparing Feedback-Evoked Brain Potentials

Same as Experiment 1: the ERP analysis was conducted on 3 separate events: (1) screen-touch with immediate target-feedback, (2) screen-touch with delayed target-feedback, and (3) target-feedback following delay. The present experiment, however, prevented vision of hand in all conditions. Thus, no visual feedback whatsoever was available at screen-touch in the immediate and delayed feedback conditions. Furthermore, "target-feedback" consisted of the appearance of two vertical lines as opposed to just one. As before, the analysis focused on differences within each event that were evoked by two factors: phase (1-6) and accuracy (hit, small miss, big miss). Differences in respect to those two factors *between* feedback events are addressed in the discussion section. Percentage of hits, small misses, and big misses across each phase of both feedback conditions is shown in Figure A19. Difference waves with 95% CIs used to determine differences between levels of accuracy and phase are shown in the Appendix section.

3.3 Results

3.3.1 Adaptation and De-Adaptation: Slopes and Intercepts

The analysis revealed a significant effect of exposure condition on slope, $F(1.6, 33.5) = 25.9$, $p < .001$, ${}_p\eta^2 = .56$. Figure 3.2 shows the relationship between trial number and error and Table 3.2 shows the mean slope, SE, and 95% CI for each exposure condition. Pairwise comparisons revealed that both the Prism-right and the Prism-left conditions differed from all other slopes ($p < .05$), however, sham conditions and baseline did not differ. The analysis also revealed a significant effect of exposure condition on intercepts, $F(1.3, 26.7) = 26.9$, $p < .001$, ${}_p\eta^2 = .57$. Table 3.3 shows the mean intercept, SE, and 95% CI for each exposure condition. Pairwise comparisons revealed that all intercepts differed from each other except between baseline and sham(right).

A two-way ANOVA comparing absolute slope scores between prism-right, prism-left, sham(right), and sham(left) revealed and effect of exposure (prism vs. sham) on absolute slopes, $F(1, 20) = 39.1$, $p < .001$, ${}_p\eta^2 = .66$, such that prism slopes were larger than sham slopes. The analysis revealed no effect of direction (left vs. right) on absolute slopes, $F(1, 20) = 0.48$, $p = .5$, ${}_p\eta^2 = .02$, and no interaction effect, $F(1, 20) = 0.56$, $p = .46$, ${}_p\eta^2 = .03$. A two-way ANOVA comparing absolute intercept scores between prism-right, prism-left, sham(right), and sham(left) revealed an effect of exposure (prism vs.

sham) on absolute intercepts, $F(1, 20) = 30.1$, $p < .001$, ${}_p\eta^2 = .6$, such that prism intercepts were larger than sham intercepts. The analysis revealed no effect of direction (left vs. right) on absolute intercepts, $F(1, 20) = 0.94$, $p = .34$, ${}_p\eta^2 = .05$, and no interaction effect, $F(1, 20) = 2.2$, $p = .15$, ${}_p\eta^2 = .1$.

In summary, the results indicate that the prism-right condition resulted in a negative slope reflecting the reduction of large positive-value (right) errors across trials; and the prism-left condition resulted in a positive slope reflecting the reduction in large negative-value (left) errors across trials. Both sham conditions, however, produced smaller slopes no different than baseline, and intercepts equal to (i.e. sham(right)), or nearly equal to (i.e. sham(right)) baseline.

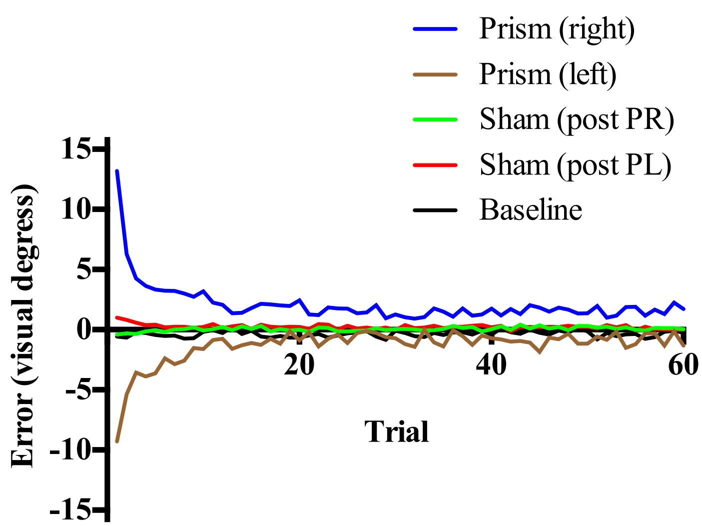

Figure 3.2 Mean error size in visual degrees across all trials, averaged according to Prism (left, right), Sham (left, right), and Baseline sham conditions.

Table 3.2 Error-by-trial linear regression slopes for prism, sham, and baseline exposure conditions

Condition	Slope	SE	95% CI
Baseline	0.002	0.003	-0.005, 0.009

Prism right	-0.050	0.012	-0.074, -0.025
Prism left	0.044	0.007	0.029, 0.058
Sham (right)	0.005	0.001	0.002, 0.007
Sham (left)	-0.005	0.002	-0.009, -0.001

Table 3.3 Error-by-trial linear regression intercepts for prism, sham, and baseline exposure conditions

Condition	**Intercept**	**SE**	**95% CI**
Baseline	-0.42	0.18	-0.79, -0.05
Prism right	3.70	0.86	1.92, 5.49
Prism left	-2.70	0.40	-3.53, -1.86
Sham (right)	-0.09	0.05	-0.20, 0.01
Sham (left)	0.40	0.09	0.21, 0.59

3.3.2 Immediate vs. Delayed PA Feedback: Error

The analysis of error-by-trial slopes revealed no difference between immediate feedback (mean = -.04, SE = .008) and delayed feedback (mean = -.04, SE = .007), t(20) = 0.64, p = .53. The analysis of error-by-trial intercepts also revealed no difference between immediate (mean = 4.5, SE = 0.56) and delayed (mean = 4.3, SE = 0.49) feedback, t(20) = 0.59, p = .56. The relationship between trial and absolute error for both conditions is illustrated in Figure 3.3.

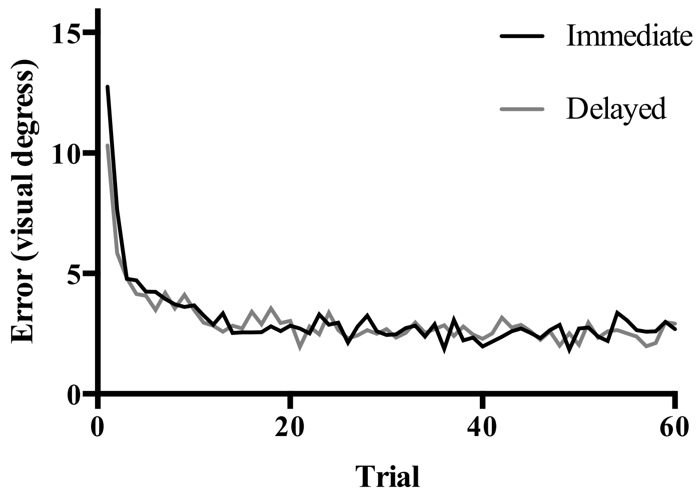

Figure 3.3 Mean error across trials for the immediate and delayed feedback conditions.

Absolute errors submitted to a 2x6 repeated-measures ANOVA with feedback (immediate, delayed) and phase (1-6) as factors revealed a significant effect of phase on error size, $F(1.7, 33.8) = 40.7$, $p < .001$, ${}_p\eta^2 = .67$. Bonferroni-adjusted pairwise comparisons revealed that mean errors in P1 were significantly larger than all other phases, however, no other phases differed from each other. The analysis also revealed no significant effect of feedback condition on error size, $F(1, 20) = 0.08$, $p = .77$, ${}_p\eta^2 = .004$, nor any interaction between phase and feedback, $F(2.2, 43.3) = 0.9$, $p = .42$, ${}_p\eta^2 = .04$. Table 3.4 shows means, SE, and 95% CI for errors across phase and feedback conditions. Likewise, Figure 3.4 illustrates the mean errors in a bar graph.

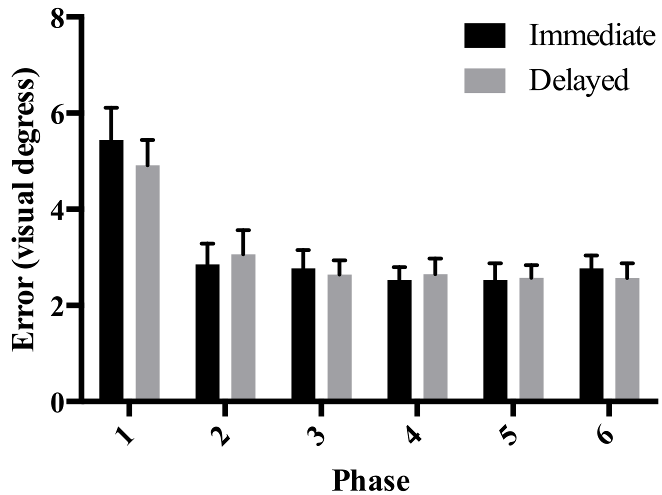

Figure 3.4 Mean error size across phases for immediate and delayed target-feedback PA blocks. Error bars indicate standard error.

Table 3.4 Absolute errors in each phase of both PA feedback conditions.

Feedback	Phase	Mean	SE	95% CI
Immediate	1	5.45	0.66	4.06, 6.83
	2	2.85	0.43	1.96, 3.75
	3	2.77	0.38	1.98, 3.56
	4	2.53	0.27	1.97, 3.09
	5	2.53	0.35	1.81, 3.25
	6	2.77	0.27	2.20, 3.33
Delayed	1	4.92	0.53	3.82, 6.02
	2	3.06	0.50	2.01, 4.11
	3	2.64	0.29	2.03, 3.25
	4	2.65	0.33	1.97, 3.33
	5	2.58	0.26	2.03, 3.12
	6	2.57	0.31	1.93, 3.21

3.3.3 Immediate vs. Delayed PA Feedback: RT

A 2x6 repeated-measures ANOVA with feedback (immediate, delayed) and phase (1-6) as factors revealed no effect of phase on RT, $F(2.1, 43.5) = 1.1$, $p = .34$, $_p\eta^2 = .05$, no effect of feedback on RT, $F(1, 20) = 0.5$, $p = .82$, $_p\eta^2 = .002$, and no interaction between the two factors, $F(3.2, 65.3) = 1.5$, $p = .68$, ${}_p\eta^2 = .02$. Table 3.5 shows RT means, SE, and 95% CI.

Table 3.5 Reaction time in each phase of both PA feedback conditions.

Feedback	Phase	Mean (ms)	SE (ms)	95% CI (ms)
Immediate	1	665	008	648, 682
	2	664	010	643, 685
	3	667	012	642, 692
	4	671	012	646, 695
	5	668	011	645, 691
	6	669	013	642, 696
Delayed	1	667	007	653, 680
	2	665	010	645, 685
	3	665	011	642, 688
	4	666	010	644, 688
	5	674	013	647, 700
	6	671	008	654, 688

3.3.4 Immediate vs. Delayed PA Feedback: MT

A 2x6 repeated-measures ANOVA with feedback (immediate, delayed) and phase (1-6) as factors revealed an effect of feedback on MT, $F(1, 20) = 6.3$, $p < .05$, ${}_p\eta^2 = .24$. The delayed feedback condition produced slightly longer MTs (mean = 362ms, SE = .037ms) compared to the immediate feedback condition (mean = 315ms, SE = .043ms). There was no effect of phase on MT, $F(5, 100) = 0.7$, $p = .59$, ${}_p\eta^2 = .04$, nor any interaction between factors $F(3.1, 62.6) = 0.6$, $p = .58$, ${}_p\eta^2 = .03$. Table 3.6 shows mean MTs, standard errors, and 95% confidence intervals.

Table 3.6 Movement time in each phase of both PA feedback conditions

Feedback	Phase	Mean (ms)	SE (ms)	95% CI (ms)
Immediate	1	320	035	247, 394

	2	306	033	237, 375
	3	320	037	242, 397
	4	324	040	241, 408
	5	308	042	219, 396
	6	315	041	230, 400
Delayed	1	344	043	254, 434
	2	356	047	258, 455
	3	358	045	265, 451
	4	368	041	282, 454
	5	365	043	277, 454
	6	378	045	285, 471

3.3.5 Immediate vs. Delayed PA Feedback: Aftereffects

A 2x2 repeated-measures ANOVA with preceding PA direction (prims-left, prism-right) and preceding PA feedback (immediate, delayed) as factors revealed a significant effect of feedback on mean PVSA error, $F(1, 20) = 9.5$, $p < .01$, ${}_p\eta^2 = .32$ on mean PVSA error. Specifically, the immediate feedback condition produced slightly larger PVSA errors than the delayed feedback condition. There was no effect of prism adaptation direction, $F(1, 20) = 0.1$, $p = .76$, ${}_p\eta^2 =.005$, and no interaction effect, $F(1, 20) = 0.07$, $= p = .79$, ${}_p\eta^2 = .003$, on mean PVSA errors. Means, SE, and 95% CI are presented in Table 3.7.

Table 3.7 PVSA errors produce by both PA feedback conditions and their respective direction of prism shift

Feedback	**Prism Direction**	**Mean**	**SE**	**95% CI**
Immediate	Right	1.78	0.21	1.35, 2.21
	Left	1.84	0.26	1.31, 2.37
Delayed	Right	1.25	0.25	0.73, 1.77
	Left	1.38	0.26	0.84, 1.92

3.3.6 PA ERPs: Screen-Touch with Immediate Target-Feedback

The event of touching the screen with immediate target feedback yielded one ERP component sensitive to accuracy (Figure 3.5). Visual inspection of waveforms did not reveal any components sensitive to phase. This latter observations was tested below by submitting mean voltage 200-350ms post-screen-touch (see Figure 3.6) and mean voltage 350-500ms post-screen-touch separately to a repeated-measures ANOVA with two factors: phase (1-6) and electrode site (FPz, FCz, Cz, CPz, Pz, POz, Oz).

3.3.6.1 Accuracy-Sensitive ERP component

Mean voltage 225-375 ms post-touch at electrode FCz was sensitive to accuracy, $F(2,42) = 27.85$, $p > .001$, $\eta p2 = .57$. Means, SE, and 95% CI corresponding to each level of accuracy are presented in Table 3.8. Bonferroni-adjusted post hoc comparisons revealed that all levels of accuracy differed from each other ($p < .05$). Furthermore, a contrasts analysis revealed a linear trend across each level of accuracy, suggesting amplitude became more negative as error size increased, $F(1,21) = 40.40$, $p < .017$, $\eta p2 = .66$. These results support the hypothesis that an FRN component was evoked at screen touch on miss trials during the immediate feedback condition.

Table 3.8 Accuracy-sensitive negative-going ERP component. Evoked by screen-touch with immediate target-feedback. Amplitude measured at FCz, 225-375ms post-touch for each level of accuracy

Feedback	**Error**	**Mean (μV)**	**SE (μV)**	**95% CI (μV)**
Immediate	Hit	12.0	1.8	8.2, 15.9
	Small Miss	9.3	1.5	6.2, 12.5
	Big Miss	7.4	1.5	4.3, 10.5

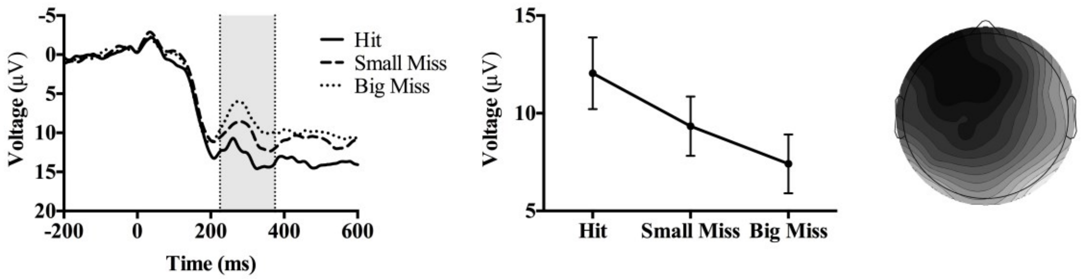

Figure 3.5 **Left**: average waveforms at FCz corresponding to each level of accuracy evoked by screen-touch with immediate feedback. The gray window corresponds to the time-window used to calculate mean difference between levels of accuracy. **Centre**: mean voltage 225-375ms at FCz corresponding to each levels of accuracy. Error bars represent standard error of the mean. **Right**: scalp topography derived by subtracting hits from all misses and corresponding to maximal difference. Darker tone indicates negative-going voltage.

3.3.6.2 Absent Phase-Sensitive ERP component

The repeated-measures ANOVA, with phase and electrode site as factors, revealed no effect of phase for mean voltage 200-350ms post-touch, $F(2.9, 61.3) = 1.27$, $p = .28$, $\eta p2 = .06$, and no interaction between phase and electrode site, $F(6.8, 143) = 0.74$, $p = .63$, $\eta p2 = .03$. Similarly, for mean voltage 350-500 ms post-touch, there was no effect of phase, $F(2.9, 62.3) = 0.48$, $p = .69$, $\eta p2 = .02$, and no interaction between phase and electrode site, $F(7.2, 152) = 1.67$, $p = .12$, $\eta p2 = .07$. Figure 3.6 illustrates the null effect of phase 200-350 ms post-touch at electrode site POz.

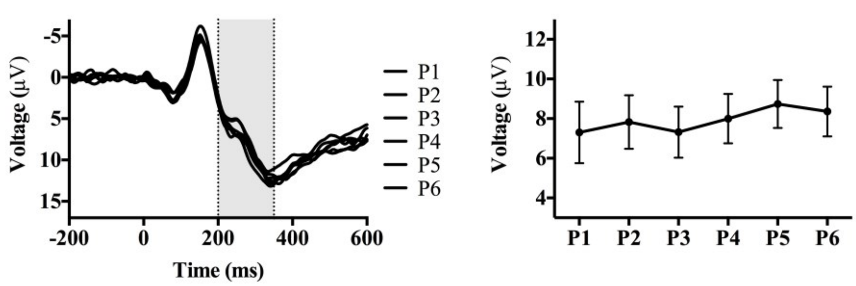

Figure 3.6 **Left**: average waveforms at POz corresponding to each level of accuracy evoked by screen-touch with immediate feedback. The gray window corresponds to the time-window used to calculate mean difference between levels of accuracy. **Right**: mean voltage 200-350ms at POz corresponding to each levels of accuracy. Error bars represent standard error of the mean

3.3.7 PA ERPs: Screen-Touch with Delayed Target-Feedback

The event of touching the screen with delayed target-feedback yielded no observable ERP components sensitive to either accuracy or phase. To test this observation, the same FRN-sensitive time range and electrode site observed during immediate feedback was tested here. The absence of sensitivity to phase was tested by submitting mean voltage 200-350ms post-screen-touch and mean voltage 350-500ms post-screen-touch separately to a repeated-measures ANOVA with two factors: phase (1-6) and electrode site (FPz, FCz, Cz, CPz, Pz, POz, Oz).

3.3.7.1 Absent Accuracy-Sensitive ERP component

Mean voltage 225-375 ms post-touch at electrode FCz was not sensitive to accuracy, $F(2,42) = 0585$, $p = .564$, $\eta p2 = .03$. Figure 3.7 illustrates this null effect.

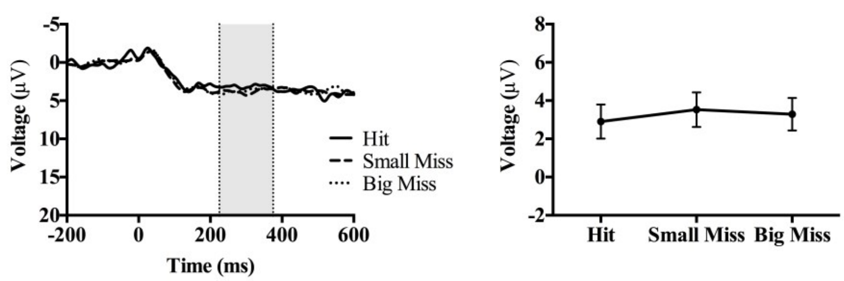

Figure 3.7 **Left**: average waveforms at FCz corresponding to each level of accuracy evoked by screen-touch with delayed feedback. The gray window corresponds to the time-window used to calculate mean difference between levels of accuracy. **Right**: mean voltage 225-375ms at FCz corresponding to each levels of accuracy. Error bars represent standard error of the mean.

3.3.7.4 Phase-Sensitive ERP component

Contrary to visual inspection, mean voltage 200-350ms post-touch ($F(5, 105) = 3.44$, $p = .006$, $\eta p2 = .14$) and 350-500 ms post-touch ($F(5, 105) = 2.29$, $p = .05$, $\eta p2 = .1$) were both sensitive to phase. There was no interaction between phase and electrode site, $F(5.98, 125.31) = 0.47$, $p = .83$, $\eta p2 = .02$ and $F(6.73, 141.43) = .46$, $p = .86$, $\eta p2 = .02$, respectively. The difference manifested as a negative-going voltage during P1 compared to all other phases. The difference appears present over the course of most of the ERP after 0ms as well as at all electrodes tested. Thus, while this suggests a component of the ERP is sensitive to phase, it does not match the same parieto-occipital component that diminishes across phase observed in Experiment 1. In fact, the negative-going voltage across the entire epoch might suggest the difference does not reflect a discrete neural event, but rather an artifact of some sort during P1. Figure 3.8 illustrates this effect at electrode POz. This result, however, will not be further addressed in the discussion.

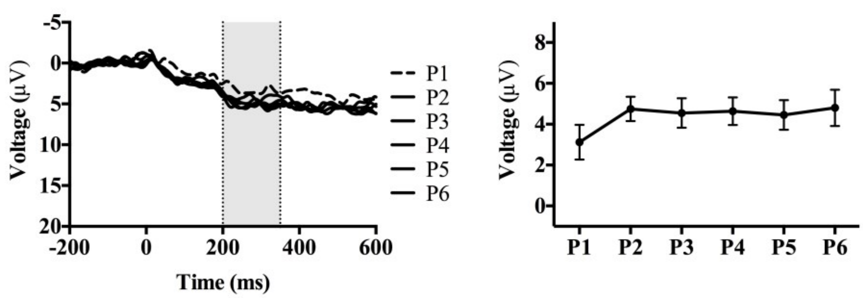

Figure 3.8 **Left**: average waveforms at POz corresponding to each level of phase evoked by screen-touch with delayed feedback. The gray window corresponds to the time-window used to calculate mean difference between levels of phase. **Right**: mean voltage 200-350ms at POz corresponding to each level of phase. Error bars represent standard

error of the mean.

