

No-Report Rivalry: The ERP Correlates of Probe-Mediated Perceptual Reversals

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Preface

This thesis is a continuation of Jeff Nestor's 2022 thesis *ERP Correlates of Perceptual Reversals During Binocular Rivalry: A No-Report Paradigm*. In Jeff's thesis, the experimental setup for this study was verified and pilot data was collected.

List of Abbreviations

BOLD	Blood oxygen level dependent
BR	Binocular rivalry
CSP	Cumulative smooth pursuit
EEG	Electroencephalogram
EOG	Electrooculogram
ERP	Event related potential
HEOG	Horizontal electrooculogram
LGN	Lateral geniculate nucleus
NCC	Neural correlates of consciousness
OKN	Optokinetic nystagmus
PSP	Postsynaptic potential
RHT	Reverse hierarchy theory
RL	Reversal latency
RN	Reversal negativity
V1	Primary visual cortex
VAN	Visual awareness negativity
VEOG	Vertical electrooculogram
fMRI	Functional magnetic resonance imaging

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Abstract

Binocular rivalry (BR) is a type of perceptual bistability commonly used to investigate the neural correlates of consciousness (NCC) as it allows for a high level of control in laboratory studies. When viewing BR, one's conscious vision regularly alternates between two differing perceptions, despite the physical stimuli remaining unchanged. Previous studies have relied on participants reporting of their perception during BR to sort the data for neural comparisons, however, this approach potentially confounds data interpretation as the neural processes behind perceptual reversals are difficult to isolate from those related to the attentional, decisional, and motor processes of reporting. In the present study, electroencephalography (EEG) data were recorded during a "no-report" BR study in which probes were used to trigger perceptual reversals and moving stimuli were used such that eye-tracking could serve as an indirect measure of perception in a no-report condition. Event related potentials (ERPs) were time-locked to probe onset and separated into stable (when probes were delivered to the currently dominant image) and reversal (when probes were delivered to the suppressed image) trials.

Three ERP components were analyzed: N1, reversal negativity (RN), and the P3b. The results suggested that N1 amplitude is related to whether the probe is presented to the dominant or suppressed eye (reduced N1 amplitudes were found for suppressed eye probes). The present study was also the first to demonstrate an RN in the absence of report, providing further evidence that it is a neural signal closely linked with perceptual reversals. Finally, the results suggested that the P3b, once commonly thought to be a potential correlate of conscious perception, was present and robust in the report condition but strongly attenuated in the absence of report – suggesting that it is most likely linked with downstream cognitive and motor processes required to report one's conscious perception.

This thesis is dedicated to my dad. Thank you for setting me back on my feet after every bump in the road, and for always giving me the strength to keep going when I'm ready to give up. I love you.

1. Introduction

1.1 NCCs

Within the field of cognitive neuroscience, an increasing focus has been placed on identifying the neural correlates of consciousness (NCC). An NCC can be loosely defined as the “minimal neuronal mechanisms jointly sufficient for one specific conscious percept,” (Koch, 2004). This definition is exceedingly broad as being conscious is the subjective concept of ‘what it is like’ to have an experience. It can refer to several aspects of phenomenal perceptions, such as auditory, visual, somatosensory, and so on. Conscious experience also includes less ‘concrete’ perceptions like dreams, thoughts, and emotions (Koch et al., 2016). The study of NCCs can be challenging for two main reasons. The first being that conscious perception is highly subjective, making it difficult to collect objective and quantifiable data that can be manipulated in a research setting. The second reason is that in order to isolate NCCs, it is imperative that neural activity related to consciousness of one particular perceptual object be distinguished from activity pertaining to unconscious processes, attention, or unrelated perception.

It has been proposed that one of the best approaches for studying NCCs is by focusing on visual perception (Crick & Koch, 1998). Visual perception stands out as a tool for identifying NCCs as much is already known about the visual system since it’s the dominant sensory modality in humans, and there are several visual phenomena that allow for highly controlled manipulations, e.g., in which the images presented are unchanging whilst the subject’s conscious perception changes, broadly referred to as ‘perceptual bistability’ (Blake et al., 2014). One particularly useful type of perceptual bistability for controlled laboratory studies with concurrent brain recordings is binocular rivalry.

1.2 Binocular Rivalry

Binocular rivalry is a phenomenon in which two differing monocular images are presented to each eye and, rather than the images melding into one, they rival each other such that only one image is perceived at a time while the other image is suppressed from one's awareness (Tong, 2001). The first documented example of binocular rivalry occurred in the 18th century when a researcher viewed a piece of blue fabric in one eye and a piece of yellow fabric in the other. Rather than perceiving green as expected, his perception alternated between seeing the blue and then the yellow piece of fabric (DuTour, 1760, translated by O'Shea, 1999). While perception switches spontaneously every few seconds between the two percepts, there are factors such as motion, contrast, brightness, and density of contours that can influence the dominance duration of a given percept over the other (Blake & Logothetis, 2002).

While binocular rivalry requires a setup that presents images to each eye individually, Figure 1 shows an example of monocular rivalry. To get a better understanding of how perception switches in binocular rivalry, try fixating on the monocular rivalry image (Fig 1d) without moving your eyes for 20-30 sec. Your perception should switch between seeing the orange gratings in the foreground, and the green gratings in the foreground, with transitions between the two every ~3-6 sec or so. Staring at it long enough may even make it appear as if the currently suppressed (background) color has completely disappeared from your view. Binocular rivalry (e.g., if only the orange grating were presented to the left eye and only the green to the right eye, via a stereoscope) creates an even stronger perceptual dominance/suppression effect. In both cases, the most important feature of rivalry is that the physical image never changes, while perception fluctuates between the two very different alternatives.

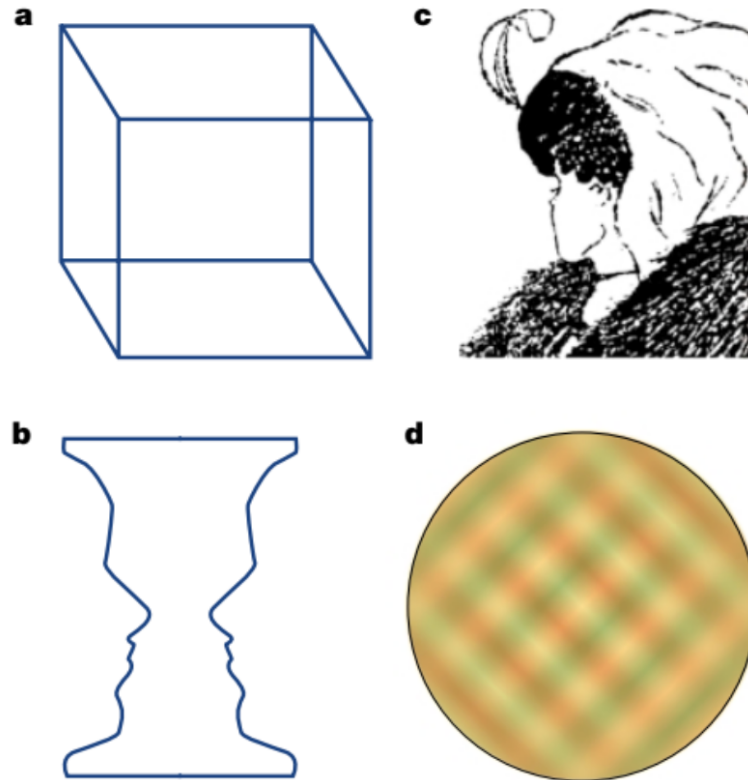


Figure 1: Well-known ambiguous figures.

a) Necker's cube: perception of this cube can vary between a view from above and a view of the side. **b)** Rubin's face/vase: this figure can be viewed as a vase when the edges are "owned" by the central object or as two face profiles when the center region is viewed as the background. **c)** Boring's old lady/young woman: figure can be seen as a young woman turning her head away from view or as the profile of an old woman. **d)** Monocular rivalry: two opposing patterns overlaid compete for perceptual dominance (image from Blake & Logothetis, 2002).