3.3.8 PA ERPs: Target-Feedback Onset

The onset of target feedback after a period of delay yielded one ERP component sensitive to accuracy (Figure 3.9). Visual inspection of waveforms did not reveal a component sensitive to phase. This latter observation was tested by submitting mean voltage 200-350ms post-screen-touch and mean voltage 350-500ms post-screen-touch separately to a repeated-measures ANOVA with two factors: phase (1-6) and electrode site (FPz, FCz, Cz, CPz, Pz, POz, Oz).

3.3.8.1 Accuracy-Sensitive ERP component

Mean voltage 230-330 ms post-target-onset at electrode FCz was sensitive to accuracy, $F(2,42) = 11.52$, $p > .001$, $\eta p2 = .35$. Means, SE, and 95% CI corresponding to each level of accuracy are presented in Table 3.9. Bonferroni-adjusted post hoc comparisons revealed a significant difference between Hits and both Big and Small misses ($p < .05$). A contrasts analysis also revealed a linear trend across each level of accuracy, lending some evidence that amplitude became more negative as error size increased, $F(1,21) = 14.48$, $p = .001$, $\eta p2 = .41$. These results suggest an FRN component was evoked on miss trials by onset of target-feedback after a delay period.

Table 3.9 Accuracy-sensitive negative-going ERP component. Evoked by target onset after delay. Amplitude measured at FCz, 230-330ms post-touch for each level of accuracy

Feedback	**Error**	**Mean (μV)**	**SE (μV)**	**95% CI (μV)**
Immediate	Hit	11.1	1.6	7.7, 14.5
	Small Miss	8.1	1.4	5.1, 11.1
	Big Miss	7.2	1.2	4.8, 9.7

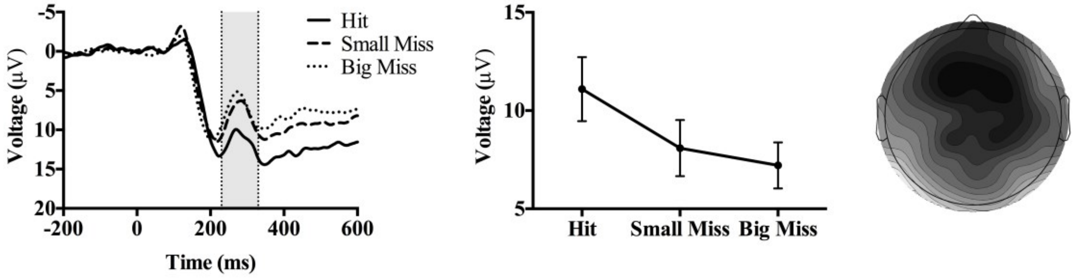

Figure 3.9 **Left**: average waveforms at FCz corresponding to each level of accuracy evoked by screen-touch with immediate feedback. The gray window corresponds to the time-window used to calculate mean difference between levels of accuracy. **Centre**: mean voltage 230-330ms at FCz corresponding to each levels of accuracy. Error bars represent standard error of the mean. **Right**: scalp topography derived by subtracting hits from all misses and corresponding to maximal difference. Darker tone indicates negative-going voltage.

3.3.8.2 Absent Phase-Sensitive ERP component

Both voltage 200-350ms post-touch ($F(5, 105) = 1.80$, $p = .120$, $\eta p2 = .08$) and 350-500 ms post-touch ($F(5, 105) = 0.87$, $p = .505$, $\eta p2 = .04$) were not sensitive to phase. There was, however, a moderate interaction between phase and electrode site for mean voltage 200-350ms, $F(6.93, 145.65) = 2.62$, $p = .014$, $\eta p2 = .11$, but not for 350-500ms, $F(7.45, 156.21) = 1.54$, $p = .151$, $\eta p2 = .07$. No electrodes, particularly at parieto-occipital or parieto-central sites showed a response that diminished in amplitude across phases. Thus, target-onset after a delay also did not appear evoke a phase-sensitive component similar to those observed during screen-touch in Experiment 1. Figure 3.10 illustrates the null effect at POz for mean voltage 200-350 ms post-target-onset.

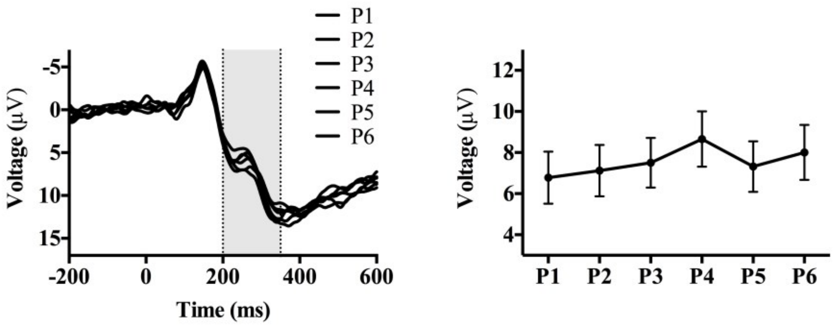

Figure 3.10 **Left**: average waveforms at POz corresponding to each level of phase evoked by screen-touch with delayed feedback. The gray window corresponds to the time-window used to calculate mean difference between levels of phase. **Right**: mean voltage 200-350ms at POz corresponding to each level of phase. Error bars represent standard error of the mean.

3.4 Discussion

Experiment 2 required participants to perform blocks of memory-guided prism adaptation with either immediate or delayed target-feedback. Unlike Experiment 1, participants' reaching limb was fully occluded – they were unable to see any portion of their arm, hand, or finger during the reaching movement. Thus, "target-feedback" in the present experiment involved not only a vertical target line, but also a simultaneous second target-like line indicating where the participants' finger touched the screen. The purpose of Experiment 2 was to compare the effect of immediate and delayed feedback conditions when direct hand-feedback is not available, and, furthermore, contrast these results to those obtained in Experiment 1 when direct hand-feedback was available. Importantly, "hand-feedback" here specifically refers to direct vision of hand, and not indirect hand-feedback.

Because view of the reaching hand was considered a critical factor in the results from Experiment 1, behavioural results from Experiment 2 were predicted to better resemble Kitazawa et al. (1995). Thus, it was predicted that during PA participants would show a greater reduction of errors across trials in the immediate feedback condition compared to the delayed feedback condition. It would also be predicted that the immediate feedback condition would result in larger aftereffects compared to the delayed condition. It was evidently still predicted that participants would successfully adapt to the prism without direct hand-feedback however. That being said, it was also hypothesized that aftereffects in both feedback conditions would be substantially smaller than those observed in Experiment 1.

Following the behavioural predictions, it was hypothesized that both immediate and delayed target-feedback would evoke an FRN. Neither target-feedback event was predicted to evoke a phase-sensitive P300 component similar to that observed in MacLean et al. (2015), nor a phase-sensitive parieto-occipital component observed in Experiment 1. Finally, it was also predicted that screen-touch with delayed target-feedback would not evoke any components sensitive to accuracy or phase seeing as no visual feedback information is available during that event in Experiment 2.

Results from the present experiment did indeed resemble Kitazawa et al. (1995) more than did Experiment 1. While the immediate and delayed feedback conditions did not differ in respect to errors across trials, the immediate feedback condition did however produce slightly larger aftereffects than the delayed feedback condition. This result, along with Kitazawa's results, suggest that delays in visual feedback only impact aftereffects if (1) target-feedback is the only source of error information, or (2) if hand- and target-feedback are both delayed. Thus, it again highlights the importance of hand-feedback, seeing as when the two conditions share identical provision of hand-feedback, regardless of differences in target-feedback (immediate, delayed), their aftereffects are the same.

Similar to Experiment 1, there were no difference in RTs but the delayed condition did have slower MTs than the immediate condition. Although the main purpose of the study was not to investigate MTs, this result warrants some discussion given how it was addressed in Experiment 1. It was hypothesized that, in Experiment 1, the increased attention towards hand-feedback, suggested by the ERPs, may have caused participants to make very mild movement corrections near the end of their reach thus increasing MT and reducing errors slightly. Here, however, there was no provision of hand-feedback and no difference in error between the delayed and immediate condition. This leads to two possibilities: (1) the increased MTs in the delayed feedback conditions were caused by different factors in Experiment 1 and Experiment 2, or (2) the increased MTs in the delayed feedback conditions in both experiments were caused by the same factor, which evidently cannot be attributed to differences in how hand-feedback was processed. Delaying explicit hand-feedback may thus simply lead to differences in post-trial processing and motor planning that results in slower MT. To better understand the differences between feedback conditions, future studies should collect kinematic data to determine what components of the reaching movement are prolonging MTs. Differences in, for example, the ballistic phase of the reach might suggest that delayed target-feedback is mainly affecting the movement plan rather than online movement corrections.

Analysis of error-by-trial intercepts and slopes in PA, sham, and baseline exposure conditions suggests that Experiment 2 evoked slightly atypical adaption, aftereffects, and de-adaptation compared to Experiment 1. Figure 3.11 compares error-by-trial adaptation in Experiments 1 and 2. While, prism-right and prism-left indeed produce large errors at the onset of blocks in the predicted directions (respectively, right and left) and showed error correction across trials, there appeared to be an overall lesser degree of adaptation compared to Experiment 1. For example, prism-right and prism-left adaptation slopes in Experiment 2 were, respectively, -0.05 and 0.04, compared to -0.08 and 0.08 in Experiment 1. Intercepts were also larger in Experiment 1, however. Thus, increased adaptation slopes in Experiment 1 are perhaps an effect of larger errors specifically at the onset of PA blocks compared to Experiment 2. Mean absolute errors in P6 for both feedback conditions in Experiment 2 (2.7 and 2.5), however, were larger than those observed in Experiment 1 (1.8 an 1.5), suggesting larger errors were not just isolated to early phases in Experiment 2.

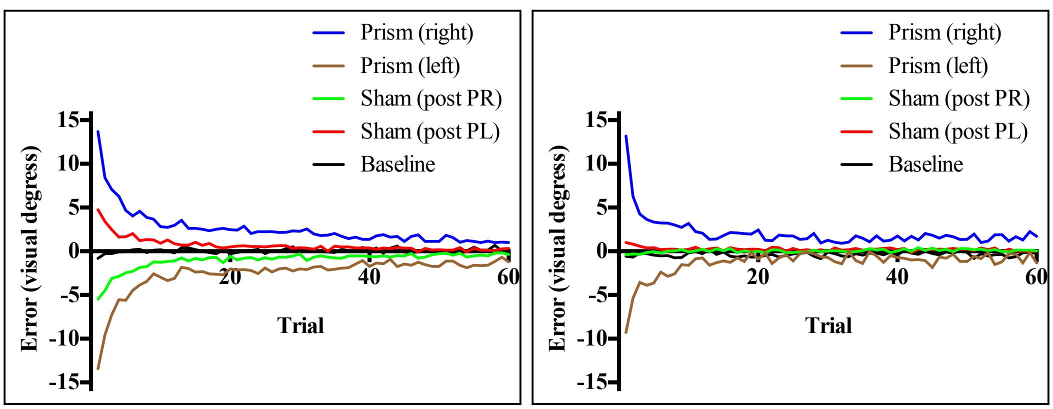

Figure 3.11 **Left**: Error-by-trial adaptation in Experiment 1. **Right**: Error-by-trial adaptation in Experiment 2.

An interesting difference between Experiments 1 and 2 was that error correction only seemed to take place over the course of P1 in Experiment 2 (e.g. no difference across P2-P6). On the other hand, in Experiment 1, participants were able to further correct errors from P2 to P6. These results would thus suggest that feedback conditions involving vision of hand produce better error correction caused by prisms than feedback without vision of hand. Specifically, without vision of hand, participants seem able to only undergo early rapid compensation for large errors but are not able to continue improving after that initial compensation.

Importantly, significantly smaller aftereffects were generated from PA blocks in the present experiment compared to Experiment 2. For example, sham blocks in Experiment 2 showed much smaller intercept and slopes compared to Experiment 1. Furthermore, mean PVSA error was substantially smaller in the present experiment compared to Experiment 1. Collapsed between feedback conditions, the mean PVSA error in Experiment 1 was 5.6 (SE = 0.4) whereas mean PVSA error in Experiment 2 was 1.5 (SE = 0.2). Thus, although Experiment 2 successfully induced direct effects in the PA blocks and participants underwent compensation for those large errors, subsequent aftereffects were not as strong as previously reported in Experiment 1. As discussed in the introduction, this latter result is consistent with effect of symbolic hand representation during PA on aftereffects.

The ERPs evoked by target-feedback were consistent with our predictions. Screen-touch with immediate target-feedback resulted in an FRN component, sensitive to errors, peaking ~300ms post-touch at fronto-central electrode sites. Delayed target feedback also evoked an FRN component sensitive to errors with a similar timing and scalp distribution to screen-touch with immediate target-feedback. Neither of these two events produced a P300-like component sensitive to phase, like thart observed in MacLean et al (2015), nor a central or parieto-occipital component observed in Experiment 1. There was no evidence of an early ERN, or subsequent Pe response either. Indeed, screen-touch with delayed target-feedback did not produce any ERP components sensitive to accuracy or phase resembling the ERN, Pe, or P300. This latter result further cements the importance of hand-feedback during screen-touch in evoking the ERN and positive-going Cz-to-POz/Oz components in response to errors, and in evoking the P300/parieto-occipital component in response to different phases.

Together, the results support the theory that the phase-sensitive parieto-occipital component observed in Experiment 1, with hand-feedback available, may only be evoked when the assumption of unity is met. Furthermore, the weak aftereffects in Experiment 2 and the absence of phase-sensitive parieto-occipital components lend support to the idea that when the assumption of unity is met, the observed parieto-occipital component in prior conditions reflects a process associated with spatial realignment, or perceptual learning, leading to stronger aftereffects.

It is thus also interesting that the FRN component was still evoked by instances of target-feedback when participants missed the target. Participants evidently processed errors because adaptation (error correction) across trials was still observed. The results suggest the neural processes underlying the FRN component are not critical to engaging spatial realignment or perceptual learning that leads to strong aftereffects, although they suffice to compensate for errors caused by the prismatic visual shift. The FRN components observed on error-trials might therefore engage compensatory mechanisms akin to recalibration (Redding & Wallace, 2002). Importantly, recalibration has been suggested to result in compensation to prism glasses, but not necessarily yield robust aftereffects (Redding & Wallace, 1993; 1997). Therefore, while the phase-sensitive parieto-occipital component continues to show promise as an index of realignment and perceptual learning, the FRN component may in fact suggest participants are engaging in compensatory strategies like recalibration that can hinder the strength of subsequent aftereffects despite leading to error correction.

The association between the aforementioned ERPs and different adaptive processes can be further elucidated by a paradigm in which explicit target-feedback is not available to the participants, whereas hand-feedback is still available. Under such conditions, participants may show no FRN response to miss-reaches, but still show a phase-sensitive parieto-occipital component evoked by hand-feedback. With target-feedback and the FRN absent, the subsequent strength of aftereffects would then reveal whether those accuracy-sensitive neural processes (e.g. FRN) are critical to producing robust aftereffects. Experiment 3 investigates these hypotheses.

CHAPTER 4: EXPERIMENT 3

4.1 Introduction

Experiment 2 investigated ERP components evoked by target-feedback that did not meet the assumption of unity described by Welch and Warren (1980). Specifically, no direct hand-feedback was made available to participants at the end of the reach. As predicted, both immediate and delayed target-feedback conditions produced much smaller aftereffects compared to Experiment 1. Furthermore, neither immediate nor delayed target-feedback evoked a phase-sensitive parieto-occipital component hypothesized to reflect realignment or perceptual learning. No Pe-like component or early ERN was evoked either. Target-feedback did however produce an accuracy-sensitive FRN component in both the immediate and delayed conditions.

These results confirm the importance of hand-feedback in eliciting strong aftereffects and may support its role in generating a phase-sensitive parieto-occipital component. The results also lead to an important question concerning target-feedback and the FRN component: is explicit accuracy information (i.e. target-feedback) and the neural process generating the FRN critical to producing robust aftereffects? Experiment 2 certainly showed that explicit accuracy (i.e. error) information, indicating distance between hand and target, evoked an FRN and that this information is sufficient to engage visuo-motor compensation to the prism glasses. However, with the absence of strong aftereffects, the adaptive systems involved in Experiment 2 might not be critical to engaging any form of spatial realignment or perceptual learning. The importance of target-feedback and the FRN cannot be excluded, however, seeing as both were observed in Experiment 1 when aftereffects were indeed large.

The FRN, as described by Holroyd and Coles (2002; 2008) is suggested to reflect a reward-sensitive signal evoked by phasic dopaminergic firing in the ventral tegmental area (VTA), similarly to that observed in non-human primates (Schultz et al., 1997). Holroyd and Coles theorized the FRN is produced by a neural prediction error: the earliest indication that the outcome of a selected action is worse than predicted. This theory follows from reinforcement learning (RL) models. Basic RL theory suggests we learn from the outcome of our actions (Sutton & Barto, 1998). Actions yielding high-value rewards are reinforced, and those yielding low-value rewards are not reinforced. Indeed, the *prediction error* is a central component of RL models that prompts a system (e.g. brain) to perform a different action in similar future situations. Thus, the FRN response to visuo-motor errors suggests the brain has processed a low-value reward (e.g. missed target) and must adjust future actions to elicit high-value rewards (hit target).

Different models of learning, however, other than RL have been suggested to guide behaviour. Indeed, Redding and Wallace (1997), in describing prism adaptation, drew attention to the categories of learning described by Bedford (1993). Bedford classified learning under a number of categories, two of which were “world learning”, and “perceptual learning”. World learning is the process of learning from experience, or explicit memories of events. For example, by pressing a lever and receiving a treat, a mouse learns to press to the leaver again. World learning thus closely resembles the basic parameters of RL. Perceptual learning, however, reflects adjustments in physiological domains that are beyond deliberate, conscious control. Bedford, not surprisingly, cites prism adaptation as an example of perceptual learning. Perceptual learning may describe instances when the brain undergoes changes without deliberate trial and error experience.

Indeed, PA may present an example of a visuo-motor task that can be improved with either world-learning or perceptual learning. Evidence thus far would suggest that under typical conditions of PA, both types of learning are recruited (Redding & Wallace, 2002).

Considering the evidence that spatial realignment – assumed here to reflect a form of perceptual learning – is critical to developing robust aftereffects, PA paradigms that appeal only to perceptual learning, and not world learning or RL, may thus enhance those aftereffects. Interestingly, a study by Michel et al. (2007) observed PA in healthy participants by subjecting them to small increments of visual prism shifts in such a way that they were reported to not make any explicit aiming errors and to not be aware of any visual displacements. Participants in this "multiple-step" condition ultimately showed larger aftereffect compared to a group subjected to typical PA conditions where errors were large at the onset of the task. This provides evidence that appealing exclusively to perceptual learning processes, i.e. without need to undergo trial-and-error learning, during PA may actual enhance aftereffects.

The following study investigates the effect of providing hand-feedback, but not target-feedback during PA in an effort to reduce involvement of the RL-system purported to evoke the FRN response. Participants thus might recruit primarily perceptual learning processes (e.g. realignment) to compensate for the prismatic shift, and thereby enhance subsequent aftereffects. To that end, hand-feedback would still be expected to evoke a parieto-occipital component, or P300, sensitive to phase of adaptation given our hypothesis that this component is associated with some form of perceptual learning. Results from the delayed target-feedback condition in Experiment 1, however, might suggest that the absence of target-feedback will only cause participants to attribute explicit error information to hand-feedback instead. If that were the case, hand-feedback should evoke an ERN and thus suggest participants were still undergoing some form of internal error evaluation, perhaps based on memory of target location. Holroyd and Coles (2002) would in fact suggest that the ERN is also indicative of activity of a neural RL system.

In Experiment 3, participants performed memory-guided reaching with prism glasses as in Experiments 1 and 2. Participants reached below an occlusion board that allowed them to see the tip of their finger upon making contact with the screen, providing direct hand-feedback. Here, however, they received no target-feedback whatsoever. Thus, upon making contact with the screen, the target never reappeared. It should be noted, however, and will be discussed below, that there were still a number of visual landmarks available for participants to make accuracy judgments in respect to the remembered target location upon seeing their finger.

Participants were also subjected to conditions of "full" target-feedback that closely resembled MacLean et al. (2015) for comparison with the no-target-feedback condition. Here, participants did not perform memory-guided reaching, but instead were able to see the target during the entire trial.

It was hypothesized that the full target-feedback condition would result in typical adaptation and large aftereffects resembling those in Experiment 1, and would produce an ERN component on miss-trial. The ERN component was hypothesized to peak at approximately ~75ms post-touch, as in MacLean et al. (2015), thus suggesting its evoking stimulus could be the onset of hand-feedback rather than screen-touch. Screen-touch in the full target-feedback condition was also predicted to evoke a P300-like component sensitive to phase, or a more parieto-occipital component sensitive to phase, similar to that reported in MacLean et al (2015) and Experiment 1. The no-target-feedback condition was hypothesized to result in equally large, but perhaps larger, aftereffects to those produce by PA with full target-feedback. The important question was whether hand-feedback, or screen-touch, would (1) evoke an ERN or FRN component sensitive to accuracy without any provision of target-feedback, and (2) evoke a parieto-occipital component sensitive to phase. While the ERN/FRN result in the no-target-feedback condition was difficult to predict, it was hypothesized that a parieto-occipital component sensitive to phase would indeed be evoked by screen-touch.

The potential absence of the ERN or FRN component in the no-target-feedback condition was hypothesized to have implication on participants' behavioural adaptation too. Although strong aftereffects were expected in the no-target-feedback condition, the absence of any accuracy-sensitive ERPs (i.e. ERN, FRN) might reflect poorer error processing, and thus lead to overall poorer error correction across adaptation blocks. Regardless of the ERN result, the lack of target-feedback would likely make the task harder and thus error were predicted to be slightly larger in the no-target-feedback-condition compared to full-target-feedback.

Finally, because hand-feedback was available, it was also predicted that screen-touch might evoke central to parieto-occipital ERP components like those reported in Experiment 1 with delayed feedback in response to errors - Pe-like components. Likewise, the predicted parieto-occipital component sensitive to phase might be preceded by a centro-maximal component similar to that evoked by screen-touch with immediate feedback in Experiment 1 in the P2 time-range.

4.2 Methods

4.2.1 Participants

The study recruited 22 participants (mean age = 20, SD = 1.9, 21 females, 1 left hander). As in Experiment 2, one participant's behavioural data was unusable due to a recording error. Their behaviour during the experiment was observed to be normal, thus the EEG data were kept in the analysis to increase power. As a result, the behavioural analysis reflects 21 participants, whereas the EEG analysis reflects 22 participants. All participants were students at Dalhousie University who voluntarily participated in the study for extra credit points going towards Psychology & Neuroscience classes. Participants provided informed consent consistent with requirements from the Nova Scotia Health Authority Research Ethics Board. All participants reported having corrected or corrected-to-normal vision, no neurological illness, not being under any medications affecting cognitive performance, and not having any upper body impairment preventing reaching movements with their dominant arm.

4.2.2 Materials

The materials are identical to Experiments 1. Importantly, the occlusion board prevented vision of reaching movement until 3 cm immediately before the monitor (except for PVSA blocks). EEG data were collected from the same system reported above.

4.2.3 Procedure and Design

The procedure and design were very similar to Experiments 1 and 2. The experiment was designed to measure differences between goal directed reaching performed with a visible target during the entire reach (full target-feedback) and without a visible target during and after the reach (no-target-feedback). Thus the experiment employed a within-subject design with feedback (target, no target) as the main factor. As in the previous experiments, participants underwent 4 blocks of prism adaptation. Two blocks provided full target-feedback on each trial, while the other 2 blocks provided no target-feedback on each trial.

See Figure 4.1 for a typical full target-feedback trial, and Figure 4.2 for a typical no-target-feedback trial. Trial procedure closely resembled Experiments 1 and 2. In the full target-feedback condition, the target remained visible for the entire trial. In the no-target-feedback condition, the target remained on the screen for 700-900 ms as in Experiments 1 and 2. In the no-target-feedback condition, after target offset, the screen remained blank for 1000-1200 ms before the participants heard an auditory cue (1000 Hz, .05 ms, 30dB). In the full target-feedback condition, there was a 700-900 ms delay between target onset and the auditory cue. Participants reached below the occlusion board and were only able to see the tip of their finger at the very end of their reaching movement. In the full target-feedback condition, when participants made contact with the screen, they were instructed to hold their finger where it landed until they simultaneously saw the target disappear and heard an auditory cue identical to the "go-cue"1000 ms after screen-touch. In the no-target-feedback condition, participants were instructed to hold their finger where it landed until they heard an auditory cue identical to the "go-cue", also taking place 1000 ms after screen-touch. These events signaled the trial was complete and participants could return to the spacebar to initiate the next trial.

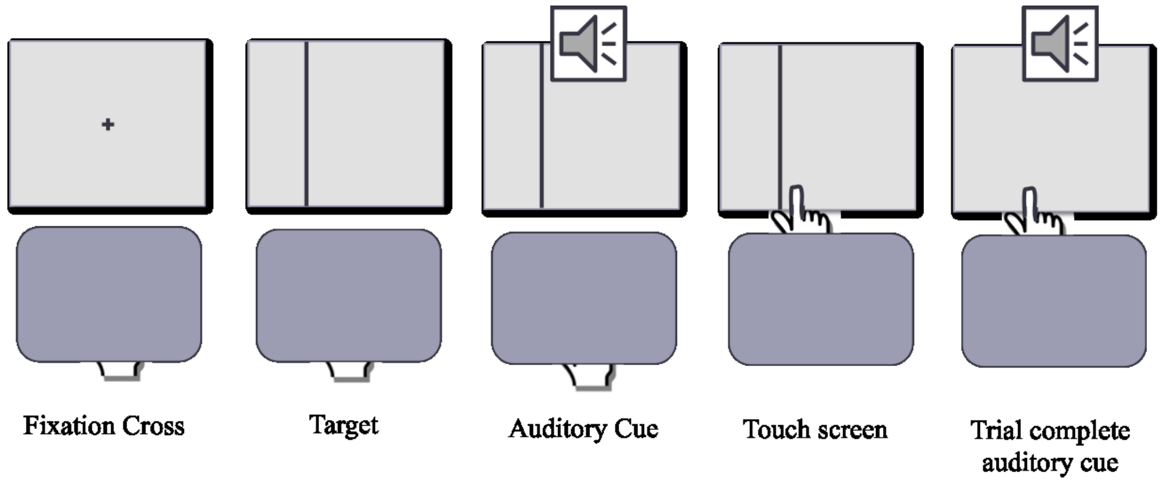

Figure 4.1 A typical PA trial (from left to right) with full target-feedback after touching the screen.

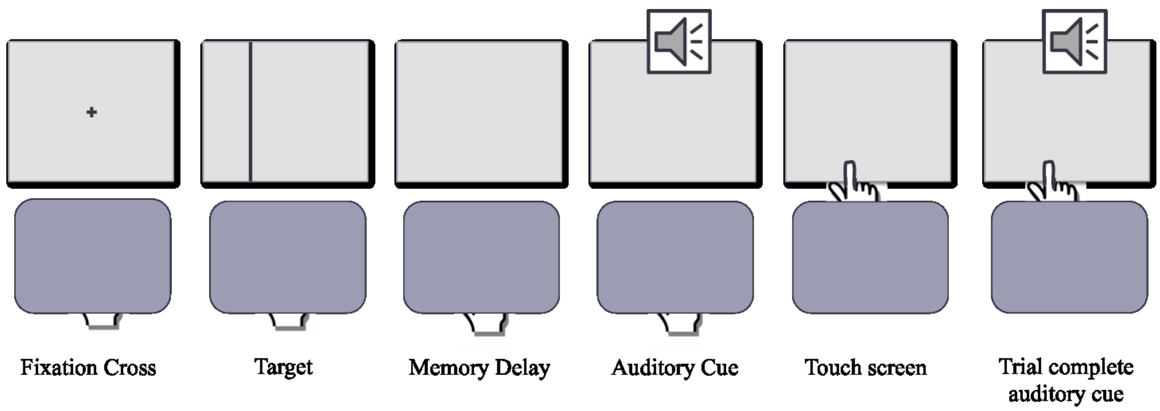

Figure 4.2 A typical PA trial (from left to right) with no target-feedback after touching the screen.

As in Experiment 1 and 2, every PA block was followed by a PVSA block measuring strength of aftereffects. The PVSA blocks were identical to those described in Experiment 1 and 2.

After every PVSA block, participants performed a sham block identical to those in Experiment 1 and 2, in order to de-adapt to the prism exposure they just experienced. Thus, while feedback delay was not a factor in the PA blocks, immediate and delayed target-feedback was randomized within sham blocks. This kept de-adaptation conditions consistent across all three experiments, thereby facilitating comparisons across experiments.

Participants also began every experiment with a baseline PVSA and a baseline sham block – identical to those described above. The entire experiment thus consisted of a total of 14 blocks (See Table 4.1).

Table 4.1 Sequence of blocks in Experiment 3.

Block	Condition	Trials
1	PVSA (BL)	10
2	Sham (BL)	60
3	Prism	60
4	PVSA	10
5	Sham	60
6	Prism	60
7	PVSA	10
8	Sham	60
9	Prism	60
10	PVSA	10
11	Sham	60
12	Prism	60
13	PVSA	10
14	Sham	60

4.2.4 Behavioural Data Collection and Analysis

Same as Experiments 1 and 2. Table A3 shows percentage of each participant's behavioural data that were removed prior to final analyses.

4.2.5 Measuring Adaptation and De-Adaptation

Same as experiments 1 and 2.

4.2.6 Immediate vs. Delayed PA Feedback: Error, RT, MT

This analysis closely resembled Experiments 1 and 2, however absolute error-by-trial slopes and intercepts were submitted to paired sample t-tests comparing full target-feedback and no-target-feedback blocks (as opposed immediate and delayed feedback blocks). Here, prism-right and prism-left were collapsed together.

Absolute errors were then submitted to a 2 x 6 repeated-measure ANOVA with the following factors: feedback (target, no target) and phase (1-6). MT and RT were also separately submitted to a 2 x 6 repeated-measure ANOVA with feedback (target, no target) and phase (1-6) as factors.

4.2.7 Immediate vs. Delayed PA Feedback: Aftereffects

To compare magnitude of aftereffect produced by the both feedback condition, absolute corrected PVSA errors (PVSA – baseline PVSA) for each participant were submitted to a 2x2 repeated-measures ANOVA with the following factors: preceding PA feedback (target, no target) and direction of preceding PA displacement (prism-right, prism-left).

4.2.8 Electroencephalography Data Analysis

Same as Experiment 1 and 2.

4.2.9 Electroencephalography Data Analysis

Same as Experiments 1 and 2. Table A3 shows percentage of each participant's ERP data that were removed prior to final analyses.

4.2.10 Comparing Feedback-Evoked Brain Potentials

An ERP analysis was conducted separately on the 2 feedback events that participants experience during PA blocks: (1) screen-touch with full target-feedback throughout the reach, and (2) screen-touch with no-target-feedback. The ERP analysis does not compare grand average differences between each event. Rather, as with Experiment 1 and 2, the analysis focuses on differences within each event that are evoked by two factors: phase (1-6) and accuracy (hit, small miss, big miss). Differences in respect to those two factors *between* feedback events are addressed in the discussion section. The rest of the analysis is consistent with Experiments 1 and 2. Percentage of hits, small misses, and big misses across each phase of both feedback conditions is shown in Figure A19. Difference waves with 95% CIs used to determine differences between levels of accuracy and phase are shown in the Appendix section.

4.3 Results

4.3.1 Adaptation and De-Adaptation: Slopes and Intercepts

The analysis revealed a significant effect of exposure condition on slope, $F(1.5, 30.9) = 89.9$, $p < .001$, ${}_{p}\eta^2 = .82$. Figure 4.3 shows the relationship between trial number and error. Table 4.2 shows mean slopes, SE, and 95% CIs for each condition. A repeated-measures ANOVA also revealed a significant effect of exposure on slope intercepts, $F(1.5, 29.8) = 122.4$, $P < .001$, ${}_{p}\eta^2 = .86$. Table 4.3 shows mean intercepts, SE, and 95% CIs for each condition. Bonferroni-adjusted pairwise comparisons revealed that all Prism and Sham slopes and intercepts significantly differed from Baseline ($p < .05$).

A two-way ANOVA comparing absolute slope scores between prism-right, prism-left, sham(right), and sham(left) revealed an effect of exposure (prism vs. sham) on absolute slope, $F(1, 20) = 36.3$, $p < .001$, ${}_{p}\eta^2 = .65$, such that prism slopes were larger than sham slopes. The analysis revealed no effect of direction (left vs. right) on absolute slopes, $F(1, 20) = 0.55$, $p = .46$, ${}_{p}\eta^2 = .03$, and no interaction effect, $F(1, 20) = 1$, $p = .33$, ${}_{p}\eta^2 = .05$. A two-way ANOVA comparing absolute intercept scores between prism-right, prism-left, sham(right), and sham(left) revealed an effect of exposure (prism vs. sham) on absolute intercepts, $F(1, 20) = 63.1$, $p < .001$, ${}_{p}\eta^2 = .76$, such that prism intercepts were larger than sham intercepts. The analysis revealed no effect of direction (left vs. right) on absolute intercepts, $F(1, 20) = 0.11$, $p = .74$, ${}_p\eta^2 = .006$, and no interaction effect, $F(1, 20) = 0.63$, $p = .44$, ${}_p\eta^2 = .03$.

In summary, both the Prism-right and Sham-left conditions produced positive-value intercepts and negative slopes, indicating early rightward (positive) errors that diminished across trials. Conversely, Prism-left and Sham (right) conditions produced negative value intercepts and positive slopes, indicating early leftward (negative) errors that diminished across trials. Slopes and intercepts in the sham conditions were smaller than those in the prism conditions ($p < .05$).

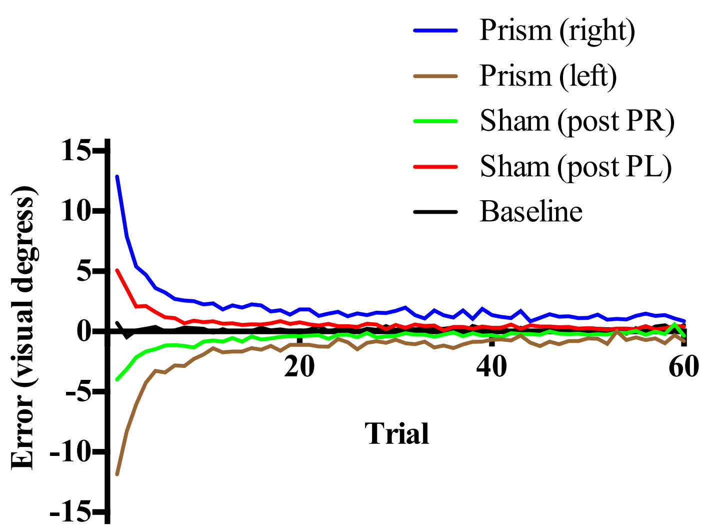

Figure 4.3 Mean error size in visual degrees across all trials, averaged according to Prism (left, right), Sham (left, right), and Baseline sham conditions.

Table 4.2 Error-by-trial linear regression slopes for prism, sham, and baseline exposure conditions

Condition	Slope	SE	95% CI
Baseline	0.001	0.001	-0.002, 0.004
Prism right	-0.061	0.007	-0.075, -0.047
Prism left	0.067	0.008	0.051, 0.084
Sham (right)	0.029	0.003	0.023, 0.034

Sham (left)	-0.028	0.002	-0.033, -0.023

Table 4.3 Error-by-trial linear regression intercepts for prism, sham, and baseline exposure conditions

Condition	Intercept	SE	95% CI
Baseline	0.13	0.08	-0.03, 0.30
Prism right	3.89	0.36	3.14, 4.64
Prism left	-3.67	0.38	-4.45, -2.88
Sham (right)	1.54	0.12	1.28, 1.79
Sham (left)	-1.43	0.12	-1.68, -1.19

4.3.2 Full Target vs. No Target PA Feedback: Error

The analysis of absolute error-by-trial slopes revealed no difference between full target-feedback (mean = -0.06, SE = 0.005) and no target-feedback (mean = -0.06, SE = 0.008), t(20) = 0.35, p = .73. The analysis of absolute error-by-trial intercepts also revealed no difference between full target-feedback (mean = 3.9, SE = 0.23) and no target-feedback (mean = 4.4, SE = 0.35), t(20) = 1.7, p = .09. The relationship between trial and absolute Error for both conditions is illustrated in Figure 4.4.

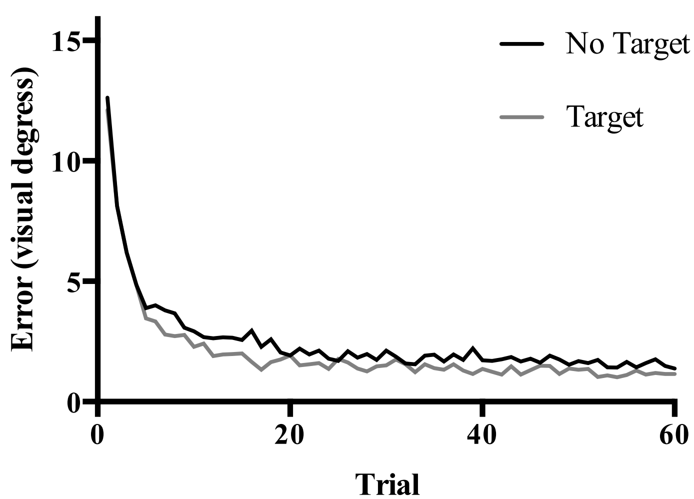

Figure 4.4 Mean error across trials for the full target- and no target-feedback conditions.

Absolute errors submitted to a 2x6 repeated-measures ANOVA with feedback (target, no target) and phase (1-6) as factors revealed a significant effect of phase on error size, $F(1.3, 27.1) = 110.7$, $p < .001$, ${}_{p}\eta^2 = .85$. Bonferroni-adjusted pairwise comparisons revealed that mean errors in phase 1 were significantly larger than all subsequent phase ($p < .001$), and, similarly, mean errors in phase 2 were larger than all subsequent phases ($p < .05$). Mean error in phases 3, 4, and 5 did not differ. Mean error in phase 6 differed from phase 1, 2, 3, and 4, but not from phase 5. The analysis also revealed a significant effect of feedback condition on error size, $F(1, 20) = 13.1$, $p < .01$, ${}_{p}\eta^2 = .40$. Specifically, mean errors in the No Target feedback condition were consistently larger than the Target feedback condition. The analysis revealed no interaction between phase and feedback, $F(1.8, 37.3) = 0.3$, $p = .72$, ${}_{p}\eta^2 = .02$. Table 4.4 shows means, SE, and 95% CIs for error across phase and feedback conditions. Likewise, Figure 4.5 illustrates the mean errors across phase and feedback conditions in a bar graph.

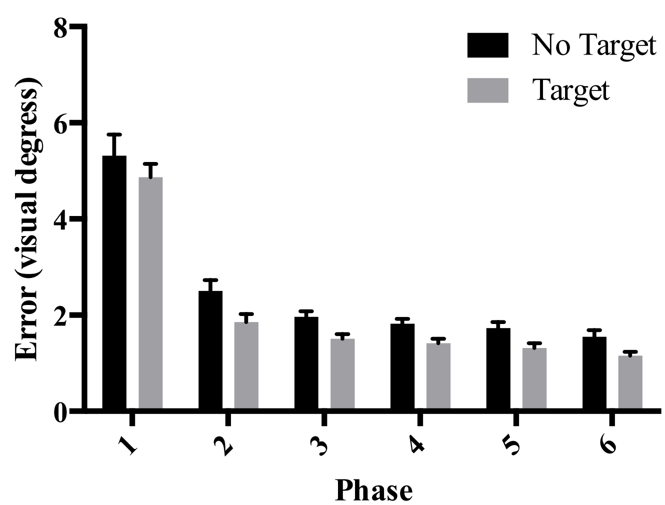

Figure 4.5 Mean error size across phases for full target- and no target-feedback PA blocks. Error bars indicate standard error of the mean.

Table 4.4 Absolute errors in each phase of both PA feedback conditions.

Feedback	Phase	Mean	SE	95% CI
No Target	1	5.31	0.44	4.40, 6.24
	2	2.50	0.23	2.03, 2.98
	3	1.96	0.12	1.70, 2.22
	4	1.82	0.10	1.62, 2.03
	5	1.73	0.12	1.47, 1.99
	6	1.55	0.14	1.27, 1.83
Target	1	4.87	0.27	4.30, 5.44
	2	1.86	0.17	1.52, 2.20
	3	1.51	0.10	1.30, 1.71
	4	1.42	0.10	1.22, 1.62
	5	1.31	0.10	1.10, 1.53
	6	1.16	0.08	0.98, 1.33

4.3.3 Full Target vs. No Target PA Feedback: RT

A 2x6 repeated-measures ANOVA with feedback (target, no target) and phase (1-6) as factors revealed no significant effect of phase on RT, $F(1.4, 29.4) = 2.6$, $p = .13$, ${}_p\eta^2 = .10$, no effect of feedback on RT, $F(1, 20) = 3.4$, $p = .08$, ${}_p\eta^2 = .14$, and no interaction between the two factors, $F(1.6, 32.2) = 2.2$, $p = .13$, ${}_p\eta^2 = .10$. Table 4.5 shows RT means, SE, and 95% CIs.

Table 4.5 Reaction time in each phase of both PA feedback conditions.

Feedback	Phase	Mean (ms)	SE (ms)	95% CI (ms)
No Target	1	671	013	644, 699
	2	664	010	643, 684
	3	666	013	638, 694
	4	667	010	646, 689
	5	668	013	641, 695
	6	670	012	645, 696
Target	1	696	021	652, 740
	2	687	022	642, 733
	3	677	014	647, 708
	4	671	012	646, 696

5	670	009	651, 689
6	671	011	648, 695

4.3.4 Full Target vs. No Target PA Feedback: MT

A 2x6 repeated-measures ANOVA with feedback (target, no target) and phase (1-6) as factors revealed no significant effect of feedback on MT, $F(1, 20) = 0.02$, $p = .87$, ${}_p\eta^2 = .001$, and no significant effect of phase on MT, $F(2.8, 56.8) = 0.31$, $p = .81$, ${}_p\eta^2 = .015$. There was, however, an interaction effect between feedback conditions, $F(5, 100) = 3.9$, $p < .01$, ${}_p\eta^2 = .16$. Bonferroni-adjusted pairwise comparisons revealed that mean MT was longer in the Target feedback condition compared to No Target feedback in phase 1, but not in any other phases. Table 4.6 shows mean MTs, SE, and 95% CIs.

Table 4.6 Movement time in each phase of both PA feedback conditions.

Feedback	Phase	Mean (ms)	SE (ms)	95% CI (ms)
No Target	1	258	030	194, 321
	2	268	031	203, 334
	3	271	032	205, 338
	4	270	036	195, 345
	5	265	034	195, 335
	6	281	037	203, 359
Target	1	293	029	232, 355
	2	260	030	196, 323
	3	266	033	198, 335
	4	268	034	197, 339
	5	275	034	205, 345
	6	263	034	193, 333

4.3.5 Full Target vs. No Target PA Feedback: Aftereffects

A 2x2 repeated-measures ANOVA with preceding PA direction (prims-left, prism-right) and preceding PA feedback (target, no target) as factors revealed a mild effect of prism adaptation feedback on mean PVSA error, $F(1, 19) = 3.8$, $p = .06$, ${}_p\eta^2 = .18$. Specifically, the no target-feedback condition produced slightly smaller PVSA errors than the full target-feedback condition. There was no effect of prism adaptation direction, $F(1, 19) = 1.06$, $p = .31$, ${}_p\eta^2 =.05$, and no interaction effect, $F(1, 19) = 0.13$, $= p = .72$, ${}_p\eta^2 = .007$, on mean PVSA errors. Means, standard errors, and 95% confidence intervals are presented in Table 4.7.