1.2.1 Mechanisms behind binocular rivalry

Modern theories for the neural mechanisms underlying binocular rivalry typically fall into one of two categories: low-level models and high-level models. The first of these two models argues that binocular rivalry occurs in the primary visual cortex (V1) or lateral geniculate nucleus (LGN) as a result of low-level interocular competition between monocular neurons (Tong et al., 2006). In other words, low-level models for binocular rivalry suggest that neurons pertaining to the right and left eyes in early visual processing reciprocally inhibit each other

such that one percept is suppressed before it is able to reach higher-level visual processing. The mechanism underlying this theory, *reciprocal interocular inhibition*, is neatly summed up in the diagram below (Fig. 2).

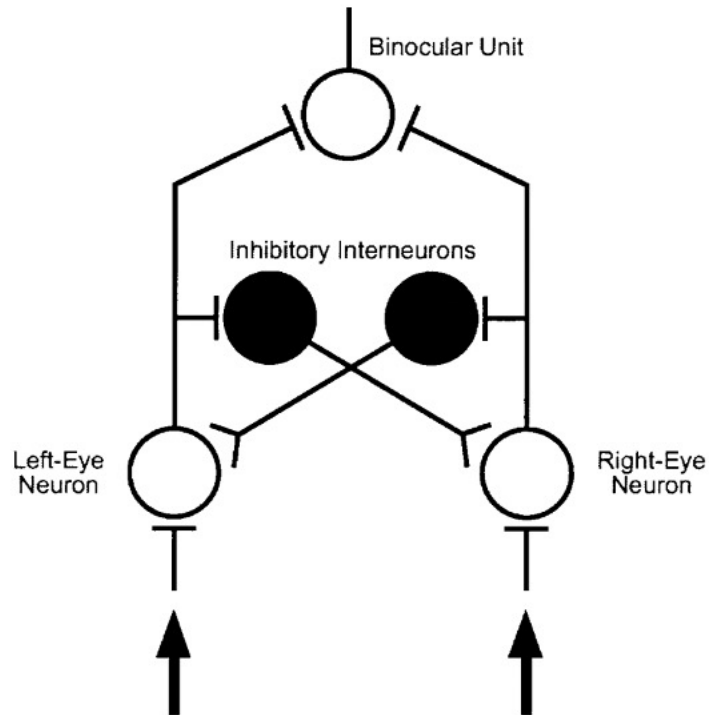


Figure 2: Schematic of reciprocal interocular inhibition

This diagram shows a stimulus (represented by the arrows) presented to each eye. Inhibitory neurons then inhibit the contralateral eye neuron before the stimulus is viewed as a binocular unit (image from Tong, 2001).

Within this model of binocular rivalry, spontaneous reversals are believed to occur due to the inhibitory action of the neurons contralateral to the present dominant percept becoming habituated over time. Thus, as the firing rates of these neurons decrease and the inhibition of the suppressed percept weakens, the opposing pathway is able to take over and inhibit the previously dominant pathway - initiating a perceptual reversal (Stollenwerk & Bode, 2003). It is important for theories of binocular rivalry to account for stereopsis, which is the fusing of two binocular images to create depth. In other words, the theory must answer the question of why some binocular images fuse together while others cause rivalry. In the low-level model, it is proposed that a separate mechanism for stereopsis detects how much the inputs from each eye are correlated, which

in turn modulates the strength of interocular inhibition (Lehky, 1988). This is to say that when binocular inputs are similar enough, the images will fuse because interocular inhibition is not strong enough to cause rivalry. Binocular rivalry is strongest when the images differ greatly (for example, lines of different colors and different orientations), whereas stereopsis occurs when the images are sufficiently similar (e.g., similar colors, similar orientations).

The low-level theory's strength lies in its simplicity and testability. For example, when a vertical grating that is presented to the left-eye is dominant whereas a horizontal grating presented to the right eye is suppressed, the perception of the left-eye image is what participants report seeing, which suggests that rivalry is a result of the eyes rather than the pattern (Blake et al., 1980). Furthermore, the low-level model is able to account for hemifield asymmetry. A hemifield is one half of a visual field, with the temporal hemifield referring to the input from the contralateral eye and the nasal hemifield referring to the input from the ipsilateral eye. Hemifield asymmetry refers to the finding that when a stimulus is presented to the temporal hemifield and nasal hemifield, the image presented to the temporal hemifield dominates over that of the nasal hemifield (Fahle, 1987). Interocular inhibition is supported by this finding as an analogous asymmetry is found in ocular dominance columns in the V1 with there being a greater representation of inputs from the temporal hemifield than those of the nasal hemifield. It is proposed that this asymmetry is the result of the visual deprivation that occurs naturally as a result of the nose partially blocking view, thus causing the brain to resolve conflict by favoring the hemifield less likely to be blocked (LeVay et al., 1985).

Unfortunately for diehard interocular inhibition advocates, this theory fails to account for certain phenomena. One such phenomenon is that of visual aftereffects, which are visual illusions that occur when the visual system adapts to a certain kind of stimulus (be it color, orientation, motion, or otherwise) such that when one looks away from the previous stimulus, the perception of new visual stimulus is temporarily altered, such that the resulting perception appears to have unexpected visual qualities reminiscent of those of previous stimulus (Laparra & Malo, 2015). The most famous example of this is the waterfall effect, in which upon being presented with a still image of an object or pattern

immediately after viewing a waterfall (downward motion) for 20 seconds or so, the still image appears to move in the opposite direction (upward motion) as the waterfall. When studying visual aftereffects in binocular rivalry, it has been observed that visual tilt and local-motion aftereffects are equally strong when the image is periodically suppressed versus when the image is continually seen (Lehmkuhle and Fox, 1975; Wade and Wenderoth, 1978). Furthermore, when the image is removed from view for a period of time similar to that of a suppression period, the strength of the aftereffects is significantly weakened (Tong, 2001). These findings are important to our understanding of the neural mechanisms underlying binocular rivalry as they imply that not only is higher level visual processing playing a role in binocular rivalry from the presence of aftereffects, but that suppressed stimuli are still being registered in the brain despite being obscured from conscious perception. Furthermore, neural mechanisms associated with higher-level processing which interocular inhibition alone cannot account for have been shown to be instrumental in binocular rivalry.

This leads into the second model for the neural mechanisms underlying binocular rivalry: the high-level or “global” model. This model accounts for the role that higher-level mechanisms, such as pattern-completion and attention, have on perception during binocular rivalry. According to reverse hierarchy theory (RHT), conscious visual perception takes a top-down approach beginning with high-level visual mechanisms that then provide feedback (potentially in the form of sensory predictions) to low-level input mechanisms (Hochstein & Ahissar, 2002). In other words, low-level visual processing is modulated by a feedforward phase in which implicit visual information is processed for “vision at a glance”, whereas high-level visual processing is modulated by a feedback phase in which visual perception becomes more detailed with explicit “vision with scrutiny”. Thus, it is possible that high-level processes play a role in perception in a low-level mechanism of rivalry, but it’s more likely that a high-level mechanism of rivalry has effects at low levels of visual processing (Wolf & Hochstein, 2011). That being said, high-level models theorize that binocular rivalry is due to pattern competition rather than competition between the eyes. Pattern competition theory suggests that binocular rivalry arises after the images have been processed in the V1 and result from competition between neural

representations of the stimuli in higher levels of the visual system (Logothetis, 1998). This theory likens the mechanisms underlying binocular rivalry to other well-known reversal illusions, such as the Necker's cube (Fig. 1a) and Rubin's face/vase (Fig. 1b).

The pattern competition theory is strongly supported by physiological research in monkeys. A study conducted by Lehky & Maunsell found that when viewing binocular rivalry, there is no activity correlated with rivalry in the LGN of alert monkeys (1996). Furthermore, in a study using single-cell recordings in the visual cortex of monkeys, it was found that only 20% of percept related cells in the early cortical areas V1/V2 were active during binocular rivalry reversals, meaning that majority of neurons in V1/V2 don't correlate with the subject's reported percept, but rather with the sensory input from the images presented to the two eyes. Interestingly, the same study found a significantly higher percentage of single cell activity in V4 (40%) and MT/MST (40%) that correlated with the reported dominant percept (Leopold & Logothetis, 1996). These findings suggest that binocular rivalry is not (solely) a result of low-level interocular inhibition since one would expect to see the majority of neural activity that correlates with the perceptual reports to be found in the LGN and V1/V2 according to that model. Most strikingly, Logothetis' lab also found that 90% of neurons recorded in the inferior temporal cortex (IT) and superior temporal sulcus (STS) – areas that are correlated with the brain's neural representation of complete objects - showed firing rates that correlated with the reported dominant perception during rivalry (Sheinberg & Logothetis, 1997). Given that a higher percentage of cells in higher-level areas exhibited modulated activity that correlated with the reported dominant percepts, it is highly unlikely that binocular rivalry is resolved via low-level interocular inhibition alone. Even so, none of this is to say that low-level mechanisms do not play a significant role in binocular rivalry.

As previously mentioned, attention plays a significant role in binocular rivalry. Chong et al. found that when participants paid specific attention to one stimulus by doing an attentionally demanding task, the dominance period of that stimulus was longer (2005). Although attention is not able to prevent a stimulus from being suppressed, it is able to prolong the portion of time that the stimulus

is in view. Not only can attention impact dominance periods, but evidence also suggests that attention is necessary for sustained rivalry. A study that tracked the cortical representations of binocular rivalry using electroencephalogram (EEG) frequency-tagging found that when attention to the dichoptic stimuli was withdrawn, rivalry was no longer observed (Zhang et al., 2011). This study verified that rivalry was not being observed by including replay conditions in which the stimuli were presented monocularly and physically switched to mimic the perceptual switches reported by participants during attended rivalry. When the subjects withdrew their attention from the replay condition, the EEG signals from their eyes were still modulated in counterphase. The authors of this study concluded that in the early stages of visual processing, attention is necessary for the resolution of interocular conflict. While this finding is important to our understanding of rivalry, the necessity of attention for the participant's ability to report complicates this finding somewhat.

Interestingly, functional magnetic resonance imaging (fMRI) studies in humans have suggested that the frontoparietal region of the brain plays a role in binocular rivalry. Lumer et al. (1998) conducted a study in which fMRI scans from participants were taken in one of two conditions: rivalry and replay. Replay in this case refers to a condition in which the stimuli presented to the participant are meant to closely match how the participant's perception was changing during the rivalry condition but is done by physically alternating the stimuli such that there is no interocular inhibition occurring. It was found that in the rivalry condition, there was significantly more frontoparietal activity than in the replay condition. This led the authors to the conclusion that this area of the brain plays a role in perception that extends beyond spatial processing. While these results are interesting, the experimental design is flawed. It has been pointed out that replay conditions that mimic rivalry have abrupt transitions between percepts when in reality, the transitions between rivalry stimuli are often dynamic with the two stimuli overlapping before complete dominance/suppression takes place, which is a phenomenon known as piecemeal rivalry (Blake et al., 2014). Thus, participants who are instructed to report the dominant percept via button-press may be confused during this period of time and uncertain of how to report their percept. This confusion leads

to heightened attention, and therefore causes an increase in frontoparietal activity. Knapen et al. recreated the previous study with a replay condition that more closely mimicked the transitions seen in binocular rivalry. With the addition of mixture periods in the replay condition, they found that participants had similar levels of frontoparietal activity in the rivalry and replay conditions (2011). It is also worth noting that when comparing rivalry to replay conditions, perceptual changes are occurring in both cases, and when the brain activity is compared between the two conditions, potential NCCs may cancel out (since the perceptual changes are common to both conditions). This is not to say that frontoparietal activity plays no role in binocular rivalry, but rather the extent to which it plays a role is difficult to decipher given these limitations of previous studies. While participant reports are typically key to understanding binocular rivalry, the act of reporting in itself requires additional attentional and motor processes that make it difficult to parse through what neural mechanisms are solely responsible for rivalry.

Despite binocular rivalry being a well-researched phenomenon, there is still no true consensus on the neural mechanism underlying it. This is most likely due to the differing interpretations of data that are confounded by attentional and motor processes related to the task of reporting (Naber et al., 2011). While the currently accepted theory tends to be a mix of both the low-level and high-level models, the extent to which researchers attribute the impact of these neural processes varies greatly. Furthermore, it is particularly difficult to parse through data regarding high-level neural processes as it is so heavily influenced by attentional and motor processes related to the task of reporting. In order to truly understand the neural mechanisms behind binocular rivalry and the implications this holds for the NCCs, it is necessary to study binocular rivalry in the absence of perceptual-reporting tasks.

1.3 OKN

In the search for the NCCs, researchers tend to rely on reports from subjects during data collection to sort the trials with concurrent brain recordings

into “conscious” vs. “unconscious” (e.g., “seen” vs. “unseen” for vision) or “conscious of A vs. B” (e.g., seeing one of the two stimuli presented during rivalry). Tsuchiya et al. (2015) have pointed out that this has led much of the research into NCCs to be more so about the neural correlates of perceptual reports. Thus, it is imperative to this field of research that no-report paradigms be used when possible to paint a clearer picture of the true NCCs. Tsuchiya et al. (2015) point out that with report paradigms, there are many ways to overestimate NCCs by mistakenly including post-perceptual processes (such as judgment, decision-making, executive processes, self-monitoring, motor preparation/execution). A promising solution to this problem is to make use of optokinetic nystagmus (OKN).

OKN is a pattern of eye-movements characterized by a repeating sequence of periods of the eyes moving in the direction of a moving stimulus (known as smooth pursuit) followed by the eyes quickly moving back in the opposite direction (known as a saccade). OKN can be used when stimuli rival each other in direction of motion (e.g., a left-moving stimulus to one eye and a right-moving stimulus to the other eye). When a perceptual reversal occurs within binocular rivalry, it is accompanied by a change in the direction of both components of OKN in the direction of the dominant percept (Aleshin et al., 2019). In other words, the eye movements follow the stimulus that is consciously seen, such that conscious perception from moment-to-moment can be indirectly inferred by measuring eye movements, rather than requiring online overt reports from the subjects. Frassle et al., (2014) confirmed that OKN reliably measured subjective perception by comparing participant reports to eye-tracking data. They found that OKN matched the reported percept $82 \pm 2\%$ of the time. When comparing OKN to participant reports, it is important to account for the latency between a perceptual switch and the act of reporting (e.g., by a button-press). Frassle et al. found that this latency tended to be 400-500ms, which was used in their analysis of the accuracy of OKN. Furthermore, by using a replay condition they also found that the latency in objective measures (OKN) was significantly shorter than that of subjective measures (participant reports). While replay conditions are known to be confounding, in this case any effect that longer

periods of piecemeal rivalry would have equally affected the report-based and OKN-based data.