Table 4.7 PVSA errors produce by both PA feedback conditions and their respective direction of prism shift

Feedback	Prism Direction	Mean	SE	95% CI
No Target	Right	5.04	0.27	4.47, 5.61
	Left	4.90	0.33	4.21, 5.59
Target	Right	5.42	0.35	4.69, 6.15
	Left	5.46	0.34	4.76, 6.16

4.3.6 PA ERPs: Screen-Touch with Full Target-Feedback

The event of touching the screen with full target-feedback throughout the reach yielded three ERP components sensitive to accuracy (Figure 4.6), and one ERP component sensitive to phase (Figure 4.7).

4.3.6.1 Accuracy-Sensitive ERP component (1)

Mean voltage 30-130ms post-touch at electrode FCz was sensitive to accuracy, $F(2,42) = 9.18$, $p > .001$, $\eta p2 = .30$. Means, SE, and 95% CI corresponding to each level of accuracy are presented in Table 4.8. Bonferroni-adjusted post hoc comparisons revealed that Hits differed from both Small and Big Misses ($p < .05$). A contrasts analysis revealed a linear trend across each level of accuracy, lending some evidence that amplitude became more negative as accuracy worsened, $F(1,21) = 9.78$, $p = .005$, $\eta p2 =$

.32. These results support the hypothesis that an early ERN is evoked at screen touch on miss trials while the target is visible, and replicate the results reported in MacLean et al. (2015).

Table 4.8 First accuracy-sensitive negative-going ERP component. Evoked by screen- touch with full target-feedback. Amplitude measured at FCz, 30-130ms post-touch for each level of accuracy.

Feedback	**Error**	**Mean (μV)**	**SE (μV)**	**95% CI (μV)**
Full Target	Hit	7.2	0.9	5.4, 9
	Small Miss	5.2	0.8	3.4, 7
	Big Miss	4.7	0.9	2.8, 6.6

4.3.6.2 Accuracy-Sensitive ERP component (2)

Mean voltage 180-280ms post-touch at electrode Cz was also sensitive to accuracy, $F(1.3,27.33) = 9.58$, $p > .001$, $\eta p2 = .31$. Means, SE, and 95% CI corresponding to each level of accuracy are presented in Table 4.9. Bonferroni-adjusted post hoc comparisons revealed that Big Misses differed from both Small Misses and Hits ($p < .05$). A contrasts analysis revealed a linear trend across each level of accuracy, such that amplitude became more positive as accuracy worsened, $F(1,21) = 7.63$, $p = .012$, $\eta p2 = .28$. However, this effect is likely driven by the difference between big misses and both hits/small misses. These results may suggest that a Pe component was evoked at screen touch on large miss trials after the ERN response while the target was visible. Or, as postulated in Experiment 1, the component may simply reflect centro-maximal activity in the P2 time-range.

Table 4.9 Second accuracy-sensitive positive-going ERP component. Evoked by screen- touch with full target-feedback. Amplitude measured at Cz, 180-280ms post-touch for each level of accuracy

Feedback	Error	Mean (μV)	SE (μV)	95% CI (μV)
	Hit	16.8	1.3	14.1, 19.5
Full Target	Small Miss	16.3	1.2	13.8, 18.9
	Big Miss	19.9	1.2	17.4, 22.5

4.3.6.3 Accuracy-Sensitive ERP component (3)

Finally, mean voltage 270-370ms post-touch at electrode POz was sensitive to accuracy as well, $F(2,42) = 11.72$, $p > .001$, $\eta p2 = .36$. Means, SE, and 95% CI corresponding to each level of accuracy are presented in Table 4.10. Bonferroni-adjusted post hoc comparisons revealed that Big Misses differed from both Small Misses and Hits ($p < .05$). A contrasts analysis revealed a linear trend across each level of accuracy, such that amplitude became more positive as accuracy worsened, $F(1,21) = 11.15$, $p = .003$, $\eta p2 = .35$. As with the previous component, the linear trend is likely mainly driven by the difference between big misses and both hits/small misses. These results may suggest that a later parieto-occipital Pe component was evoked at screen touch on large miss trials after the initial ERN and first positive-going central component. Although the scalp distribution is more occipital than typically reported for a P300, it is noteworthy that the timing is consistent with a P300 component.

Table 4.10 Third accuracy-sensitive positive-going ERP component. Evoked by screen- touch with full target-feedback. Amplitude measured at POz, 270-370ms post-touch for each level of accuracy

Feedback	Error	Mean (μV)	SE (μV)	95% CI (μV)
	Hit	10.7	1.2	8.2, 13.1
Immediate	Small Miss	10.6	1.0	8.5, 12.7
	Big Miss	13.9	1.1	11.5, 16.3

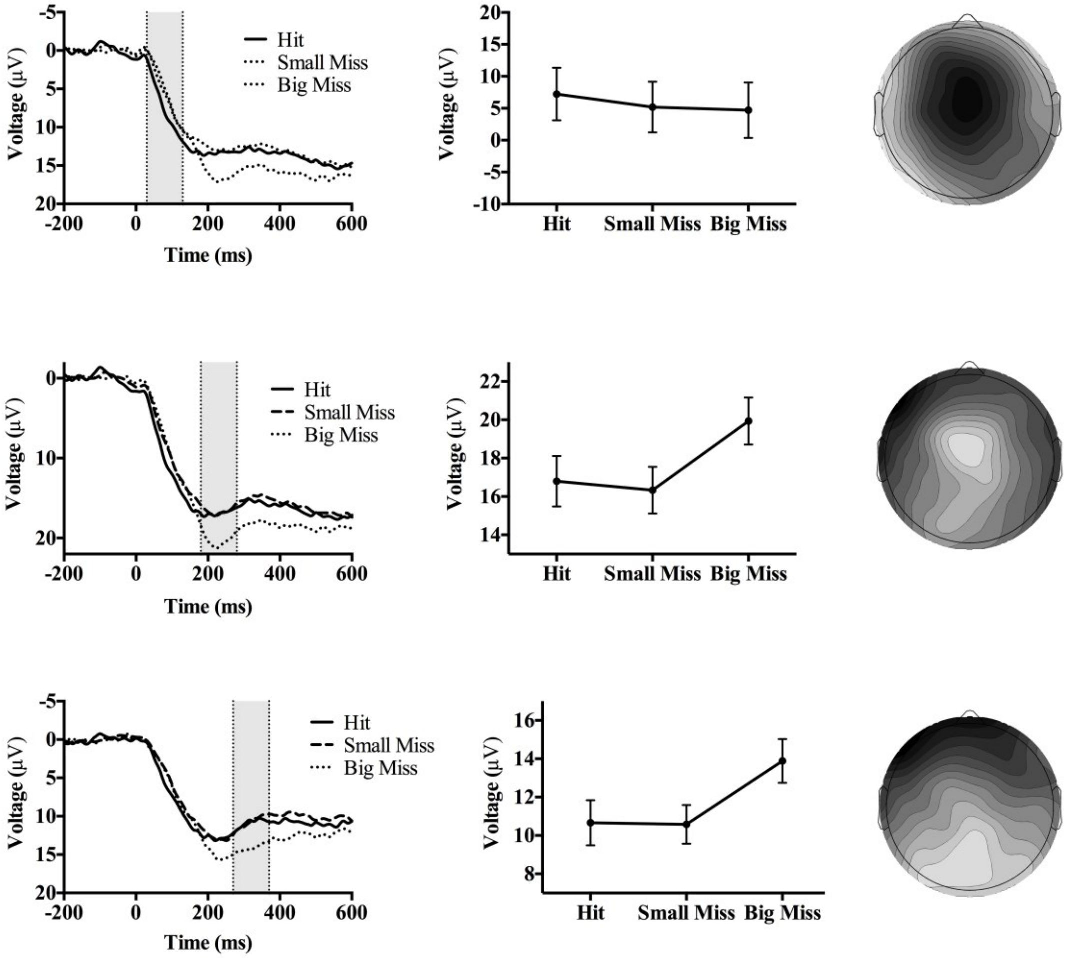

Figure 4.6 **Top Left**: average waveforms at FCz corresponding to each level of accuracy evoked by screen-touch with full target-feedback. The gray window corresponds to the time-window used to calculate mean difference between levels of accuracy. **Top Centre**: mean voltage 30-130ms at FCz corresponding to each levels of accuracy. Error bars represent standard error of the mean. **Top Right**: scalp topography derived by subtracting hit data from all miss data and corresponding to maximal difference 30-130ms. Darker tone indicates negative-going voltage. **Middle Left**: average waveforms at Cz corresponding to each level of accuracy evoked by screen-touch with full target-feedback. The gray window corresponds to the time-window used to calculate mean difference between levels of accuracy. **Middle Centre**: mean voltage 180-280ms at Cz corresponding to each levels of accuracy. Error bars represent standard error of the mean. **Middle Right**: scalp topography derived by subtracting hit data from all miss data and corresponding to maximal difference 180-280ms. Lighter tone indicates positive-going voltage. **Bottom Left**: average waveforms at POz

corresponding to each level of accuracy evoked by screen-touch with full target-feedback. The gray window corresponds to the time-window used to calculate mean difference between levels of accuracy. **Bottom Centre**: mean voltage 270-370ms at POz corresponding to each levels of accuracy. Error bars represent standard error of the mean. **Bottom Right**: scalp topography derived by subtracting hit data from all miss data and corresponding to maximal difference 270-370ms. Lighter tone indicates positive-going voltage.

4.3.7.4 Phase-Sensitive ERP component

Mean voltage 280-380ms post-touch at electrode CPz was sensitive to phase, $F(5,105) = 8.11$, $p > .001$, $\eta p2 = .28$. Means, SE, and 95% CI corresponding to each level of accuracy are presented in Table 4.11. Bonferroni-adjusted post hoc comparisons only revealed that P1-P4 differed from P5 ($p < .05$). A contrasts analysis, however, revealed a linear trend across each level of phase, such that amplitude became less positive from P1 to P6, $F(1,21) = 17.78$, $p = .001$, $\eta p2 = .46$. These results suggest that a parietal component was evoked by screen-touch with visible target and was largest in amplitude during early trials but diminished with adaptation. While this component may reflect similar phase-sensitive neural processing observed in earlier conditions at electrodes Oz and POz, the current scalp distribution (maximal at CPz) is more consistent with the traditional P300 component.

Table 4.11 Phase-sensitive positive-going ERP component. Evoked by screen-touch with full target-feedback. Amplitude measured at CPz, 280-380ms post-touch for each phase of adaptation

Feedback	Phase	Mean (μV)	SE (μV)	95% CI (μV)
Full Target	1	18.7	1.1	16.4, 21.1
	2	15.9	1.3	13.1, 18.6
	3	16.2	1.2	13.7, 18.8
	4	14.9	1.5	11.9, 17.9
	5	14.9	1.3	12.2, 17.7
	6	13.0	1.4	10.1, 15.8

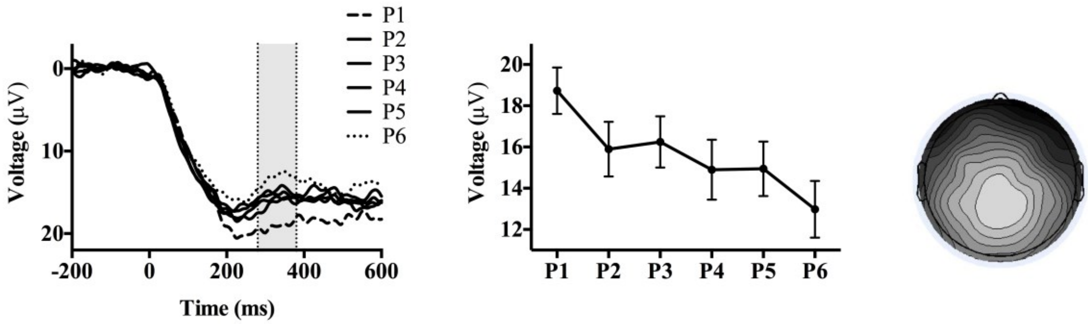

Figure 4.7 **Left**: average waveforms at CPz corresponding to each level of phase evoked by screen-touch with full target-feedback. The gray window corresponds to the time-window used to calculate mean difference between levels of phase. **Centre**: mean voltage 280-380ms at CPz corresponding to each levels of phase. Error bars represent standard error of the mean. **Right**: scalp topography derived by subtracting P6 data from P1 data and corresponding to maximal difference 280-380ms. Lighter tone indicates positive-going voltage.

4.3.7 PA ERPs: Screen-Touch with No Target-Feedback

The event of touching the screen without any target-feedback yielded two ERP components sensitive to accuracy (Figure 4.8), and one ERP component sensitive to phase (Figure 4.10).

4.3.7.1 Accuracy-Sensitive ERP component (1)

Mean voltage 155-205ms post-touch at electrode Cz was sensitive to accuracy, $F(2,42) = 8.36$, $p = .001$, $\eta p2 = .28$. Means, SE, and 95% CI corresponding to each level of accuracy are presented in Table 4.12. Bonferroni-adjusted post hoc comparisons revealed that only Hits and Big Misses differed from each other ($p < .05$). A contrasts analysis revealed a linear trend across levels of accuracy, lending some evidence that amplitude became more positive as accuracy worsened, $F(1,21) = 13.38$, $p = .001$, $\eta p2 =$

.34. These results suggest that a centro-maximal component, similar to a Pe, was evoked at screen touch on miss trials without target-feedback. As noted previously, the component may also simply reflect central error-sensitivity in the P2 time-range.

Table 4.12 First accuracy-sensitive positive-going ERP component. Evoked by screen- touch with no target-feedback. Amplitude measured at Cz, 155-205ms post-touch for each level of accuracy

Feedback	**Error**	**Mean (μV)**	**SE (μV)**	**95% CI (μV)**
No Target	Hit	10.5	1.3	7.9, 13.1
	Small Miss	12.2	1.0	10, 14.4
	Big Miss	13.4	1.2	11, 15.8

4.3.7.2 Accuracy-Sensitive ERP component (2)

Mean voltage 270-370ms post-touch at electrode POz was also sensitive to accuracy, $F(2,42) = 8.14$, $p = .001$, $\eta p2 = .28$. Means, SE, and 95% CI corresponding to each level of accuracy are presented in Table 4.13. Bonferroni-adjusted post hoc comparisons revealed that Big Misses differed from both Hits and Small Misses ($p < .05$). A contrasts analysis revealed a linear trend across each level of accuracy, such that amplitude became more positive as accuracy worsened, $F(1,21) = 13.61$, $p = .001$, $\eta p2 = .39$. These results suggest that a later more parieto-occipital component was also evoked at screen touch on miss trials without target visible after the centro-maximal component. As noted before, the component may reflect a late Pe but also has timing consistent with the P300 – albeit more occipital than normally reported.

Table 4.13 Second accuracy-sensitive positive-going ERP component. Evoked by screen- touch with no target-feedback. Amplitude measured at POz, 270-370ms post-touch for each level of accuracy.

Feedback	**Error**	**Mean (μV)**	**SE (μV)**	**95% CI (μV)**
No Target	Hit	6.98	1.23	4.42, 9.54
	Small Miss	7.85	0.84	6.11, 9.59

Big Miss	9.52	0.85	7.76, 11.28

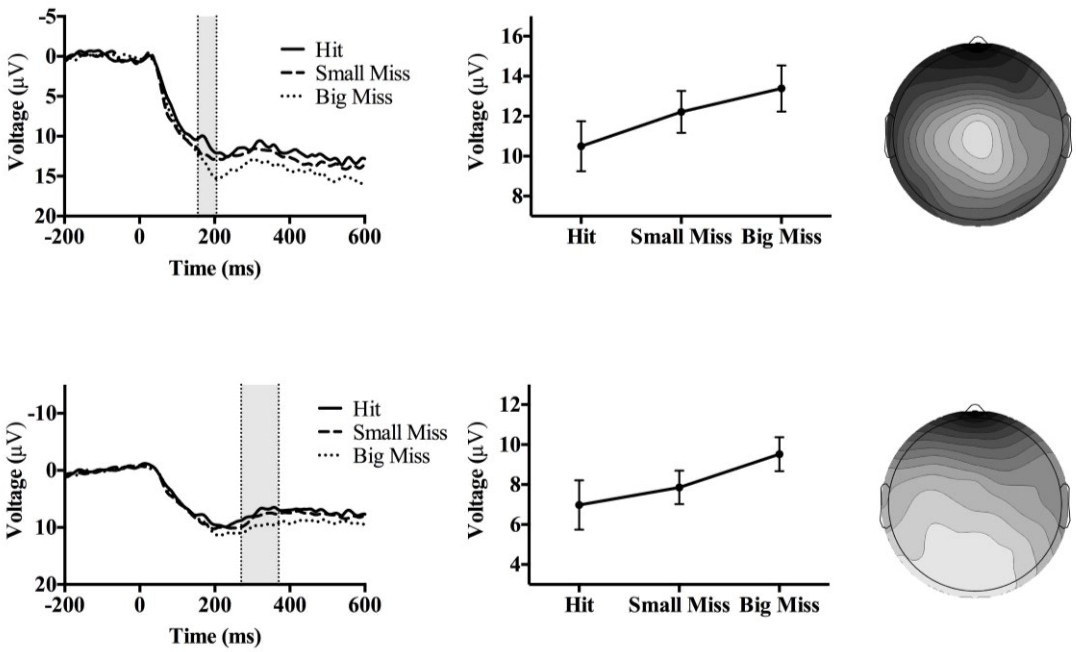

Figure 4.8 **Top Left**: average waveforms at Cz corresponding to each level of accuracy evoked by screen-touch with no target-feedback. The gray window corresponds to the time-window used to calculate mean difference between levels of accuracy. **Top Centre**: mean voltage 155-205ms at Cz corresponding to each levels of accuracy. Error bars represent standard error of the mean. **Top Right**: scalp topography derived by subtracting hit data from all miss data and corresponding to maximal difference 155-205ms. Lighter tone indicates positive-going voltage. **Bottom Left**: average waveforms at POz corresponding to each level of accuracy evoked by screen-touch with no target-feedback. The gray window corresponds to the time-window used to calculate mean difference between levels of accuracy. **Bottom Centre**: mean voltage 270-370ms at POz corresponding to each levels of accuracy. Error bars represent standard error of the mean. **Bottom Right**: scalp topography derived by subtracting hit data from all miss data and corresponding to maximal difference 270-370ms. Lighter tone indicates positive-going voltage.

4.3.7.4 Absent ERN

Visual inspection of accuracy waveforms did not reveal an ERN component evoked by screen-touch with no target-feedback. To confirm this observation, mean voltage 30-130ms post-touch at electrode FCz (latency and electrode of ERN response in previous condition) was submitted to a repeated-measures ANOVA with accuracy as the only factor. The analysis revealed no effect of accuracy at that time-range, $F(2,42) = 2.16$, $p = .128$, $\eta p2 = .09$. Figure 4.9 illustrates this null effect.

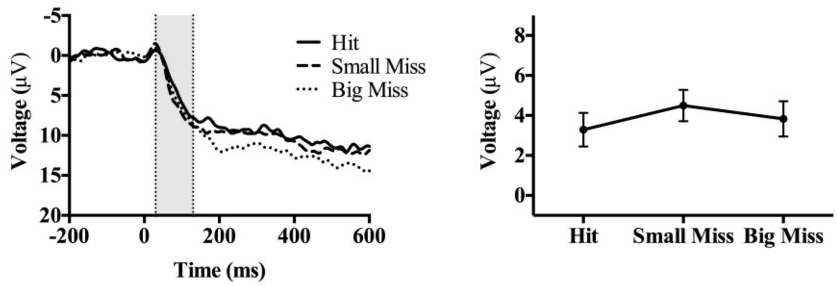

Figure 4.9 **Top Left**: average waveforms at FCz corresponding to each level of accuracy evoked by screen-touch with delayed feedback. The gray window corresponds to the time-window used to calculate mean difference between levels of accuracy. **Top Centre**: mean voltage 30-130ms at FCz corresponding to each levels of accuracy. Error bars represent standard error of the mean. **Top Right**: scalp topography derived by subtracting hit data from all miss data and corresponding to maximal difference 30-130ms. Darker tone indicates negative-going voltage.

4.3.7.4 Phase-Sensitive ERP component

Mean voltage 210-310ms post-touch at electrode CPz was sensitive to phase, $F(5,105) = 6.92$, $p < .001$, $\eta p2 = .25$. Means, SE, and 95% CI corresponding to each level of accuracy are presented in Table 4.14. Bonferroni-adjusted post hoc comparisons only revealed that P1 differed from P3, P4, and P6 ($p < .06$). A contrasts analysis revealed a linear trend across each level of phase, such that amplitude became less positive from P1 to P6, $F(1,21) = 14.23$, $p = .001$, $\eta p2 = .40$. The evidence suggests that a parietal component was sensitive to phase of adaptation. While this component may reflect similar phase-sensitive neural processing observed in earlier conditions at electrodes Oz and POz, the current scalp distribution (maximal at CPz) is more consistent with the traditional P300 component.

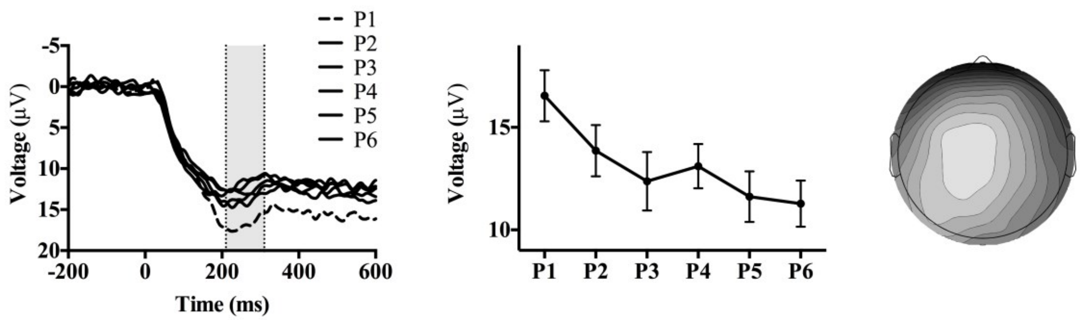

Figure 4.10 **Left**: average waveforms at CPz corresponding to each level of phase evoked by screen-touch with delayed feedback. The gray window corresponds to the time-window used to calculate mean difference between levels of phase. **Centre**: mean voltage 210-310ms at CPz corresponding to each levels of phase. Error bars represent standard error of the mean. **Right**: scalp topography derived by subtracting P6 data from P1 data and corresponding to maximal difference 210-330ms. Lighter tone indicates positive-going voltage.