Given this information, utilizing eye-tracking in place of self-report measures can allow for data collection without the potentially confounding post-perceptual brain activity associated with self-reporting tasks.

1.4 Probe mediated reversals

As previously mentioned, there are several factors that might cause one stimulus to remain more dominant over another. Brightness, motion, contrast, and density of contours are all factors that can influence stimulus dominance. A probe mediated reversal occurs when a visual probe, such as an increase in brightness, triggers a reversal (Metzger et al., 2017). It has been found that probes presented to the suppressed eye trigger a reversal, while probes presented to the dominant eye tend to prolong the dominance period (Blake, Westendorf, & Fox, 1990). Typically, probe-mediated reversal experiments trigger a reversal by overlaying the probe directly on top of the stimulus being viewed. This then calls into question whether the probe is effective because it appears in the eye or in the object being viewed, which links back to the interocular inhibition vs. pattern competition debate.

To get a better understanding of the mechanisms behind probe-mediated reversals, Metzger et al. (2020) examined the effects of probes on vs. off objects on the dominance periods observed in rivalry in a series of two experiments. The probes used in these experiments were a texture overlay and a face overlay. The first experiment examined the dominance period durations in suppressed eye probes vs. dominant eye probes both as on-object probes and off-object probes. They found that with both on-object and off-object probes, probes presented to the suppressed eye created significantly shorter dominance periods relative to probes presented to the dominant eye, and that probes presented to the dominant eye extended the dominance period duration. That being said, they found that this effect was much larger for the on-object probes relative to the off-object probes (Fig. 3).

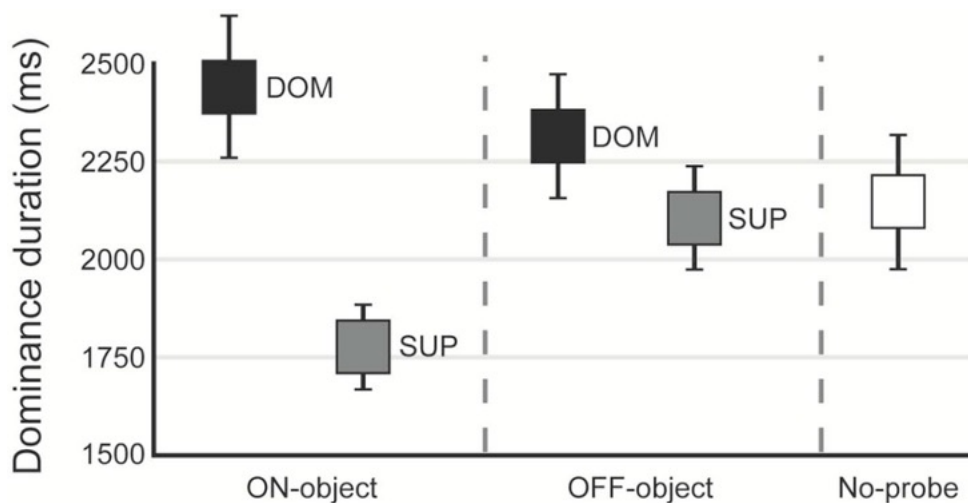


Figure 3: Dominance durations of a probe in the dominant eye vs. the suppressed eye with the probe on vs. off the object in view (Metzger et al., 2020)

The second experiment in this study examined off-object probes efficacy as a function of distance. Interestingly, the median dominance periods of suppressed and dominant eye probes did not vary as a function of the distance of the off-object probe. To summarize the findings of these experiments, on-object probes are more effective than off-object probes, but off-object probes still produce a difference in median dominance periods when compared to no-probes.

Probe mediated reversal is an important tool for two reasons. First, as just described, probes allow for an increased level of experimental control compared to spontaneous perceptual reversals: probes presented to the currently suppressed stimulus will cause a reversal, while probes presented to the currently dominant stimulus will not. Second, when recording brain activity with time-resolved measures (such as EEG, MEG, ECoG, single-cell recording) the abrupt probe onsets can provide a precisely controlled timestamp of from which neural activity can time-locked and analyzed. In the present study, which employed concurrent EEG recordings, the probe mediated reversal approach was combined with OKN measures that allowed for a “no-report” condition.

1.5 EEG

Many of the studies on binocular rivalry mentioned thus far have either utilized fMRI or single cell recordings as a measure of brain activity. As Pitts & Britz (2011) point out, fMRI has both good spatial resolution and good spatial coverage (whole brain) but suffer from poor temporal resolution. Single cell recordings on the other hand, have excellent temporal and spatial resolution but poor spatial coverage, and are invasive (requiring neurosurgery) so are only applicable in non-human animal models and in rare cases of human epileptic patients (who already require neurosurgery and electrode implants for clinical reasons). Scalp EEGs offer a nice compromise in that they provide high levels of temporal resolution with whole-brain coverage, and a decent level of spatial precision, whilst being noninvasive.

Scalp EEG data are acquired by placing an electrode cap on a participant's head. Each electrode corresponds to a certain location on the scalp and allows for a fairly reliable estimation of the location of brain activity (at the centimeter level). As for the temporal aspect, event-related potentials (ERPs) are time-locked electrical changes in the brain that can be identified using EEG. Measurable ERPs come from the sum of many postsynaptic potentials (PSPs), which allow for direct and nearly instantaneous measurement of neurotransmission-mediated neural activity. The immediacy of ERPs provides another temporal advantage over fMRI, which makes use of blood oxygen level-dependent (BOLD) signals. BOLD signals are a secondary consequence of neural activity, delayed by 4-6 sec, and are thus not ideal candidates for studies in which temporal changes are being investigated (Luck, 2014). This poor temporal resolution would make OKN and probe-mediated reversals unhelpful as they serve as precise time markers to carefully track the flow of sensory processing by the millisecond, thus making EEG the ideal candidate for data collection in the present study.

1.5.1 Relevant ERPs

There are several ERPs associated with perceptual changes in binocular rivalry. The present study looks at three specific ERP components: N1, RN, and

P3b. The N1 component, which is a negative wave that occurs approximately 100-200 ms after stimulus onset that occurs at posterior (occipital) electrode sites. The N1 component is believed to be involved in early visual processing (Luck, 2014). In a study investigating the effects of spatial attention on early visually evoked ERPs, it was found that the N1 amplitude was significantly larger for trials in which the participants were cued to attend to a stimulus vs. when the participants were paying attention to a different stimulus (Luck et al., 1994). This finding, as well as many others like it, suggests that the N1 is modulated by top-down attention.