Table 4.14 Phase-sensitive positive-going ERP component. Evoked by screen-touch with no target-feedback. Amplitude measured at CPz, 210-310ms post-touch for each phase of adaptation

Feedback	**Phase**	**Mean (μV)**	**SE (μV)**	**95% CI (μV)**
No Target	1	16.5	1.2	14, 19.1
	2	13.9	1.3	11.3, 16.5
	3	12.4	1.4	9.4, 15.3
	4	13.1	1.1	10.9, 15.4
	5	11.6	1.2	9.1, 14.2
	6	11.3	1.1	8.9, 13.6

4.4 Discussion

The purpose of Experiment 3 was to investigate the effect of undergoing PA with hand-feedback, but not target-feedback at the termination of reaching movements. Participants performed memory-guided reaching without onset of target-feedback at screen-touch. Participants also performed more traditional bocks of PA with the target visible during and after the entire reach. This latter condition was a replication of MacLean et al. (2015) and primarily served as a control condition. Importantly, it was hypothesized that both conditions would produce equal magnitude of aftereffects, although the no-target-feedback condition might show larger errors across adaptation blocks.

As observed in MacLean et al. (2015), it was predicted that the full-feedback condition would evoke an early ERN-like component on miss trials, as well as a P300-like component sensitive to phase of adaptation. It was difficult to predict whether no-target-feedback would evoke an early ERN. The no-target-feedback condition, however, was designed to limit explicit error processing thus also designed to eliminate contribution from the ERN and FRN generating system. A P300-like component sensitive to phase, or a more parieto-occipital component, however, was still predicted to be evoked by hand-feedback in the no-target-feedback condition.

Analysis of slopes and intercepts in the PA (collapsed across feedback conditions), sham, and baseline conditions confirm that typical direct effects, adaptation, aftereffects, and de-adaptation took place. Prism-right and Prism-left conditions, respectively, produced large errors in the rightward and leftward direction at the onset of blocks, and showed error correction towards baseline levels of accuracy across trials. Sham(right) and sham(left) both produced errors at the onset of blocks, respectively, in the leftward and rightward direction – larger than baseline, but smaller than PA blocks. Sham blocks also showed error correction towards baseline level of accuracy as trials progressed. Figure 4.11 compares adaptation slopes across all three experiments thus far.

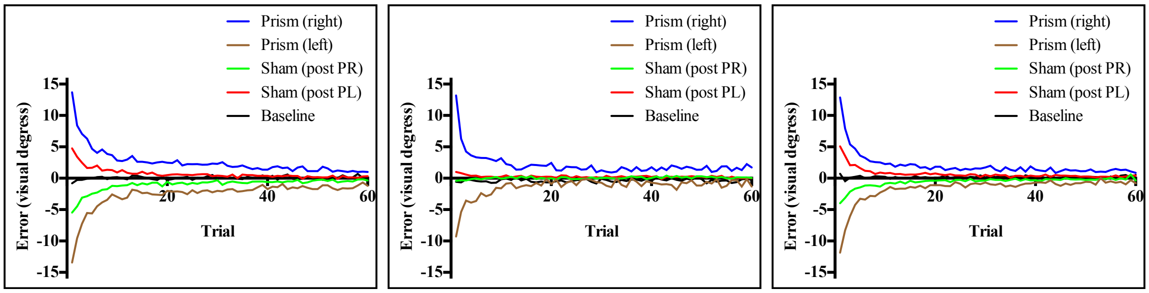

Figure 4.11 **Left**: Error-by-trial adaptation in Experiment 1. **Centre**: Error-by-trial adaptation in Experiment 2. **Right**: Error-by-trial adaptation in Experiment 3

Somewhat contrary to our hypothesis, the target-feedback and the no-target feedback conditions had similar adaptation slopes – suggesting participants were able to adapt equally well to the prism displacement whether target-feedback was made available to them during/after the reach or not. However, the analysis also revealed that mean errors across all phases in the no-target feedback condition were larger than those in the full target-feedback condition. Participants, therefore, were better at correcting errors in the full target-feedback condition. Importantly, the mean errors in PVSA blocks following both conditions were nearly identical. The full target-feedback condition showed modestly larger aftereffects, only by approximately 0.45 visual degrees. Clearly, however, the no-target-feedback condition lead to fairly robust aftereffects, much larger than those reported in Experiment 2 where direct hand-feedback was not available. Figure 4.12 compares mean PVSA error in Experiment 1, Experiment 2, and from both feedback conditions in Experiment 3. Both RT and MT were not particularly sensitive to feedback conditions, although MT was slightly slower in the target-feedback condition during Phase 1 of adaptation.

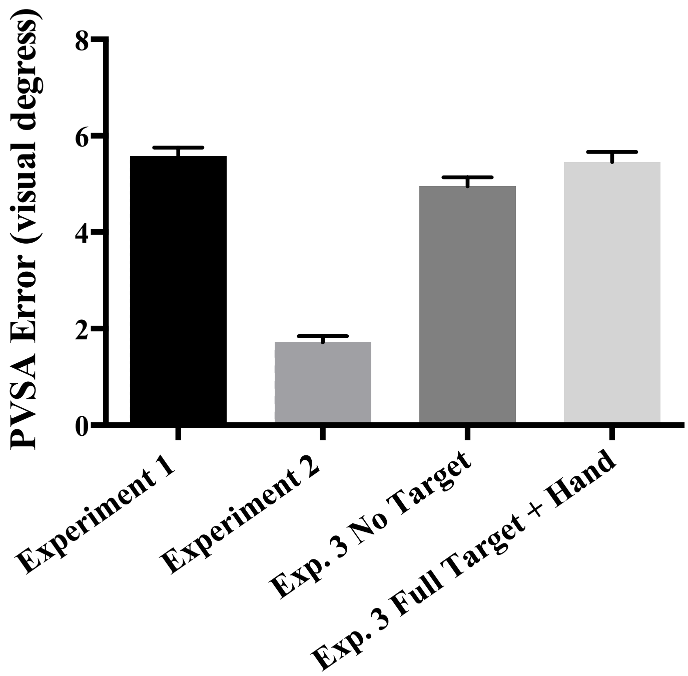

Figure 4.12 Mean PVSA errors in Experiment 1 (averaged across immediate and delayed feedback), Experiment 2 (averaged across immediate and delayed feedback), no-target-feedback in Experiment 3, and full target-feedback in Experiment 3.

The event of screen-touch with full target-feedback during the entire reach did indeed evoke an early ERN component on miss-trials similar to MacLean et al. (2015). Screen touch with full target-feedback also evoked two positive-going components sensitive to large errors: a positive voltage peaking ~190ms post touch at central electrode sites, then another positive voltage peaking ~330ms at parietal electrode sites. Consistent with our hypothesis, a parietal component sensitive to phase was also evoked by screen-touch with the target visible during the entire reach, also similar to MacLean et al. (2015), albeit maximal at slightly more centro-parietal electrode.

The ERN and parietal component results can be said to closely replicate MacLean et al. (2015), which had conditions very similar to those in Experiment 3 with full target-feedback. The phase-sensitive parietal component is particularly not surprising seeing as participants produced strong aftereffects in this condition. This result supports the possibility that the phase-sensitive parietal, parieto-occipital, and/or traditional P300 components observed across these experiments reflect adaptive perceptual learning processes.

Interestingly, the accuracy-sensitive ERP components evoked by this condition also closely match those evoked in Experiment 1 by screen-touch with delayed target-feedback. Following the early ERN component – which was perhaps evoked by onset of hand-feedback – two positive-going components were evoked at Cz, then POz. These again share some similarity to the P3a and P3b components. Therefore, in the present condition, large errors may have increased involvement of attention-related processes at screen-touch as well as subsequent information-integration processes. It is difficult to determine whether these should rather be treated as Pe-like components reflecting increased awareness of errors with the available data. As discussed in Experiment 1, these components could possibly reflect a single component that simply drifts from centro-maximal sites to parieto-occipital sites across time. The data certainly suggests that during conditions of full target-feedback, participant undergo additional feedback processing after the ERN when they miss the target by a large margin.

The fact that these ERPs resemble the condition of memory-guided PA with delayed target-feedback is important. First, it might suggest that participant in Experiment 1, with delayed feedback, were indeed recruiting a very reliable memory of target to make sound accuracy judgment upon seeing their finger. Indeed, early error processing seems identical whether target-feedback is fully available or delayed. Secondly, because conditions of *immediate* target-feedback evoked a late (~300ms peaking) FRN – likely evoked by target-feedback rather than hand-feedback – it suggests that when target-feedback is soon-to-be-available, participants withhold any sort of feedback processing until actual target-feedback onset. In other words, the *anticipation* of an upcoming stimulus (that may provide error information) will actually delay ongoing error monitoring immediately before the presentation of that anticipated stimulus. Thus, when target-feedback is fully available during the entire reach, participants respond to hand-feedback with an early ERN because they are not anticipating upcoming target information – it is already there. Likewise, when target-feedback is delayed by 800ms, hand-feedback can evoke an ERN because error monitoring is not "withheld" in anticipation of a feedback stimulus immediately at screen-touch.

Screen-touch with no target-feedback also yielded interesting results. Despite the observation that screen-touch with delayed target feedback in Experiment 1 could evoke an early ERN component, the current condition – without any target-feedback – did not evoke an ERN components. The preceding discussion would suggest that, without any anticipation of upcoming stimuli, the provision of hand-feedback would indeed evoke an early ERN component. Here, however, it appears that when participants anticipate no target-feedback at all (i.e. not even delayed) they do not undergo the type of error processing that generates an ERN component. This result, along with the absence of a later FRN, actually matches our predicted outcome and suggests that participants underwent adaptation to the prisms without involvement of a neural RL system. It would also suggest that the ERN/FRN-generating system – a neural RL system according to Holroyd and Coles – does not necessarily have to be recruited during adaptation in order to produce strong aftereffects. Finally, it would also suggest that in the absence of RL systems, other learning systems (e.g. perceptual) are sufficient to compensate for errors caused by the visual shift – albeit to a lesser degree than when the ERN is observed (e.g. see Figure 4.5).

It cannot be said, however, that participants did not undergo any error processing in the no-target-feedback condition. Indeed, the event of screen-touch did evoke two positive-going components that resemble those previously reported in Experiment 1: a positive voltage sensitive to errors first peaking ~190ms post-touch at central electrode sites, then a second positive voltage peaking ~330ms at more parietal electrode site. These components indeed match those observed in the present experiment's full target-feedback condition and Experiment 1's delayed target-feedback condition. Those results, in combination with the absence of Pe components and weaker aftereffects in Experiment 2, begin to suggest that the central to parieto-occipital response may also play some critical role in producing strong aftereffects. At minimum, there is strong evidence that the central to parieto-occipital components are evoked specifically by hand-feedback and show stronger activity in response to errors or early phases of adaptation. Although these components were not evoked by errors in the immediate feedback condition from Experiment 1 – where strong aftereffects were still produced – it is interesting that similar central to parieto-occipital components were still observed in that conditions, but sensitive to phase instead. At the very least, the present results suggest that participants undergo some form of error processing, albeit not the ERN, at screen-touch with no provision of target-feedback.

Finally, as hypothesized, screen-touch without any target-feedback evoked a P300-like component sensitive to phase, also similar to the parieto-occipital components reported in Experiment 1, diminishing in voltage from early to late trials. This result supports the ongoing evidence that a parietal P300-like component, or parieto-occipital component sensitive to phase, evoked with hand-feedback present may reflect adaptive perceptual learning, e.g. realignment, that leads to strong aftereffects. Indeed, both feedback conditions in the present experiment evoked a phase-sensitive parietal component, independent of error, and both yielded strong aftereffect exceeding those observed in Experiment 2.

The presence of both the phase-sensitive parietal component and the accuracy-sensitive central-to-parieto-occipital components in the no-target-feedback condition also suggests that the neural processes they index are sufficient to compensate for errors over the course of PA blocks. In other words, they do not just generate after effects but also enable participants to correct for large reaching errors. Because Experiment 2 also showed error compensation, but only evoked the purported RL system that generates the FRN, our results certainly confirm that adaptive behaviour, i.e. adapting to prisms, can be supported by a number of different systems.

CHAPTER 5: GENERAL DISCUSSION

Experiments 1, 2 and 3 investigated brain potentials evoked by various provisions of feedback at the end of reaching movements during blocks of prism adaptation (PA). A general goal of these studies was to identify ERP components reflecting activity of different neural systems that support perceptual-motor adaptation exhibited during PA tasks. More specifically, the studies were designed to identify ERP components reflecting perceptual learning processes – e.g. spatial realignment – that are engaged during PA and that contribute to robust aftereffects. These aftereffects have been shown to improve symptoms of visuo-spatial neglect (VSN, neglect), a condition experienced after stroke that results in difficulties attending and responding to contralesional stimuli. It was stated that PA's use as a clinical treatment for VSN could be ultimately enhanced by identifying ERP components that reflect spatial realignment, or simply perceptual learning processes. To that end, it was also stated that these experiments could ultimately further develop PA treatment for VSN by two means: (1) by improving knowledge of the basic brain processes involved in adaptation, and (2) by improving our means to understand how, or why certain persons with neglect and/or populations respond poorly to PA while others do not.

Each experiment measured ERP components across different feedback conditions that were sensitive to either accuracy (i.e. error) or phase of adaptation. Taken together, the results reveal a number of interesting finding regarding basic feedback processing during PA. First, as it has already been shown in behavioural studies, our results confirm there can be dissociation between systems that lead to error correction across trials during PA and systems that lead to strong aftereffects after PA. The results here suggest that a neural system, or simply a neural event, that generates the FRN component is not critical to producing aftereffects, but can nonetheless lead to successful compensation of errors induced by the prisms. Similarly, the absence of an ERN component in Experiment 1 with immediate feedback as well as in Experiment 3 with no-target-feedback, despite producing robust aftereffects, would suggest the ERN-generating system is also not critical to aftereffects. If Holroyd and Coles (2002) are indeed correct about the shared generator of the ERN/FRN response, this would suggest specifically that the brain's neutral RL system is not critical to producing strong PA aftereffects.

A second system, or neural event, that generates two sequential positive-going components (central to parieto-occipital) was also shown to be sensitive to error trials however. Although these components are error-sensitive, they do not appear necessary to undergo error compensation, as they were not reported in, for example, Experiment 2 where errors were nonetheless successfully corrected. There is indeed some evidence, however, that these error sensitive central-to-parieto-occipital components play some role in enhancing aftereffects. Indeed, all PA conditions that produced strong aftereffects except for one (Experiment 1, immediate target-feedback) showed the central-to-parieto-occipital response evoked by screen-touch on error trials. Furthermore, the condition of immediate target-feedback in Experiment 1 did in fact evoke central-to-parieto-occipital components, but only sensitive to phase instead. The central-to-parieto-occipital components thus require further investigation, particularly seeing as they were not reported in MacLean et al. (2015). Their response to hand-feedback in the present set of studies, however, suggests they may at minimum be sensitive to discrepancies between the proprioceptive and visual system, although their contribution to aftereffects remains to be better elucidated.

The most interesting finding pertained to a parietal/parieto-occipital component sensitive to phase that was present in all PA conditions that led to strong aftereffects and was not present in conditions that led to weaker aftereffects. This component was evoked at screen-touch only when hand-feedback was available, suggesting it may be evoked as a response to the experience of perceptual discordance induced by the prisms (e.g. between proprioception and vision). Consistent with theories on the P300 and parietal P3b component observed in other ERP studies, the P300-like component observed here might reflect the integration of critical information into participants' working model of the environment. Thus, while the parietal/occipital component here shows an association to subsequent aftereffects, and may thus reflect perceptual learning like spatial realignment, it also might simply reflect the integration of information critical to *engaging* perceptual learning processes. Indeed, seeing as the parietal/occipital component was evoked by provisions of feedback that indicate perceptual discord, it might suggest the phase-sensitive response acts as an on-switch for a supplementary adaptive process, like spatial realignment, every time perceptual discord is encountered. Thus, across phases of adaptation, the signal for the "on-switch" tapers in amplitude concomitantly with a reduction in the amount of perceptual discord encountered.

It is also important to note the relationship these ERP components may share with neural regions involved in PA. Both the ERN and FRN, which appear sensitive to error information, have been source localized to anterior cingulate cortex (Dehaene et al., 1994; Herrmann et al., 2004; Ullsperger & von Cramon, 2001; Gehring & Willoughby, 2002; Van Veen & Carter, 2002; Debener et al., 2005). Danckert et al. (2008) reported increased activity in ACC during early error correction trials of prism adaptation. Our present results thus extend evidence that frontal brain regions are involved in recalibration processes during PA. The centro-parietal and parieto-occipital components sensitive to phase of adaptation may reflect activity within the parietal-cerebellar network that has also been shown to be involved in adaptation (Pisella et al., 2004; Chapman et al., 2010; Fernandez-Ruiz et al., 2007; Martin et al., 1996; Luaute et al., 2009; Clower et al., 1996). Indeed, both Clower et al. (1996) and Luaute et al. (2009) showed parietal cortex activity that reduced across trials of adaptation in a similar manner to the P300-like component reported here. Furthermore, activity at occipital electrode sites reported here may thus also reflect feedback information processed in the cerebellum. Specifically, according to the Luaute et al. (2009) and Chapman et al. (2008), the occipital activity may reflect error signals in the cerebellum corresponding to discrepancies between proprioceptive maps and visual maps.

Each experiment was not without limitations and confounds that should also be mentioned. Future studies must better elucidate the relationship that errors may have on positive-going central and parieto-occipital components. Indeed, as is evident in Figures A19-A21, the frequency and size of error tended to decrease across phases of adaptation. Thus, while the parieto-occipital component reported to be sensitive to phase may indeed respond differently to aiming errors compared to the FRN, it is difficult to say that it is evoked entirely independent of errors. Indeed, the resemblance between the phase-sensitive components here and the P300 component reported in the literature suggests that frequency, or probability of events may also play a role in modulating the parieto-occipital component. The phase-sensitive component may simply be sensitive to probability of accurate reaches, thus as frequency of hits increases, the amplitude of the parieto-occipital component diminishes. This interpretation would also fit with the theory that the P300 component reflects allocation of attention toward its evoking stimulus. Such as the case, the phase-sensitive P300-like components observed in Experiment 1 and 3 may simply reflects diminishing attention directed towards accurate hand-feedback as the probability of that stimulus increases.

The nature of blocking feedback conditions must also be considered in the interpretation of the ERP data. Blocking, for example, immediate and delayed feedback conditions was necessary in order to compare their respective aftereffects. This approach, however, can cause participants to adopt different performance strategies in anticipation of feedback events. For example, error-monitoring systems may be engaged differently depending on participants' expectation of feedback. This was indeed the case when comparing error-related components between the delayed feedback condition in Experiment 1 and the no-target feedback condition in Experiment 3. While both feedback events were identical, only the former condition evoked an ERN response. While this of course provides insight into how the brain processes errors during different conditions of PA, it also illustrates the effect of expectancy and strategy employed by participants over the course of entire blocks when consistent feedback is provided. Feedback-evoked ERPs should thus be interpreted conservatively, seeing as the content of feedback appears to interact with participants' error monitoring strategy. Thus, in future studies for example, not all provisions of target-feedback are certain to show an FRN if some other factor, e.g. valence, is modified.

Finally, it should also be considered that the ERP data measured here are only locked to feedback events. Thus all neural processes (e.g. recalibration, realignment) discussed as being associated with these ERPs are necessarily confined to neural events evoked shortly after onset of some visual feedback. Neural processes associated with realignment, for example, may simply not be able to be captured by the time-window around feedback-evoked brain potentials used in this study. Nonetheless, feedback-evoked potentials can provide a window into critical events that, downstream, engage realignment.

In reference to the overall goals of the thesis, the parietal/occipital component sensitive to phase of adaptation, perhaps indexing a P300 as originally hypothesized, may present an opportunity to ultimately improve PA for persons with neglect. First of all, if the parietal/occipital component indeed indexes some process associated with spatial realignment, then it provides a means to assess whether a given PA paradigms is recruiting adaptive processes leading to strong aftereffects. For example, with increasing interest in brain training to improve cognitive or motor impairments (Green & Bavelier, 2008; Lusting et al., 2009), it is not surprising that a procedure like PA could end up in some computerized take-home format for persons with neglect (e.g. Champod et al., 2014). Such PA paradigms face design questions concerning how feedback can be made more interesting to a game-user. By appealing to computerized games, designers can use any number of symbolic or virtual representations of arm movement to make the PA tasks more interesting. For example, would a persons with neglect prefer a virtual volley-ball game or just a series of repetitive pointing movements towards vertical lines? The problem, of course, is that both virtual (Veilleux & Proteau, 2015) and symbolic (Wilms

& Malá, 2010) representations of hand during PA have been shown to produce relatively weak aftereffects. There might, however, be a middle ground where feedback can take on some virtual characteristics of arm movements but still maintain the purported assumption of unity described by Welch & Warren (1980). This presents an opportunity where ERPs can be used to test whether different provisions of feedback are indeed evoking the desired perceptual learning processes. An instance where a newly designed PA paradigm leads to weak aftereffects can be studies with ERPs to determine if the post-adaptation results are due to lack of perceptual learning (i.e. no phase-sensitive parietal/occipital component). This also suggests a role for other ERP components identified in the preceding experiments. Event-related potentials can show, for example, that a PA paradigm evokes error-sensitive RL processes, but not phase sensitive parietal/occipital responses. This could suggest to designers of PA paradigms that feedback provisions could be modified to reduce reliance one particular learning system in order to emphasize another. These examples need not be specific to the development of game-like PA paradigms. In fact, any PA paradigm with discrete provisions of feedback could be tested to determine what kind of learning mechanisms are being evoked. Thus by employing the ERP technique, the development of PA treatments for persons with neglect can be improved by determining what type of learning (e.g. RL vs. perceptual) is taking place.

ERPs can also be used to better understand how persons with neglect are responding to PA. There are of course many instances where persons with neglect may not respond to PA with improved symptoms (e.g. Humphreys et al., 2006; Nijboer et al., 2008). Although, a number of factors may account for how persons with neglect exhibit symptoms and respond to PA, such as differences in lesions sites (e.g. Chen et al., 2014) or even trunk orientation during tests (Karnath et al., 1991), there are limited tools to reliably determine why a person with neglect responds well or poorly to PA. The use of ERPs, which are substantially less expensive to use than other neuroimaging tools such as MRI, could thus provide a relatively quick and cost-effective means determine how persons with neglect are responding to PA treatment. Feedback-evoked brain potentials can potentially inform clinicians as to why a persons with neglect is responding poorly to PA by providing objective evidence that their perceptual learning system is not being engaged (i.e. no phase-sensitive parietal/occipital component). Evidence that a person with neglect is only sensitive to explicit error information (i.e. target-feedback errors) might suggest a need to recruit a different treatment approach, or a different PA paradigm that better suits that person's needs. At the very least, the identification of a phase-sensitive parietal/occipital component – perhaps indexing perceptual learning processes – adds one additional variable that can be looked at when assessing persons with neglect.