The second relevant ERP component is reversal negativity (RN), which is the negative difference, within the timeframe of the evoked P2 wave, between reversal and stable perceptions. RN occurs 200-350 ms after stimulus onset and is centered around posterior electrodes. The source of the RN component is likely occipital-temporal and fusiform regions of the brain (Pitts et al., 2009). In a study by Britz & Pitts (2011), the RN component was investigated through a binocular rivalry paradigm. In order to generate time-locked ERPs, an intermittent paradigm was used in which 600 ms blocks were used to time-lock EEG recording to stimulus onset rather than participant reports. They found that the RN was stronger in the reversal condition relative to the stable perception condition, suggesting that it is a signal unique to perceptual reversals.

Finally, the P3b, which is also commonly referred to as the P3, is a late positive component with an onset of approximately 300 ms after stimulus onset and an extended duration (usually lasting until about 600 ms). The P3b is associated with widespread activity in the parietal and frontal lobes and is recorded primarily by more anterior electrodes compared to the N1 and RN over central-parietal regions of the scalp (Luck, 2014). The P3b is a well-researched ERP component that is often believed to be a NCC pertaining to visual awareness. However, Pitts et al. (2014) questioned if the P3b was truly associated with visual awareness or if it was reflective of post-perceptual processes associated with the task of reporting visual perception. To investigate this, they conducted a series of EEG experiments in which neural responses to geometric shapes were recorded during an inattentive blindness paradigm. In these experiments, they investigated neural responses when the shape was task-

relevant vs. task-irrelevant. Pitts et al. (2014) found that when the shapes were clearly perceived but task-irrelevant, the P3b was absent (Fig. 4).

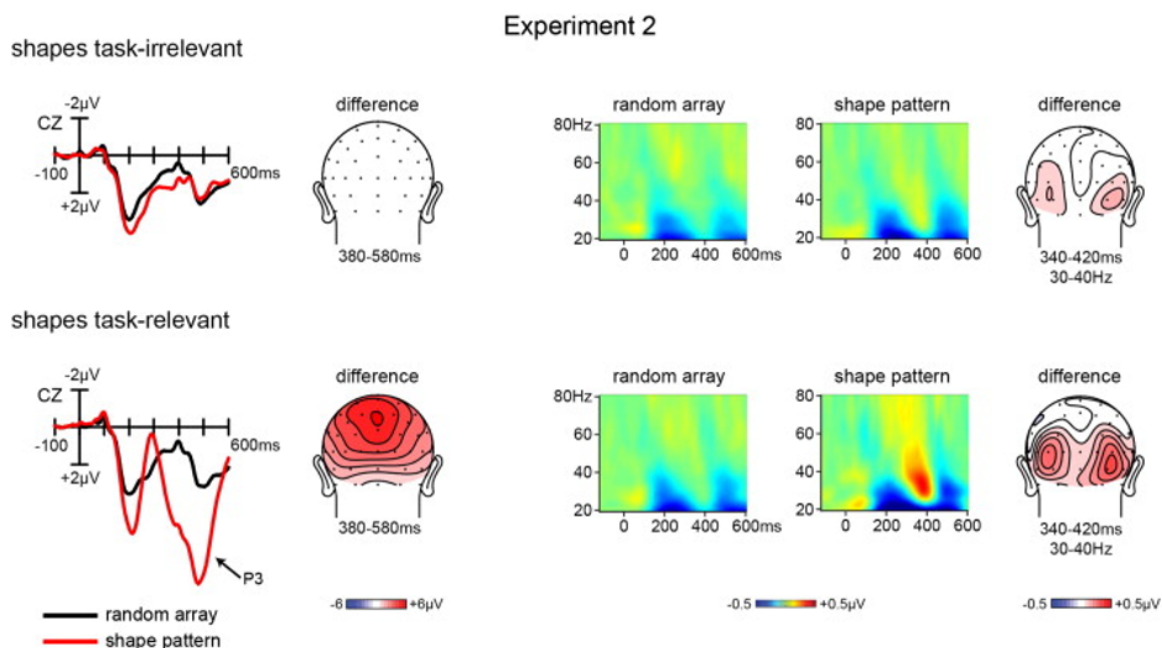


Figure 4: ERPs and difference maps from Pitts et al. (2014).

These findings indicate that because the P3b component was absent despite the shapes being clearly perceived in the task-irrelevant conditions, the P3b is not linked to visual awareness but rather the task of reporting. These findings once again highlight the importance of a no-report paradigm in experiments investigating the NCCs regarding visual awareness.

Trial-to-trial variations in the time intervals between perceptual changes in continuous binocular rivalry can make it difficult to time-lock stimulus onset. While participant reports can be used to identify stimulus onset, the act of reporting can introduce ERP components that are not related to perceptual change and create an overlap that makes it impossible to truly isolate ERP components associated with perceptual change from those associated with the task of reporting. In 2017, Metzger et al. utilized EEG in a binocular rivalry experiment to determine the NCCs associated with perceptual reversal for static stimuli. In their experiment, they looked at three ERP components: P3b, N1, and P1. The P1 component is a strongly positive wave that occurs approximately 100 ms after stimulus onset and is largest at the lateral occipital lobe electrodes. The

P1 likely originates from V1/V2 and early extra-striate cortex, which suggests it is involved in early visual processing (Luck, 2014).

Metzger et al. (2017) recorded ERPs in a probe-mediated reversal binocular rivalry paradigm in order to find out if the P3b was associated with perceptual reversal or with the probe. They found that the timing of the P3b was closely linked with the timing of the reported perceptual reversal rather than the probe. Furthermore, they found that the N1 was associated with whether the probe used for perceptual reversal occurred in the dominant or suppressed eye, and that the P1 amplitude was associated with the speed of reversal.

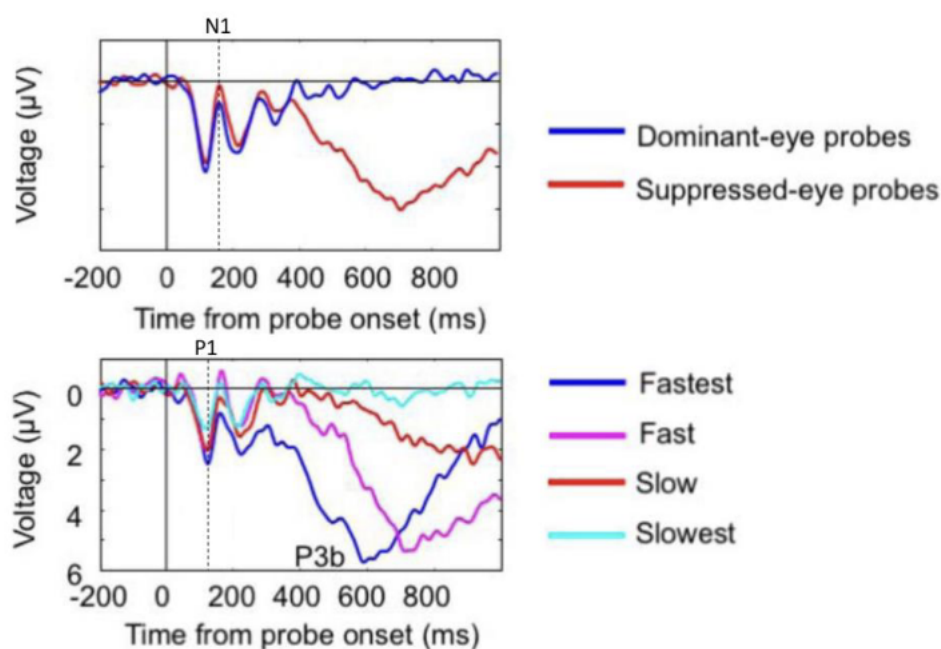


Figure 5: ERPs following probes from the Metzger et al. (2017) study.

Because this study relied on self-reporting to mark perceptual reversals, there was no condition in which perceptual reversals could be measured in binocular rivalry without self-reporting with which to compare the amplitudes of P3b ERPs. In this thesis, a design similar to Metzger et al.'s (2017) experiment will be used with the addition of moving stimuli which will allow for a no-report condition in which OKN can be used to track perceptual reversal in place of self-reporting.

In the present study, we hypothesize that we will find RN in reversal but not stable trials, the P3b will be attenuated (if not entirely absent) in the no report

condition, and that N1 amplitudes will be similar to those seen in the Metzger et al. (2017) study.

2. Methods

2.1 Participants

In the original design of this study, the plan was to collect one session's worth of EEG data from 20-30 different participants. However, due to the complicated nature of the experimental procedures, and in the interest of both time and data quality, it made more sense to have fewer participants and to collect EEG data from multiple sessions from each participant (similar to many experiments in classic human psychophysics, and in non-human primate research). In order to contribute valid data, each subject had to demonstrate clean eye-tracking, robust perceptual rivalry, clear probe-initiated reversals, high accuracy of OKN decoding, and clean EEG data. If any one of these criteria was not met, a subject must be excluded from analysis, making it very challenging to acquire valid data from 20+ subjects in the limited timeframe of the two-semester thesis. By collecting more data from fewer participants, the data will be cleaner, will allow for an increased total number of valid sessions, and will hopefully paint a clearer picture of the main ERP effects. Since this experiment does not require naïve participants, having participants who are familiar with the experimental design reduces the risk of reporting mistakes and unclean EEG recordings. Furthermore, all participants described seeing both stronger rivalry and seeing rivalry faster the more practice they had with the experiment. In short, we decided that it was more worthwhile to collect several clean EEG recordings from a few participants than to collect one EEG recording of uncertain quality from many participants.

Of the 10 participants prescreened, a total of 3 participants (all students at Reed College) participated in the full study. Participants were compensated \$10 for the 30-minute prescreening session (which tested for behavior and eye-tracking only), \$30 for the first 3-hour EEG session to verify that the ERPs were clean, and \$50 for each of the 4 subsequent 3-hour EEG sessions. Thus, each participant returned to the lab six times, once for the initial behavior/eye-

tracking screening, and five times for the main behavior/eye-tracking/EEG sessions. The participants from whom a full set of EEG data were collected are Subject 0, Subject 3, and Subject 7, with the number designated to each participant coming from the order in which the participants were prescreened.

2.1.1 Participants excluded

As previously mentioned, 3 out of 10 participants participated in the full experiment, meaning 7 participants were not invited back for further data collection. Subject 1 passed the prescreening with high accuracy and decodability (which are some of the prescreening parameters defined in section 2.4) but was not able to return due to scheduling conflicts. Subject 2 also had high decodability and accuracy but strange reversal latency distributions, indicating that the probes did not elicit reversals as expected. This was due to the participant having misunderstood the instructions to ignore the probes, which resulted in them trying to actively prevent perceptual reversals. Subject 4 (not included in data analysis or as one of the three participants) had two EEG sessions before being excluded from the study due to the presence of large alpha waves obscuring ERPs (commonly assumed to reflect fatigue or drowsiness). Subjects 5, 6, 8, and 9 did not meet decodability and/or accuracy criteria.

2.2 Apparatus

The experimental apparatus used in this experiment (Fig. 6) was adapted from Qian & Brascamp's (2017) instructions on building a dichoptic display with eye-tracking. The entire apparatus is arranged on top of a height-adjustable desk. The display is made up of two identical monitors (60 Hz, 1920x1080 px, 24") that face each other from opposite sides of the desk. The chinrest, which is mounted to the edge of the desk, is placed exactly in the middle of the two monitors. Two infrared-transparent mirrors ("cold mirrors") positioned at 45° relative to the participants midline are placed in front of the chin rest such that they reflect the monitor displays to each eye. The infrared-transparent mirrors allow for the eye-tracker to track pupil position whilst the stimuli from the monitors are reflected

to each eye. The eye-tracker (desk-mounted EyeLink 1000 plus, sampling rate 1000 Hz) is positioned directly in front of the chinrest at a distance of 45 cm.

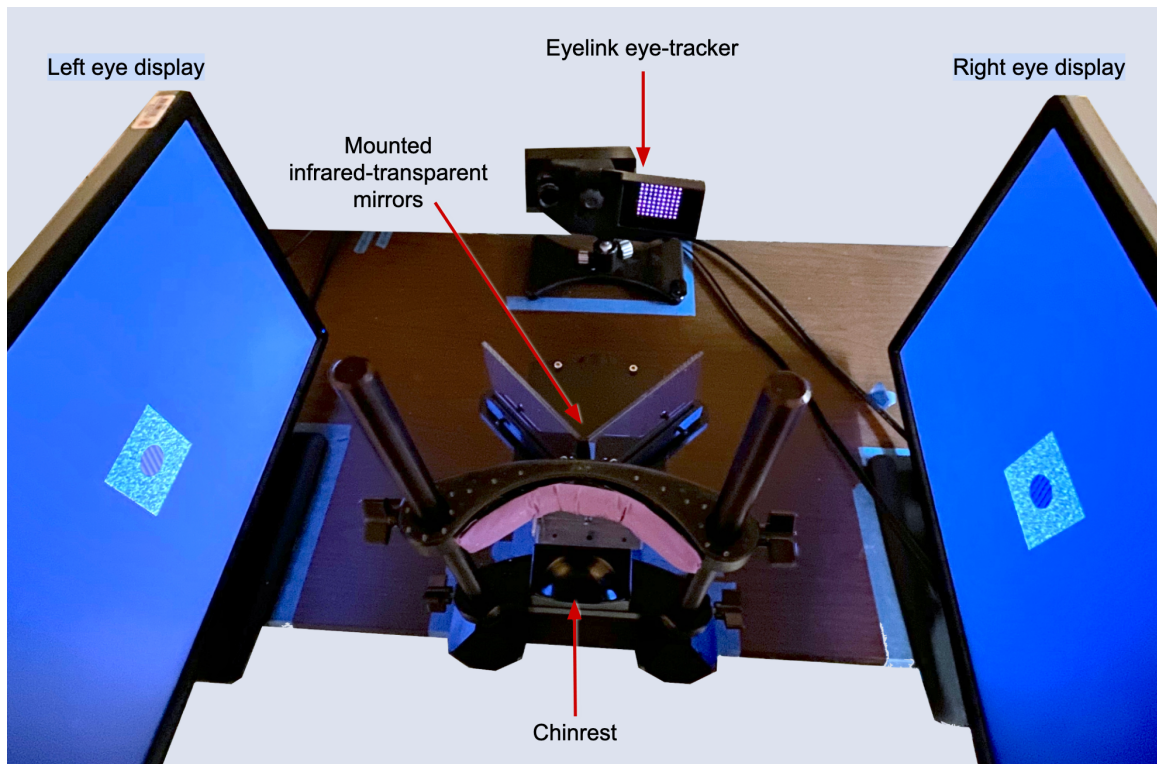


Figure 6: Apparatus in EEG recording booth.

Participants place their chins in the chinrest and view stimuli from the left and right eye display monitors through the 45° angled infrared-transparent mirrors. The EyeLink eye-tracker is placed in front of the mirrors and records eye movement from the right eye.