The preceding experiments are only the first few steps in applying the ERP methodology to PA for VSN treatment. Naturally, future studies must test similar conditions of feedback during PA with both elderly populations as well as persons who have had a stroke and are experiencing neglect symptoms. Stroke victims are predominantly older than those reported in Experiments 1, 2, and 3, thus a replication of the current findings among older participants would be necessary to have a proper control group. Although the current application of ERPs shows promise, difference between an aged brain with a lesion and a young healthy brain means ERPs may not manifest identically between the two groups. Further investigation among an older and a VSN population is certainly warranted.

REFERENCES

Angeli, V., Benassi, M. G., & Làdavas, E. (2004a). Recovery of oculo-motor bias in neglect patients after prism adaptation. *Neuropsychologia, 42(9),* 1223–34.

Angeli, V., Meneghello, F., Mattioli, F., & Ladavas, E. (2004b). Mechanisms underlying visuo-spatial amelioration of neglect after prism adaptation. *Cortex, 40,* 155–156.

Anguera, J. A., Seidler, R. D., & Gehring, W. J. (2009). Changes in performance monitoring during sensorimotor adaptation. *Journal of neurophysiology*, *102*(3), 1868-1879.

Aston-Jones, G., Rajkowski, J., & Kubiak, P. (1997). Conditioned responses of monkey locus coeruleus neurons anticipate acquisition of discriminative behavior in a vigilance task. *Neuroscience*, *80*(3), 697-715.

Aston-Jones, G., Rajkowski, J., Kubiak, P., & Alexinsky, T. (1994). Locus coeruleus neurons in monkey are selectively activated by attended cues in a vigilance task. *The Journal of Neuroscience*, *14*(7), 4467-4480.

Becker, D. E., & Shapiro, D. (1980). Directing attention toward stimuli affects the P300 but not the orienting response. *Psychophysiology*,*17*(4), 385-389. doi:10.1111/j.1469-8986.1980.tb00168.x

Bedford, F. (1993). Perceptual learning. *The psychology of learning and motivation*, *30*, 1-60.

Bediou, B., Koban, L., Rosset, S., Pourtois, G., & Sander, D. (2012). Delayed monitoring of accuracy errors compared to commission errors in ACC. *Neuroimage*, *60*(4), 1925-1936.

Bjoertomt, O., Cowey, A., & Walsh, V. (2002). Spatial neglect in near and far space investigated by repetitive transcranial magnetic stimulation. *Brain*, *125*(9), 2012-2022.

Boldt, A., & Yeung, N. (2015). Shared neural markers of decision confidence and error detection. *The Journal Of Neuroscience*, *35*(8), 3478-3484. doi:10.1523/JNEUROSCI.0797-14.2015

Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological review*, *108*(3), 624.

Bowen, A., & Lincoln, N. B. (2007). Cognitive rehabilitation for spatial neglect following stroke. Cochrane Database of Systematic Reviews Issue 2. Art. No.: CD003586.DOI: 10.1002/14651858.CD003586.pub2

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial vision*, *10*, 433-436.

Brighina, F., Bisiach, E., Oliveri, M., Piazza, A., La Bua, V., Daniele, O., & Fierro, B. (2003). 1 Hz repetitive transcranial magnetic stimulation of the unaffected hemisphere ameliorates contralesional visuospatial neglect in humans. *Neuroscience letters*, *336*(2), 131-133.

Bultitude, J. H., & Rafal, R. D. (2010). Amelioration of right spatial neglect after visuo-motor adaptation to leftward-shifting prisms. *Cortex; a journal devoted to the study of the nervous system and behavior*, *46*(3), 404.

Carlton, L. G. (1981). Visual information: The control of aiming movements. *The Quarterly Journal of Experimental Psychology*, *33*(1), 87-93.

Cazzoli, D., Müri, R. M., Schumacher, R., von Arx, S., Chaves, S., Gutbrod, K., ... & Nyffeler, T. (2012). Theta burst stimulation reduces disability during the activities of daily living in spatial neglect. *Brain*, *135*(11), 3426-3439.

Champod, A. S., Taylor, K., & Eskes, G. A. (2014). Development of a new computerized prism adaptation procedure for visuo-spatial neglect. *Journal of neuroscience methods*, *235*, 65-75.

Chen, P., Goedert, K. M., Shah, P., Foundas, A. L., & Barrett, A. M. (2014). Integrity of medial temporal structures may predict better improvement of spatial neglect with prism adaptation treatment. *Brain imaging and behavior*, *8*(3), 346-358.

Clower, D. M., & Boussaoud, D. (2000). Selective use of perceptual recalibration versus visuomotor skill acquisition. *Journal Of Neurophysiology*, *84*(5), 2703-2708.

Datié, A.-M., Paysant, J., Destainville, S., Sagez, A., Beis, J.-M., & André, J.-M. (2006). Eye movements and visuoverbal descriptions exhibit heterogeneous and dissociated patterns before and after prismatic adaptation in unilateral spatial neglect. European Journal of Neurology : The Official Journal of the European Federation of Neurological Societies, 13(7), 772–9.

Debener, S., Ullsperger, M., Siegel, M., Fiehler, K., Von Cramon, D. Y., & Engel, A. K. (2005). Trial-by-trial coupling of concurrent electroencephalogram and functional magnetic resonance imaging identifies the dynamics of performance monitoring. *The Journal of Neuroscience*, *25*(50), 11730-11737.

Dehaene, S., Posner, M. I., & Tucker, D. M. (1994). Localization of a neural system for error detection and compensation. *Psychological Science*, 303-305.

Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of neuroscience methods*, *134*(1), 9-21. doi:10.1016/j.jneumeth.2003.10.009

Dijkerman, H. C., McIntosh, R. D., Milner, A. D., Rossetti, Y., Tilikete, C., & Roberts, R. C. (2003). Ocular scanning and perceptual size distortion in hemispatial neglect: effects of prism adaptation and sequential stimulus presentation. *Experimental Brain Research, 153*(2), 220–230.

Donchin, E., & Cohen, L. (1967). Averaged evoked potentials and intramodality selective attention. *Electroencephalography & Clinical Neurophysiology*, *22*(6), 537-546. doi:10.1016/0013-4694(67)90061-2

Donchin, E., & Coles, M. G. (1988). Is the P300 component a manifestation of context updating?. *Behavioral and brain sciences, 11*(03), 357-374.

Duncan- Johnson, C. C., & Donchin, E. (1977). On quantifying surprise: The variation of event- related potentials with subjective probability. *Psychophysiology*, *14*(5), 456-467.

Dunning, J. P., & Hajcak, G. (2007). Error-related negativities elicited by monetary loss and cues that predict loss. *Neuroreport*, *18*(17), 1875-1878.

Elliott, D., Helsen, W. F., & Chua, R. (2001). A century later: Woodworth's (1899) two-component model of goal-directed aiming. *Psychological bulletin*,*127*(3), 342.

Elliott, D., & Madalena, J. (1987). The influence of premovement visual information on manual aiming. *The Quarterly Journal of Experimental Psychology*, *39*(3), 541-559.

Endrass, T., Franke, C., & Kathmann, N. (2005). Error awareness in a saccade countermanding task.*Journal Of Psychophysiology*, *19*(4), 275-280. doi:10.1027/0269-8803.19.4.275

Eskes, G. A., & Butler, B. (2006). Using limb movements to improve spatial neglect: the role of functional electrical stimulation. *Restorative neurology and neuroscience*, *24*(4), 385-398.

Facchin, A., Beschin, N., Toraldo, A., Cisari, C., & Daini, R. (2013). Aftereffect induced by prisms of different power in the rehabilitation of neglect: a multiple single case report. *Neurorehabilitation*.

Falkenstein, M., Hohnsbein, J., Hoormann, J., & Blanke, L. (1991). Effects of crossmodal divided attention on late ERP components. II. Error processing in choice reaction tasks. *Electroencephalography and clinical neurophysiology*,*78*(6), 447-455.

Farnè, A., Rossetti, Y., Toniolo, S., & Ladavas, E. (2002). Ameliorating neglect with prism adaptation: visuo-manual and visuo-verbal measures. *Neuropsychologia, 40*(7), 718-729.

Ferber, S., Danckert, J., Joanisse, M., Goltz, H. C., & Goodale, M. A. (2003). Eye movements tell only half the story. *Neurology*, *60*(11), 1826-1829.

Fortis, P., Maravita, A., Gallucci, M., Ronchi, R., Grassi, E., Senna, I., ... & Vallar, G. (2010). Rehabilitating patients with left spatial neglect by prism exposure during a visuomotor activity. *Neuropsychology*, *24*(6), 681.

Frassinetti, F., Angeli, V., Meneghello, F., Avanzi, S., & Làdavas, E. (2002). Long-lasting amelioration of visuospatial neglect by prism adaptation. *Brain*, *125*(3), 608-623.

Friedman, D., Cycowicz, Y. M., & Gaeta, H. (2001). The novelty P3: An event-related brain potential (ERP) sign of the brain's evaluation of novelty. *Neuroscience And Biobehavioral Reviews*, *25*(4), 355-373. doi:10.1016/S0149-7634(01)00019-7

Gehring, W. J., Goss, B., Coles, M. G. H., Meyer, D. E., & Donchin, E. (1993). A Neural System for Error Detection and Compensation. *Psychological Science, 4*(6), 385–390.

Gehring, W. J., & Willoughby, A. R. (2002). The medial frontal cortex and the rapid processing of monetary gains and losses. *Science*, *295*(5563), 2279-2282.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in neurosciences*, *15*(1), 20-25.

Green, C. S., & Bavelier, D. (2008). Exercising your brain: a review of human brain plasticity and training-induced learning.

Hajcak, G., McDonald, N., & Simons, R. F. (2003). To err is autonomic: Error- related brain potentials, ANS activity, and post- error compensatory behavior.*Psychophysiology*, *40*(6), 895-903.

Hajcak, G., & Simons, R. F. (2002). Error-related brain activity in obsessive–compulsive undergraduates. *Psychiatry research*, *110*(1), 63-72.

Hassall, C. D., MacLean, S., & Krigolson, O. E. (2014). Hierarchical Error Evaluation: The Role of Medial-Frontal Cortex in Postural Control. *Journal of motor behavior*, *46*(6), 381-387.

Hassall, C.D., Silver, A., and Krigolson, O.E. (2015). *Reward positivities reflect prediction errors in a four-armed bandit task.* Presented at the Cognitive Neuroscience Society Annual (CNS) Meeting, San Francisco, CA.

Heath, M. (2005). Role of Limb and Target Vision in the Online Control of Memory-Guided Reaches. *Motor Control*, *9*(3), 281-311.

Heath, M., Westwood, D. A., & Binsted, G. (2004). The control of memory-guided reaching movements in peripersonal space. *Motor Control*, *8*(1), 76-106.

Heilman, K. M., Watson, R. T., & Valenstein, E. (1993). Neglect and related disorders. *Clinical neuropsychology*, *3*, 279-336.

Heinze, H. J., Luck, S. J., Mangun, G. R., & Hillyard, S. A. (1990). Visual event-related potentials index focused attention within bilateral stimulus arrays: I. Evidence for early selection.*Electroencephalography & Clinical Neurophysiology*, *75*(6), 511-527. doi:10.1016/0013-4694(90)90138-A

Held, R., Efstathiou, A., & Greene, M. (1966). Adaptation to displaced and delayed visual feedback from the hand. *Journal of Experimental Psychology*,*72*(6), 887.

Helmholtz, H. (1909). In Tr. JPC Southall. *Treatise on physiological optics*,*3*, 505-516.

Herrmann, M. J., Römmler, J., Ehlis, A. C., Heidrich, A., & Fallgatter, A. J. (2004). Source localization (LORETA) of the error-related-negativity (ERN/Ne) and positivity (Pe). *Cognitive Brain Research*, *20*(2), 294-299.

Humphreys, G. W., Watelet, A., & Riddoch, M. J. (2006). Long-term effects of prism adaptation in chronic visual neglect: A single case study. Cognitive Neuropsychology, 23(3), 463–478.

Holroyd, C. B., & Coles, M. G. (2002). The neural basis of human error processing: reinforcement learning, dopamine, and the error-related negativity. Psychological review, 109(4), 679.

Holroyd, C. B., & Coles, M. G. (2008). Dorsal anterior cingulate cortex integrates reinforcement history to guide voluntary behavior. Cortex, 44(5), 548-559.

Holroyd, C. B., & Krigolson, O. E. (2007). Reward prediction error signals associated with a modified time estimation task. *Psychophysiology*, *44*(6), 913-917.

Jacquin-Courtois, S., Rode, G., Pisella, L., Boisson, D., & Rossetti, Y. (2008). Wheel-chair driving improvement following visuo-manual prism adaptation. Cortex, 44(1), 90–96.

Jehkonen, M., Laihosalo, M., & Kettunen, J. E. (2006). Impact of neglect on functional outcome after stroke-a review of methodological issues and recent research findings. *Restorative neurology and neuroscience*, *24*(4), 209-215.

Johnson, R., Pfefferbaum, A., & Kopell, B. S. (1985). P300 and long-term memory: Latency predicts recognition performance.*Psychophysiology*, *22*(5), 497-507. doi:10.1111/j.1469-8986.1985.tb01639.x

Karnath, H. O., Schenkel, P., & Fischer, B. (1991). Trunk orientation as the determining factor of the 'contralateral'deficit in the neglect syndrome and as the physical anchor of the internal representation of body orientation in space.*Brain*, *114*(4), 1997-2014.

Keane, S., Turner, C., Sherrington, C., & Beard, J. R. (2006). Use of fresnel prism glasses to teat stroke patients with hemispatial neglect. Archives of Physical Medicine and Rehabilitation, 87(12), 1668–1672.

Kitazawa, S., Kohno, T., & Uka, T. (1995). Effects of delayed visual information on the rate and amount of prism adaptation in the human. *The Journal of neuroscience*, *15*(11), 7644-7652.

Koch, G., Bonni, S., Giacobbe, V., Bucchi, G., Basile, B., Lupo, F., ... & Caltagirone, C. (2012). Theta-burst stimulation of the left hemisphere accelerates recovery of hemispatial neglect. *Neurology*, *78*(1), 24-30.

Kornheiser, A. S. (1976). Adaptation to laterally displaced vision: A review. *Psychological Bulletin*, *83*(5), 783-816. doi:10.1037/0033-2909.83.5.783

Krigolson, O.E., and Hassall, C.D. (2015). *Thinking fast, thinking slow, thinking alpha?.* Presented at the Cognitive Neuroscience Society Annual (CNS) Meeting, San Francisco, CA.

Krigolson, O. E., Hassall, C. D., Balcom, L., & Turk, D. (2013). Perceived ownership impacts reward evaluation within medial-frontal cortex. *Cognitive, Affective, & Behavioral Neuroscience*, *13*(2), 262-269.

Krigolson, O., & Heath, M. (2004). Background visual cues and memory-guided reaching. *Human movement science*, *23*(6), 861-877.

Krigolson, O. E., & Holroyd, C. B. (2006). Evidence for hierarchical error processing in the human brain. *Neuroscience*, *137*(1), 13-17.

Krigolson, O. E., & Holroyd, C. B. (2007a). Hierarchical error processing: Different errors, different systems. Brain Research, 1155(25), 70-80.

Krigolson, O. E., & Holroyd, C. B. (2007b). Predictive information and motor control: The role of medial-frontal cortex. Psychophysiology, 44, 586-595.

Krigolson, O. E., Holroyd, C. B., Van Gyn, G., & Heath, M. (2008). Electroencephalographic correlates of target and outcome errors. Experimental Brain Research, 190(4), 401-411.

Làdavas, E., Bonifazi, S., Catena, L., & Serino, A. (2011). Neglect rehabilitation by prism adaptation: different procedures have different impacts. *Neuropsychologia*, *49*(5), 1136-1145.

Lopez-Calderon, J., & Luck, S. J. (2014). ERPLAB: an open-source toolbox for the analysis of event-related potentials. *Frontiers in Human Neuroscience*, *8*, 213. doi:10.3389/fnhum.2014.00213

Luauté, J. H. P., Rode, G. J. C. S., & Boisson, D. (2006). Prism adaptation first among equals in alleviating left neglect: a review. *Restorative neurology and neuroscience*, *24*(4), 409-418.

Lustig, C., Shah, P., Seidler, R., & Reuter-Lorenz, P. A. (2009). Aging, training, and the brain: a review and future directions. *Neuropsychology review*, *19*(4), 504-522.

Luukkainen-Markkula, R., Tarkka, I. M., Pitkänen, K., Sivenius, J., & Hämäläinen, H. (2009). Rehabilitation of hemispatial neglect: a randomized study using either arm activation or visual scanning training. *Restorative neurology and neuroscience*, *27*(6), 665-674.

Maclean, S. J., Hassall, C. D., Ishigami, Y., Krigolson, O. E., & Eskes, G. A. (2015). Using brain potentials to understand prism adaptation: the error-related negativity and the P300. *Frontiers in Human Neuroscience*, *9*, 335.

Maier, M. E., Pellegrino, G., & Steinhauser, M. (2012). Enhanced error- related negativity on flanker errors: Error expectancy or error significance?. *Psychophysiology*, *49*(7), 899-908.

McIntosh, R. D., Rossetti, Y., & Milner, A. D. (2002). Prism adaptation improves chronic visual and haptic neglect: A single case study. Cortex, 38(3), 309–320.

Michel, C., Pisella, L., Prablanc, C., Rode, G., & Rossetti, Y. (2007). Enhancing visuomotor adaptation by reducing error signals: Single-step (aware) versus multiple-step (unaware) exposure to wedge prisms. *Journal Of Cognitive Neuroscience*, *19*(2), 341-350. doi:10.1162/jocn.2007.19.2.341

Miltner, W. H., Braun, C. H., & Coles, M. G. (1997). Event-related brain potentials following incorrect feedback in a time-estimation task: Evidence for a “generic” neural system for error detection. *Journal of cognitive neuroscience*, *9*(6), 788-798.

Mizuno, K., Tsuji, T., Takebayashi, T., Fujiwara, T., Hase, K., & Liu, M. (2011). Prism Adaptation Therapy Enhances Rehabilitation of Stroke Patients With Unilateral Spatial Neglect A Randomized, Controlled Trial. *Neurorehabilitation and neural repair*, *25*(8), 711-720.

Morris, A. P., Kritikos, A., Berberovic, N., Pisella, L., Chambers, C. D., & Mattingley, J. B. (2004). Prism adaptation and spatial attention: A study of visual search in normals and patients with unilateral neglect. Cortex, 40(4-5), 703–721.

Mutai, H., Furukawa, T., Araki, K., Misawa, K., & Hanihara, T. (2012). Factors associated with functional recovery and home discharge in stroke patients admitted to a convalescent rehabilitation ward. *Geriatrics & gerontology international*, *12*(2), 215-222.

Newport, R., & Schenk, T. (2012). Prisms and neglect: What have we learned?. *Neuropsychologia*,*50*(6), 1080-1091. doi:10.1016/j.neuropsychologia.2012.01.023

Nieuwenhuis, S., Aston-Jones, G., & Cohen, J. D. (2005). Decision making, the P3, and the locus coeruleus--norepinephrine system.*Psychological Bulletin*, *131*(4), 510-532. doi:10.1037/0033-2909.131.4.510

Nieuwenhuis, S., Ridderinkhof, K. R., Blom, J., Band, G. H., & Kok, A. (2001). Error-related brain potentials are differentially related to awareness of response errors: Evidence from an antisaccade task.*Psychophysiology*, *38*(5), 752-760. doi:10.1017/S0048577201001111

Nijboer, T. C. W., McIntosh, R. D., Nys, G. M. S., Dijkerman, H. C., & Milner, A. D. (2008). Prism adaptation improves voluntary but not automatic orienting in neglect. *Neuroreport, 19*(3), 293–298.

Nys, G. M. S., de Haan, E. H. F., Kunneman, a, de Kort, P. L. M., & Dijkerman, H. C. (2008b). Acute neglect rehabilitation using repetitive prism adaptation: a randomized placebo-controlled trial. Restorative Neurology and Neuroscience, 26(1), 1–12.

Nys, G. M., Seurinck, R., & Dijkerman, H. C. (2008a). Prism adaptation moves neglect-related perseveration to contralesional space. *Cognitive and Behavioral Neurology*, *21*(4), 249-253.

Overbeek, T. J., Nieuwenhuis, S., & Ridderinkhof, K. R. (2005). Dissociable components of error processing: On the functional significance of the Pe vis-à-vis the ERN/Ne. *Journal Of Psychophysiology*,*19*(4), 319-329. doi:10.1027/0269-8803.19.4.319

O'Connell, R. G., Dockree, P. M., Bellgrove, M. A., Kelly, S. P., Hester, R., Garavan, H., ... & Foxe, J. J. (2007). The role of cingulate cortex in the detection of errors with and without awareness: a high- density electrical mapping study. *European Journal of Neuroscience*, *25*(8), 2571-2579.

Paolucci, S., Antonucci, G., Grasso, M. G., & Pizzamiglio, L. (2001). The role of unilateral spatial neglect in rehabilitation of right brain-damaged ischemic stroke patients: A matched comparison. *Archives of Physical Medicine and Rehabilitation, 82*(6), 743-749.

Pierce, S. R., & Buxbaum, L. J. (2002). Treatments of unilateral neglect: a review. *Archives of physical medicine and rehabilitation*, *83*(2), 256-268.

Pizzamiglio, L., Guariglia, C., Antonucci, G., & Zoccolotti, P. (2006). Development of a rehabilitative program for unilateral neglect. *Restorative neurology and neuroscience*, *24*(4), 337-345.

Polich, J. (2007). Updating p300: An integrative theory of P3a and P3b.*Clinical Neurophysiology*, *118*(10), 2128-2148. doi:10.1016/j.clinph.2007.04.019

Polich, J., Howard, L., & Starr, A. (1983). P300 latency correlates with digit span. *Psychophysiology*, *20*(6), 665-669. doi:10.1111/j.1469-8986.1983.tb00936.x

Proteau, L., Marteniuk, R. G., Girouard, Y., & Dugas, C. (1987). On the type of information used to control and learn an aiming movement after moderate and extensive training. *Human Movement Science*, *6*(2), 181-199.

Redding, G. M., Rossetti, Y., & Wallace, B. (2005). Applications of prism adaptation: A tutorial in theory and method. *Neuroscience And Biobehavioral Reviews*, *29*(3), 431-444. doi:10.1016/j.neubiorev.2004.12.004

Redding, G. M., & Wallace, B. (1993). Adaptive coordination and alignment of eye and hand. *Journal Of Motor Behavior*, *25*(2), 75-88. doi:10.1080/00222895.1993.9941642

Redding, G. M., & Wallace, B. (1996). Adaptive spatial alignment and strategic perceptual-motor control. *Journal Of Experimental Psychology: Human Perception And Performance*, *22*(2), 379-394. doi:10.1037/0096-1523.22.2.379

Redding, G. M., & Wallace, B. (1997). Prism adaptation during target pointing from visible and nonvisible starting locations. *Journal Of Motor Behavior*, *29*(2), 119-130. doi:10.1080/00222899709600827

Redding, G. M., & Wallace, B. (2002). Strategic calibration and spatial alignment: A model from prism adaptation.*Journal Of Motor Behavior*, *34*(2), 126-138. doi:10.1080/00222890209601935

Redding, G. M., & Wallace, B. (2006). Prism adaptation and unilateral neglect: Review and analysis. *Neuropsychologia*, *44*(1), 1-20. doi:10.1016/j.neuropsychologia.2005.04.009

Redding, G. M., & Wallace, B. (2009). Asymmetric visual prism adaptation and intermanual transfer. *Journal Of Motor Behavior*, *41*(1), 83-94. doi:10.1080/00222895.2009.10125920

Redding, G. M., & Wallace, B. (2013). *Adaptive spatial alignment*. Psychology Press.

Robertson, I. H., McMillan, T. M., MacLeod, E., Edgeworth, J., & Brock, D. (2002). Rehabilitation by limb activation training reduces left-sided motor impairment in unilateral neglect patients: A single-blind randomised control trial. *Neuropsychological Rehabilitation*, *12*(5), 439-454.

Rode, G., Rossetti, Y., Li, L., & Boisson, D. (1998). Improvement of mental imagery after prism exposure in neglect: A case study. *Behavioural Neurology*, *11*(4), 251-258. doi:10.1155/1999/797425

Rode, G., Pisella, L., Marsal, L., Mercier, S., Rossetti, Y., & Boisson, D. (2006). Prism adaptation improves spatial dysgraphia following right brain damage. Neuropsychologia, 44(12), 2487–93.

Rossetti, Y., Rode, G., Pisella, L., Farné, A., Li, L., Boisson, D., & Perenin, M. T. (1998). Prism adaptation to a rightward optical deviation rehabilitates left hemispatial neglect. *Nature*, *395*(6698), 166-169.

Rousseaux, M., Bernati, T., Saj, A., & Kozlowski, O. (2006). Ineffectiveness of prism adaptation on spatial neglect signs. Stroke: A Journal of Cerebral Circulation, 37(2), 542–543.

San Martín, R., Manes, F., Hurtado, E., Isla, P., & Ibañez, A. (2010). Size and probability of rewards modulate the feedback error-related negativity associated with wins but not losses in a monetarily rewarded gambling task. *Neuroimage*, *51*(3), 1194-1204.

Sarri, M., Kalra, L., Greenwood, R., & Driver, J. (2006). Prism adaptation changes perceptual awareness for chimeric visual objects but not for chimeric faces in spatial neglect after right-hemisphere stroke. *Neurocase*, *12*(3), 127-135.

Sarri, M., Greenwood, R., Kalra, L., & Driver, J. (2011). Prism adaptation does not change the rightward spatial preference bias found with ambiguous stimuli in unilateral neglect. Cortex, 47(3), 353–66.

Sarri, M., Greenwood, R., Kalra, L., Papps, B., Husain, M., & Driver, J. (2008). Prism adaptation aftereffects in stroke patients with spatial neglect: pathological effects on subjective straight ahead but not visual open-loop pointing. *Neuropsychologia*, *46*(4), 1069-1080.

Schindler, I., McIntosh, R. D., Cassidy, T. P., Birchall, D., Benson, V., Ietswaart, M., & Milner, A. D. (2009). The disengage deficit in hemispatial neglect is restricted to between-object shifts and is abolished by prism adaptation. *Experimental brain research*, *192*(3), 499-510.

Schultz, W., Dayan, P., & Montague, P. R. (1997). A Neural Substrate of Prediction and Reward. Science, 275(5306), 1593–1599. doi:10.1126/science.275.5306.1593

Serino, A., Angeli, V., Frassinetti, F., & Làdavas, E. (2006). Mechanisms underlying neglect recovery after prism adaptation. *Neuropsychologia*, *44*(7), 1068-1078.

Serino, A., Barbiani, M., Rinaldesi, M. L., & Làdavas, E. (2009). Effectiveness of prism adaptation in neglect rehabilitation a controlled trial study. Stroke, 40(4), 1392-1398.

Serino, A., Bonifazi, S., Pierfederici, L., & Làdavas, E. (2007). Neglect treatment by prism adaptation: What recovers and for how long. Neuropsychological Rehabilitation, 17(6), 657–687.

Shindo, K., Sugiyama, K., Huabao, L., Nishijima, K., Kondo, T., & Izumi, S. (2006). Long-term effect of low-frequency repetitive transcranial magnetic stimulation over the unaffected posterior parietal cortex in patients with unilateral spatial neglect. *Journal of Rehabilitation Medicine*, *38*(1), 65-67.

Shiraishi, H., Muraki, T., Ayaka Itou, Y. S., & Hirayama, K. (2010). Prism intervention helped sustainability of effects and ADL performances in chronic hemispatial neglect: a follow-up study. NeuroRehabilitation, 27(2), 165–72.

Striemer, C., & Danckert, J. (2007). Prism adaptation reduces the disengage deficit in right brain damage patients. *Neuroreport*, *18*(1), 99-103.

Striemer, C. L., & Danckert, J. (2010). Dissociating perceptual and motor effects of prism adaptation in neglect. *Neuroreport*, *21*(6), 436-441.

Sutton, R. S., & Barto, A. G. (1998). *Reinforcement learning: An introduction*(Vol. 1, No. 1). Cambridge: MIT press.

Tilikete, C., Rode, G., Rossetti, Y., Pichon, J., Li, L., & Boisson, D. (2001). Prism adaptation to rightward optical deviation improves postural imbalance in left-hemiparetic patients. Current Biology : CB, 11(7), 524–8.

Turton, A. J., O'Leary, K., Gabb, J., Woodward, R., & Gilchrist, I. D. (2010). A single blinded randomised controlled pilot trial of prism adaptation for improving self-care in stroke patients with neglect. Neuropsychological Rehabilitation, 20(2), 180–96.

Ullsperger, M., & von Cramon, D. Y. (2001). Subprocesses of performance monitoring: a dissociation of error processing and response competition revealed by event-related fMRI and ERPs. *Neuroimage*, *14*(6), 1387-1401.

Usher, M., Cohen, J. D., Servan-Schreiber, D., Rajkowski, J., & Aston-Jones, G. (1999). The role of locus coeruleus in the regulation of cognitive performance. *Science*, *283*(5401), 549-554

Vangkilde, S., & Habekost, T. (2010). Finding Wally: prism adaptation improves visual search in chronic neglect. *Neuropsychologia*, *48*(7), 1994-2004.

Van Veen, V., & Carter, C. S. (2002). The anterior cingulate as a conflict monitor: fMRI and ERP studies. *Physiology & behavior*, *77*(4), 477-482.

Veilleux, L., & Proteau, L. (2015). Prism adaptation in virtual and natural contexts: Evidence for a flexible adaptive process. *The Quarterly Journal Of Experimental Psychology*, *68*(6), 1168-1182. doi:10.1080/17470218.2014.977305

Vocat, R., Pourtois, G., & Vuilleumier, P. (2008). Unavoidable errors: a spatio-temporal analysis of time-course and neural sources of evoked potentials associated with error processing in a speeded task. *Neuropsychologia*, *46*(10), 2545-2555.

Vocat, R., Pourtois, G., & Vuilleumier, P. (2011). Parametric modulation of error-related ERP components by the magnitude of visuo-motor mismatch. *Neuropsychologia*, *49*(3), 360-367.

Vossel, S., Weiss, P. H., Eschenbeck, P., & Fink, G. R. (2013). Anosognosia, neglect, extinction and lesion site predict impairment of daily living after right-hemispheric stroke. *Cortex*, *49*(7), 1782-1789.

Watanabe, S., & Amimoto, K. (2010). Generalization of prism adaptation for wheelchair driving task in patients with unilateral spatial neglect. *Archives of physical medicine and rehabilitation*, *91*(3), 443-447.

Welch, R. B., & Warren, D. H. (1980). Immediate perceptual response to intersensory discrepancy. *Psychological bulletin*, *88*(3), 638.

Westwood, D. A., Heath, M., & Roy, E. A. (2003). No evidence for accurate visuomotor memory: Systematic and variable error in memory-guided reaching. *Journal of motor behavior*, *35*(2), 127-133.

Wilms, I., & Malá, H. (2010). Indirect versus direct feedback in computer-based Prism Adaptation Therapy. *Neuropsychological Rehabilitation*, *20*(6), 830-853. doi:10.1080/09602011.2010.492711

Woodworth, R. S. (1899). Accuracy of voluntary movement. *The Psychological Review: Monograph Supplements*, *3*(3), i-114. doi:10.1037/h0092992

Yang, N. Y., Zhou, D., Chung, R. C., Li-Tsang, C. W., & Fong, K. N. (2013). Rehabilitation interventions for unilateral neglect after stroke: a systematic review from 1997 through 2012. *Frontiers in human neuroscience*, *7*, 187.

Yeung, N., Botvinick, M. M., & Cohen, J. D. (2004). The neural basis of error detection: conflict monitoring and the error-related negativity. *Psychological review*, *111*(4), 931.

Yu, R., & Zhou, X. (2006). Brain responses to outcomes of one's own and other's performance in a gambling task. *Neuroreport*, *17*(16), 1747-1751.

APPENDIX

Table A1 Percentage (rounded) of ERP and behavioural data removed for each participant in Experiment 1 before final analyses.

Subject	ERP data removed	Behavioural data removed
1	3%	1%
2	6%	1%
3	13%	0%
4	5%	1%
5	3%	0%
6	2%	1%
7	12%	1%
8	2%	3%
9	11%	1%
10	1%	0%
11	6%	0%
12	3%	1%
13	8%	0%
14	3%	0%
15	12%	0%
16	3%	1%
17	11%	0%
18	1%	0%

Table A2 Percentage (rounded) of ERP and behavioural data removed for each participant in Experiment 2 before final analyses.

Subject	ERP data removed	Behavioural data removed
1	2%	0%
2	2%	0%
3	4%	1%
4	2%	1%
5	1%	1%
6	6%	0%
7	4%	0%
8	3%	0%
9	2%	0%
10	10%	0%
11	4%	0%
12	2%	0%
13	4%	0%
14	12%	1%
15	6%	0%

16	13%	0%
17	2%	0%
18	6%	2%
19	12%	1%
20	7%	0%
21	5%	1%

Table A3 Percentage (rounded) of ERP and behavioural data removed for each participant in Experiment 3 before final analyses.

Subject	**ERP data removed**	**Behavioural data removed**
1	12%	0%
2	2%	1%
3	11%	0%
4	4%	0%
5	1%	0%
6	1%	0%
7	1%	0%
8	2%	0%
9	2%	0%
10	1%	0%
11	12%	0%
12	2%	0%
13	10%	0%
14	13%	0%
15	1%	0%
16	1%	0%
17	1%	0%
18	1%	0%
19	1%	0%
20	3%	1%
21	10%	0%

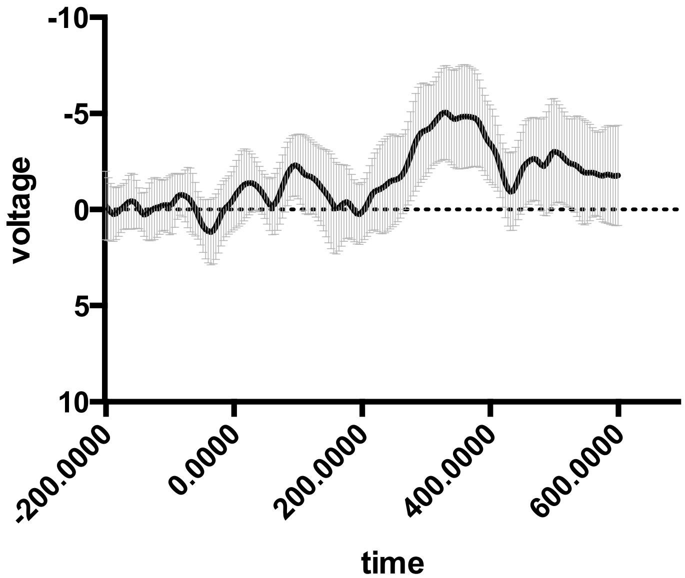

Figure A1 Accuracy difference wave at electrode FCz, evoked by screen-touch with immediate feedback in Experiment 1.

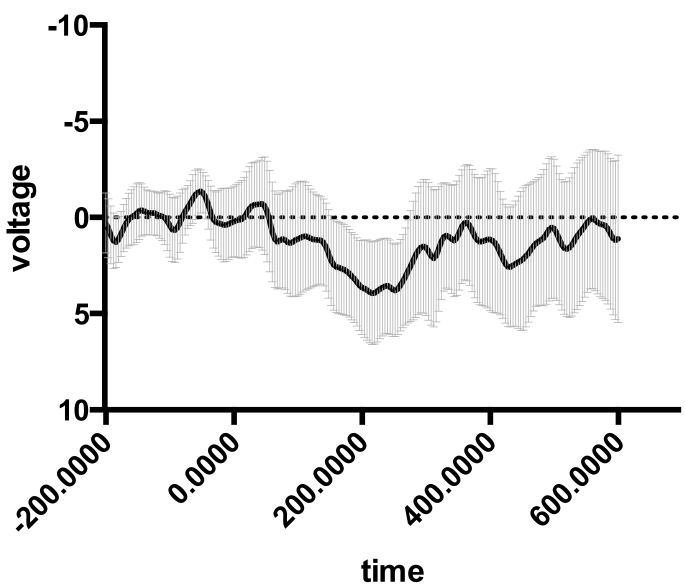

Figure A2 Phase difference wave at electrode Cz, evoked by screen-touch with immediate feedback in Experiment 1.

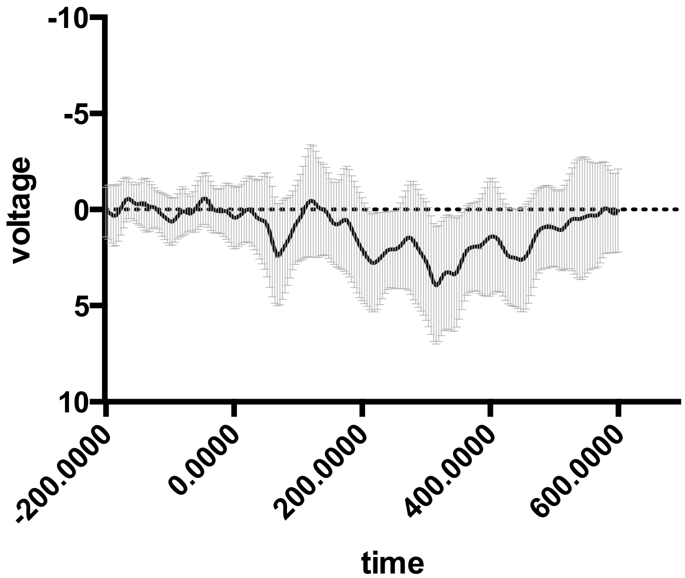

Figure A3 Phase difference wave at electrode Oz, evoked by screen-touch with immediate feedback in Experiment 1.

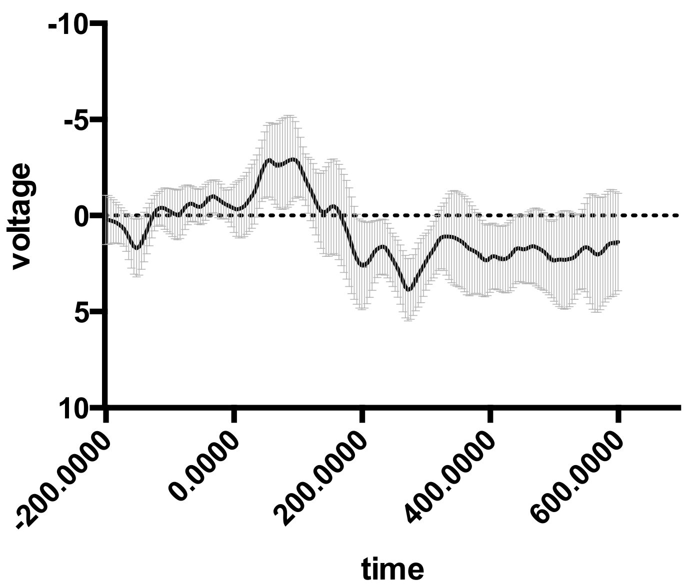

Figure A4 Accuracy difference wave at electrode FCz, evoked by screen-touch with delayed feedback in Experiment 1.

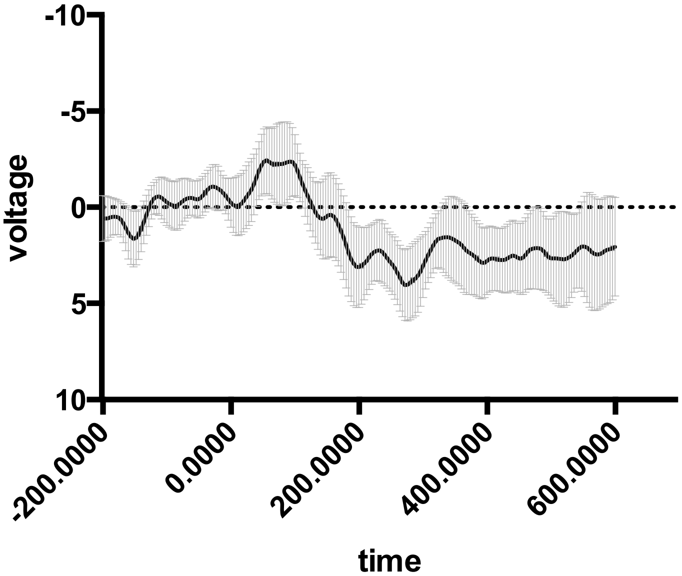

Figure A5 Accuracy difference wave at electrode Cz, evoked by screen-touch with delayed feedback in Experiment 1.

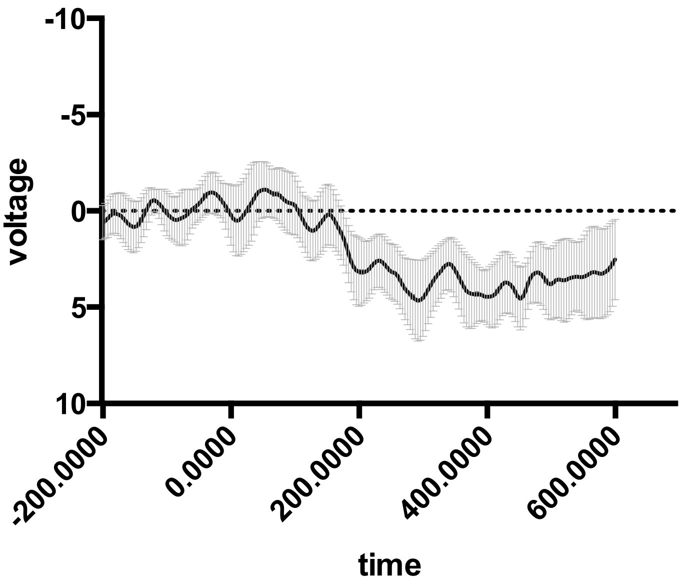

Figure A6 Accuracy difference wave at electrode POz, evoked by screen-touch with delayed feedback in Experiment 1.

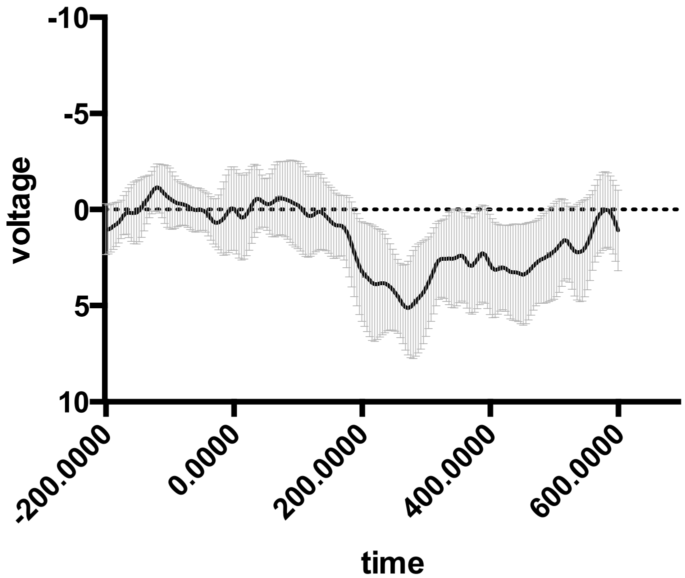

Figure A7 Phase difference wave at electrode POz, evoked by screen-touch with delayed feedback in Experiment 1.

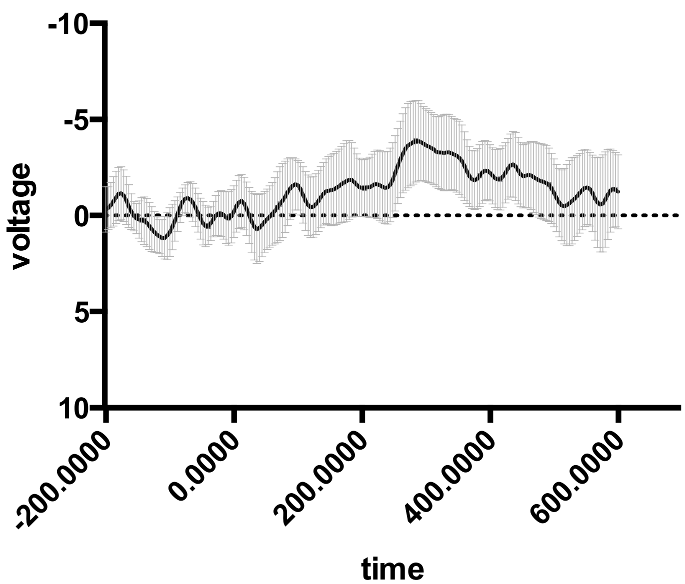

Figure A8 Accuracy difference wave at electrode FCz, evoked by onset of target feedback after a delay in Experiment 1.