2.3 Stimuli

Before the experiment begins, the monitor positions are calibrated in order to ensure that each stimulus directly falls in the center of each participant's field of view. Monitor calibration is done by presenting a white dot that is framed by identical random noise patterns and having the participant move it with the arrow keys such that it does not appear to move when it switches between the left/right eye monitors. The monitor is calibrated before each task condition to account for any changes to the participant's position.

The stimuli used in this experiment are bar gratings that are oppositely tilted by 20° and viewed through circular apertures that are framed by identical random noise patterns (Fig. 7). The bars are colored blue and yellow to increase contrast between each eye and thus strengthen the effect of rivalry. For the purpose of evoking different OKN directions, the bars move in opposite directions (left-to-right and right-to-left). The direction of motion is counterbalanced between colors/eyes across blocks. The stimuli drift at a speed of 4 cycles/second and span a visual angle of 4.7 deg with a spatial frequency of 0.94 deg/cycle.

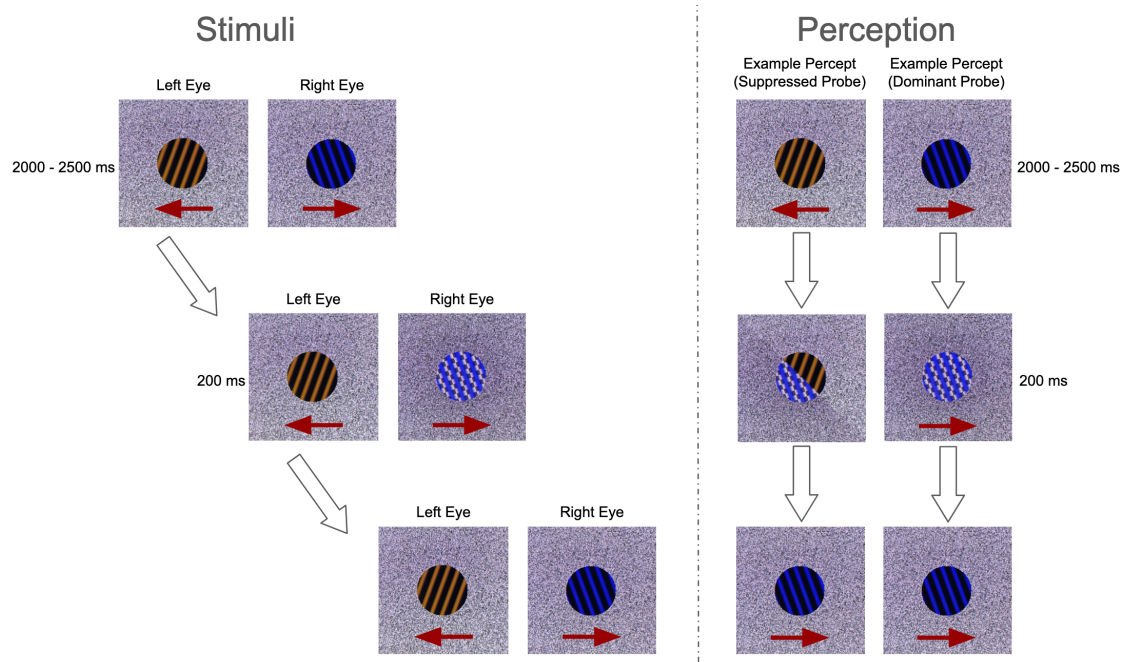


Figure 7: Stimuli, probes, and example percepts

Example of yellow and blue stimuli moving in opposite directions. Probes are presented pseudo-randomly between eyes. The stimuli (left) are an example of what is presented on the monitors, and the perception (right) are examples of what a participant sees in the cases of suppressed and dominant probes.

The probes used to trigger a reversal are a brief increase in brightness so as to not disrupt the motion of the stimuli, as well as simultaneously changing the black background stripes to gray-and-white checkerboard patterns. The checkerboard aspect of the probes was added because the brightness increase alone did not evoke typical early visual responses in the ERPs, such as the occipital P1 and N1 components, during pilot testing. The probes are presented for 200ms durations

to each eye randomly with equal probability. The intervals between probes are presented randomly from a uniform distribution of 2-2.5 seconds.

The stimuli occasionally (10% of trials) changed speed by 50% for a duration of 1 second. These motion speed changes were introduced to keep subjects attentive enough to the stimuli in the no-report condition, as pilot testing with a completely passive no-task condition led to disengagement with the stimuli to the point that OKN decoding became unreliable. In this improved no-report task, participants were asked to use the left-mouse button to report when they noticed a change in speed, which was an orthogonal stimulus feature to the alternating percepts, thereby still rendering the perceptual switches irrelevant to the task in this condition. Performance was reported to a monitor outside the recording room so that the researcher can inform participants if targets are being missed. The timing of the speed changes was on the same schedule of probe presentation such that it does not interfere with ERPs or OKN decoding during probe presentations, and all trials with a motion speed change were discarded from further analyses.

2.4 Prescreening

Due to variations across participants, a short prescreening session was conducted to verify that each participant had reliable eye-tracking data before the EEG session. The prescreening session was a shortened version of the actual experiment in which each task (report and no-report) consisted of 10 x 60-second blocks. There was a break between each block, of which the duration was determined by the participant. In the prescreening session, the report task always came first as pilot testing found that naive participants were able to better achieve rivalry and reversals when they know what to look for.

The participants were being screened to find the decodability of their eye movements, which was the percentage of time the OKN decoding pipeline was able to make a prediction about the direction of eye movements, and how accurately their eye movements matched their reported perception (with report latency being accounted for by shifting the report backwards 400ms when

compared to eye movements). If average decodability was more than 70% and accuracy was more than 75%, then participants were invited to participate in the EEG session.

It is worth noting that one participant (Subject 7) in this study did not pass the 75% accuracy threshold in the prescreening. While accuracy was an important metric for gauging the reliability of a subject's data, it was not the only indication available that the experiment worked as intended. We chose to move forward with data collection from this participant as every other prescreening target was hit, the probes reliably caused perceptual reversal, and the participant expressed after the fact that they were mainly confused/hesitant with the reporting task. Furthermore, this subject had dominance periods and reversal latencies that were within the range of the other two subjects that had passed the accuracy criteria. Finally, the initial EEG session showed that Subject 7 had ERPs on par with those of the other two subjects, and that the recorded EEG was notably clean. If this subject's eye movements did not reliably reflect their perception, then we would have expected to see ERPs inconsistent with those of other subjects and what is known from the literature.

2.5 EEG

Participants were fitted with a 64-electrode EEG cap (EasyCap, Gersching Germany). The EEG was recorded using BrainVision Recorder with a sampling rate of 1000 Hz to a computer outside of the recording room and the EEG output was time-locked to probe onset. To ensure that the data was consistent for each participant between sessions, each participant used the same electrode cap that they were fitted for in their first EEG. Data was analyzed using BrainVision Analyzer.

Before the actual experimental session began, participants did a brief 3-5 block practice in which participants reported the visually dominant stimulus to readjust to rivalry. The EEG session consisted of 30 x 60-second blocks in each task condition (1 hr of total experiment-time; with rest breaks, set-up, impedance measurements, eye tracking calibration, practice, clean-up, etc., total session time

was between 3-4 hours). The order in which task conditions were presented was alternated between sessions to ensure that there were no order effects. If the eye-tracker at any point became inconsistent with its ability to track the eyes, then it is recalibrated between blocks. If OKN became inconsistent, participants were reminded by the researcher to maintain focus between blocks.