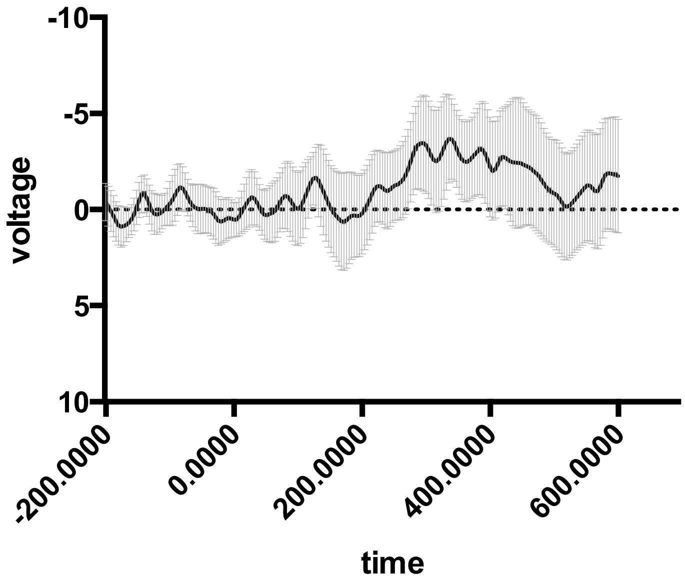

Figure A9 Phase difference wave at electrode Oz, evoked by onset of target feedback after a delay in Experiment 1.

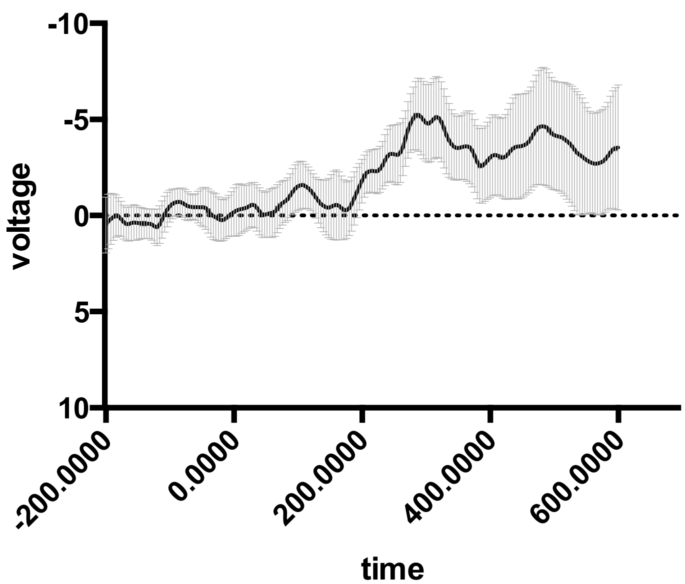

Figure A10 Accuracy difference wave at electrode FCz, evoked by screen-touch with immediate feedback in Experiment 2.

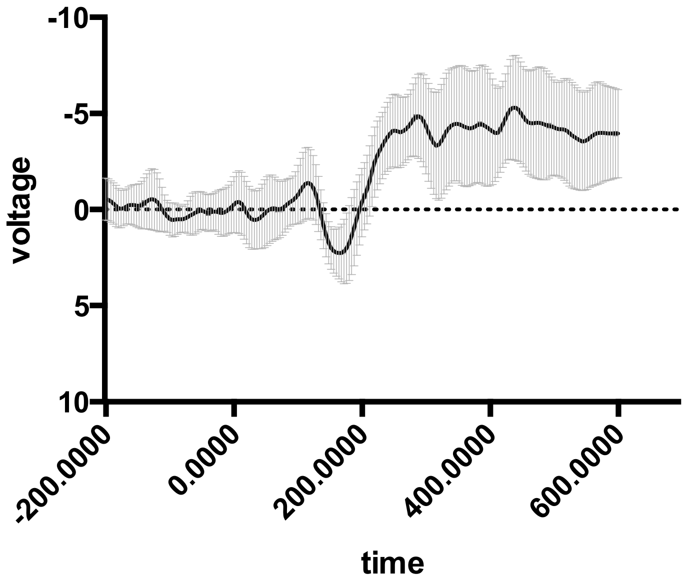

Figure A11 Accuracy difference wave at electrode FCz, evoked by onset of target feedback after a delay in Experiment 2.

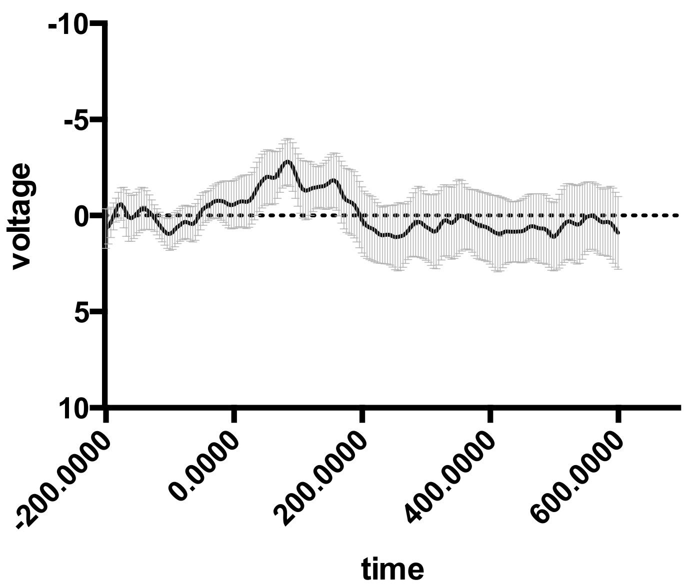

Figure A12 Accuracy difference wave at electrode FCz, evoked by screen-touch with full target feedback in Experiment 3.

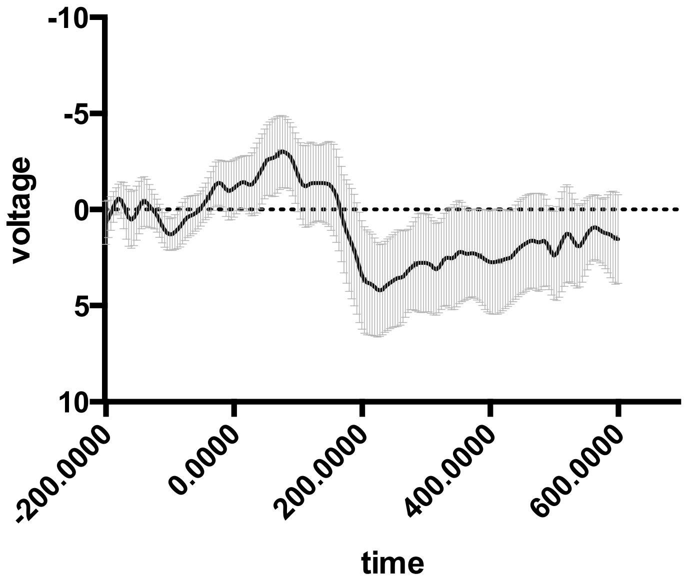

Figure A13 Accuracy difference wave at electrode Cz, evoked by screen-touch with full target feedback in Experiment 3.

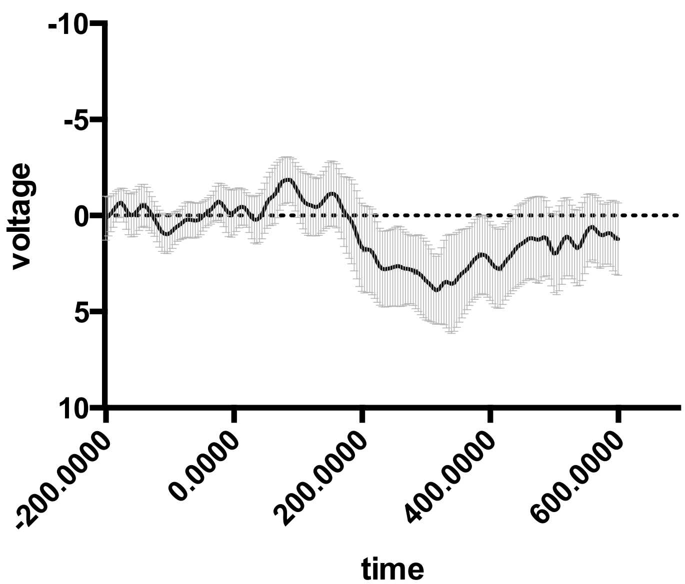

Figure A14 Accuracy difference wave at electrode POz, evoked by screen-touch with full target feedback in Experiment 3.

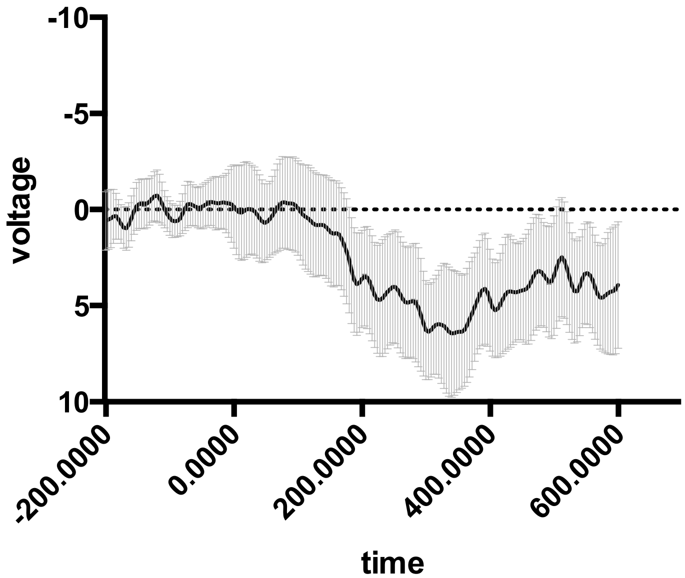

Figure A15 Phase difference wave at electrode CPz, evoked by screen-touch with full target feedback in Experiment 3.

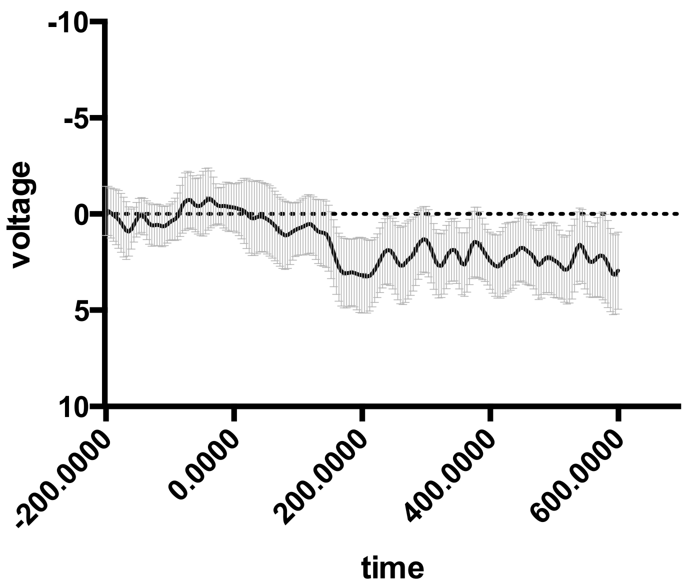

Figure A16 Accuracy difference wave at electrode Cz, evoked by screen-touch with no target feedback in Experiment 3.

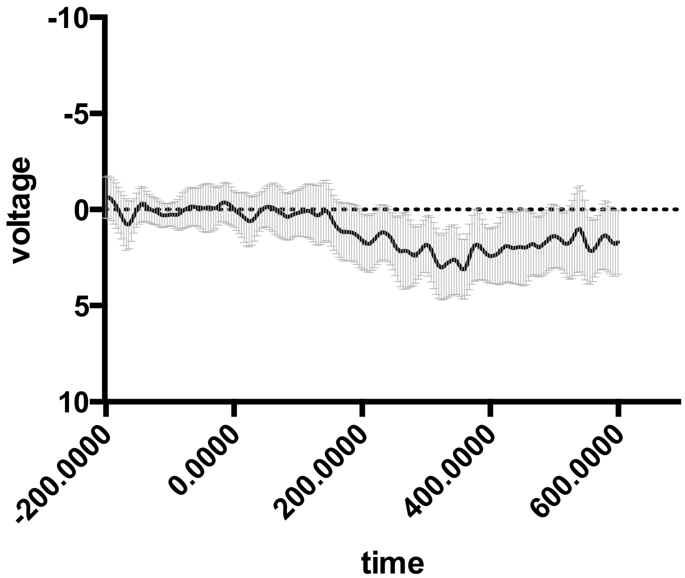

Figure A17 Accuracy difference wave at electrode POz, evoked by screen-touch with no target feedback in Experiment 3.

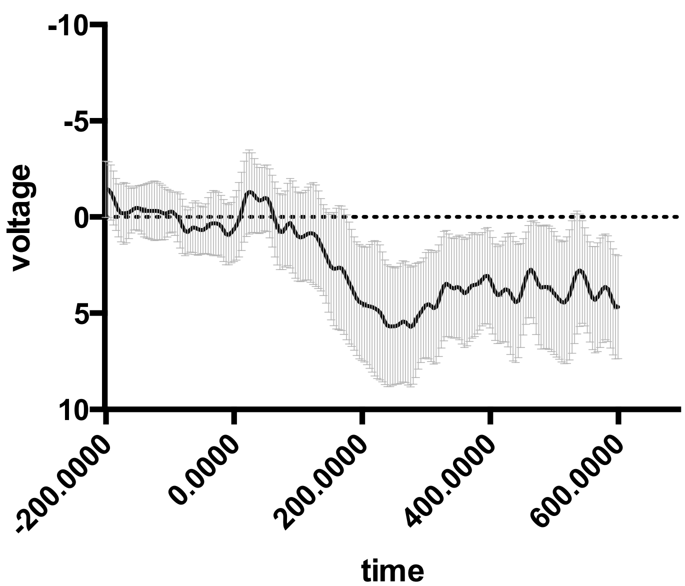

Figure A18 Phase difference wave at electrode CPz, evoked by screen-touch with no target feedback in Experiment 3.

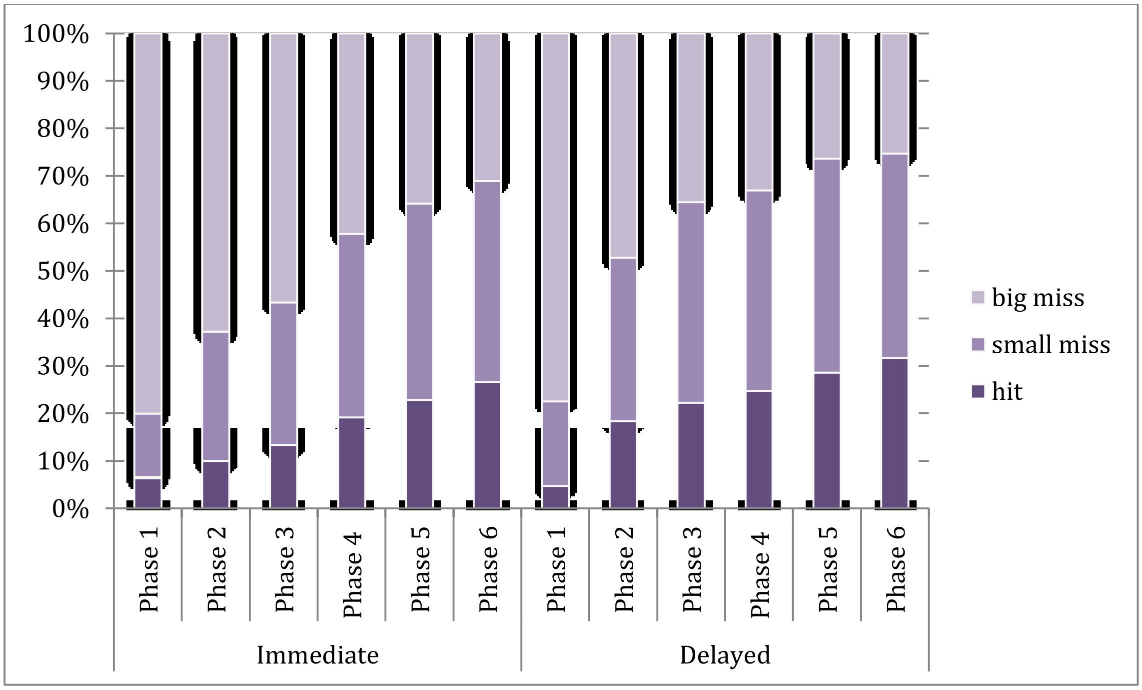

Figure A19 Percentage of hits, small misses, and big misses across each phase of prism adaptation in both feedback conditions in Experiment 1.

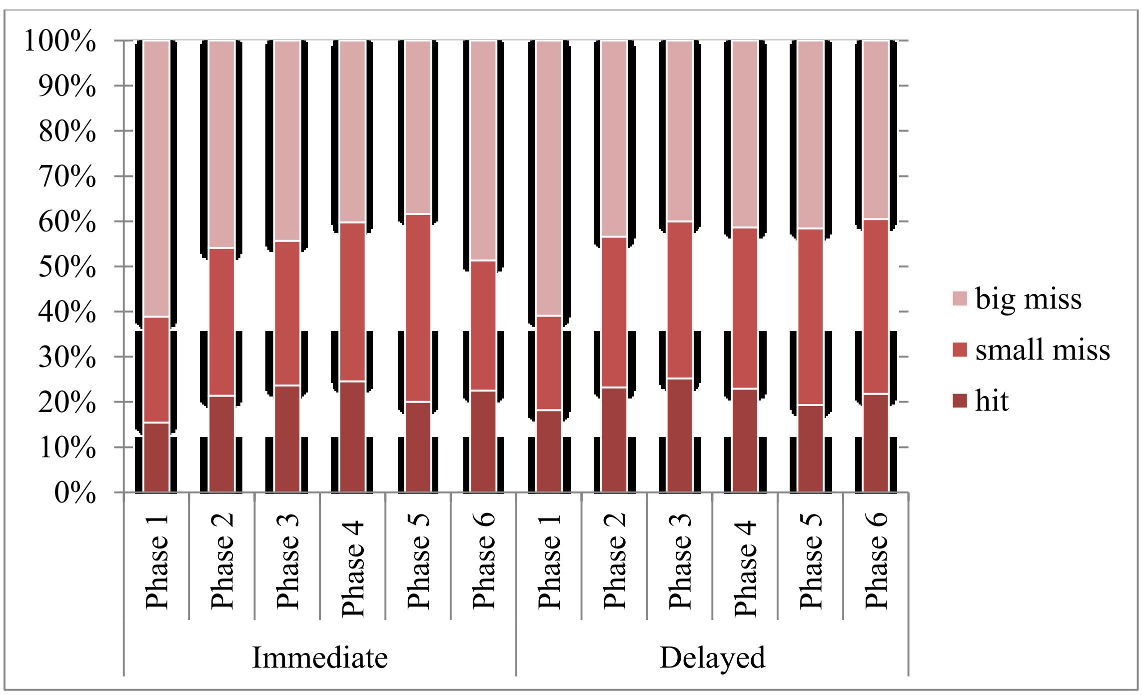

Figure A20 Percentage of hits, small misses, and big misses across each phase of prism adaptation in both feedback conditions in Experiment 2.

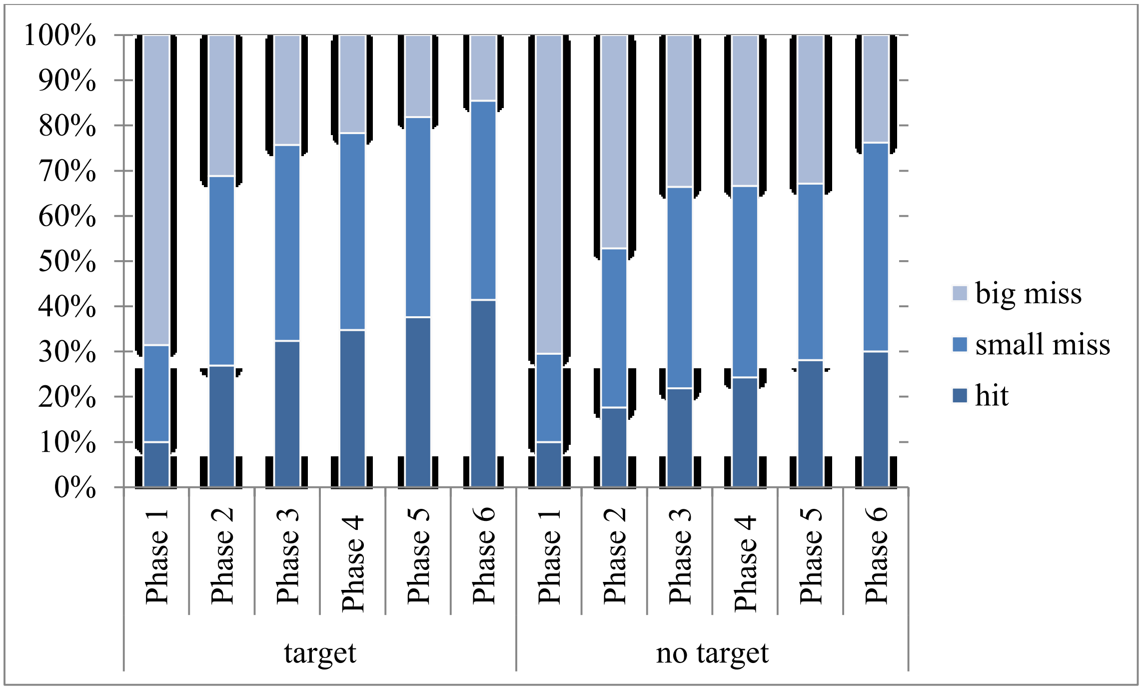

Figure A21 Percentage of hits, small misses, and big misses across each phase of prism adaptation in both feedback conditions in Experiment 3.