2.6 OKN/ERP analysis

Analysis of OKN was directly adapted from Aleshin et al. (2022). This analysis is referred to as cumulative smooth-pursuit (CSP) analysis. As previously mentioned, OKN has periods of smooth pursuit followed by a saccade backward. Aleshin et al.'s analysis identifies these periods of smooth pursuit and joins them into one segment through probabilistic analysis that accounts for physiological factors such as blinks and saccades, as well as eye-tracker related factors such as artefacts and signal losses. This is done by the pipeline making a series of velocity estimates, which can be split into two categories: pursuit dominance and pursuit transitions. The pursuit dominance phase is the ~1-2s period of dominance during rivalry, while the pursuit transition phase is a quick shift indicative of a perceptual reversal.

After the eye-tracker file was analyzed using code primarily from Aleshin et al. (2022), the resulting file was combined with the EEG files to produce a "decoded" EEG with event codes that showed perceptual reversals as identified from OKN. During EEG recording, the MATLAB program presenting the stimuli to the recording booth input event-markers into the EEG recording which denoted the onset of the checkerboard probes and which eye the probe was presented to. The completed EEG recording was then combined with the decoded eye-tracking data, which used the probe onset event-markers in the EEG file to label segments as either reversal trials or stable trials. When a segment is categorized as a stable or reversal trial, the resulting ERPs are time-locked to the onset of the probe.

Before obtaining ERPs, the decoded EEG files were preprocessed. The first step of preprocessing was topographic interpolation, in which bad (noisy, poor

impedance, or dead) channels were replaced with the average signal of the closest surrounding electrodes. The same channels were interpolated across both report and no report tasks in a given session for the sake of data consistency. Next, the markers were segmented according to the Booleans in the following section. A high-pass filter of 0.1 Hz was then applied before averaging the mastoid reference between both right and left mastoid electrodes. After averaging the mastoids, the electrooculogram (EOG) channels, which are the two electrodes placed next to both eyes and the one underneath the left eye, were made bipolar with vertical EOG (VEOG) and horizontal EOG (HEOG) channels being added to separate vertical eye movements (blinks) from horizontal (eyes moving right to left). The EEG was then separated into dominant and suppressed segments based on the segmentation markers previously implemented. Both segments then received baseline corrections, which was followed by a semiautomatic artifact rejection to filter out blinks (using the VEOG channel. The blink threshold was kept consistent in each individual session across suppressed and dominant segments. After blink rejection, the segments were averaged, and a low-pass filter of 25 Hz was applied. This resulted in four ERP outputs: suppressed mastoid reference, suppressed average reference, dominant mastoid reference, and dominant average reference.

2.6.1 Segmentation

The following Booleans are used to segment the EEGs for ERP analysis.

Suppressed (reversal trials):

```
(CURR(Stimulus, S11) AND (LAST(Response, *, -1, -10000).$Description=R23 AND (FIRST(Response, R24, 1, 800))))
OR (CURR(Stimulus, S10) AND (LAST(Response, *, -1, -10000).$Description=R24 AND (First(Response, R23, 1, 800))))
```

This translates to the following: If the last response 1-10000ms before right probe onset was a reversal to the left *and* the first response within 800ms after right probe onset was a reversal to the right, then the segment is considered a reversal

to the right. Similarly, if the last response 1-10000ms before left probe onset was a reversal to the right and the first response within 800ms after left probe onset was a reversal to the left, then the segment is considered a reversal to the left. "Responses" here refer to the event code markers that result from the OKN decoding.

Dominant (stable trials):

```
(CURR(Stimulus, S10) AND (LAST(Response, *, -10000, -1).$Description=R23 AND (NOT(FIRST(Response, R24, 1, 800)))))) OR (CURR(Stimulus, S11) AND (LAST(Response, *, -10000, -1).$Description=R24 AND (NOT(FIRST(Response, R23, 1, 800))))))
```

Translation: If the last response 1-10000ms before left probe onset was a reversal to the left and the first response within 800ms after left probe onset is *not* a reversal to the right, then the segment is considered dominant. Similarly, if the last response 1-10000ms before right probe onset was a reversal to the right and the first response after right probe onset is *not* a reversal to the left, then the segment is also considered a dominant trial.

3. Results

3.1 Psychophysics

3.1.1 Decodability & Accuracy

All participants exhibited OKN with a high level of decodable eye movements, and 2 participants had high levels of reporting accuracy. As previously mentioned, Subject 7 did not meet the threshold for reporting accuracy, but all other psychophysical criteria were well above threshold which indicates that the stimuli worked as expected and that the high error levels were most likely the result of the subject being unfamiliar and hesitant with the reporting task. Subject 7's dominance periods, decodability, and reversal latencies (RL) were nearly perfect and on par with the other two subjects and well-above those of other subjects prescreened who did not meet the accuracy threshold. Dominance periods were quantified by the amount of time (ms) OKN remained consistent in one direction before a perceptual reversal, and RL were quantified by the amount of time (ms) it took for the direction of OKN to switch following a probe.

The average dominance period across all sessions for all subjects was 1798 ms. While this dominance period is comparably shorter than those seen in the Metzger et al. (2017) study using static stimuli, it can be attributed to the present study using moving stimuli. This is supported by dominance periods of similar lengths (i.e. <2 seconds) being reported by Frassle et al. (2014) in their study which also uses dynamic stimuli. The average median RL of each participant for probes presented to the suppressed eye were significantly shorter than that of probes presented to the dominant eye, which suggests that the probes were functioning as intended (i.e., to trigger perceptual reversals) despite the short average dominance periods. Participant psychophysics are reported below (Table 1).

	Subject 0	Subject 3	Subject 7
Decodability	95%	91%	91%
Accuracy	89%	88%	23%
Avg. dominance period	2167 ms	1617 ms	1610 ms
Avg. median suppressed RL	358 ms	799 ms	644 ms
Avg. median dominant RL	2092 ms	1066 ms	1460 ms

Table 1: Psychophysical data averaged across all five sessions for each participant.

Each session is comprised of 60 x 60-second blocks: 30 blocks in the report task condition and 30 blocks in the no report task condition. Accuracy is the only metric unique to the report task condition. All other metrics are from the eye-tracking data for both report and no report conditions. The cell highlighted in red signifies that the Subject 7's accuracy did not meet a score of 75% or higher.

Subject 0 had ideal reversal latencies following probe presentations, with the median dominant reversal latencies on average being almost identical to the average dominance period, and the average median suppressed reversal latencies being extremely short. While not as clean as Subject 0, Subject 3 had reasonable reversal latencies following probe presentation that still indicate that the probes worked as intended. Subject 0 and Subject 3 had high levels of eye-tracker decodability and report accuracy well within the thresholds of 70% and 75% respectively.

3.1.2 Reversal Latency Distributions

To further verify that the probes functioned as intended, the coding pipelines would output three RL distributions: suppressed, dominant, and null. The suppressed and dominant RL distributions graphed the reversal latencies following probes presented to the suppressed and dominant eyes respectively. The null distribution takes the RL from across all trials and graphs what we would expect to see if there was no relationship between the probe and reversal.

RL distributions were examined for all trials included in data analysis. Subject 4, who was excluded from the study, displayed poor RL distributions which contributed to our choice to remove them from the study. Figure 8 shows an example of a particularly clean RL distribution from Subject 0.

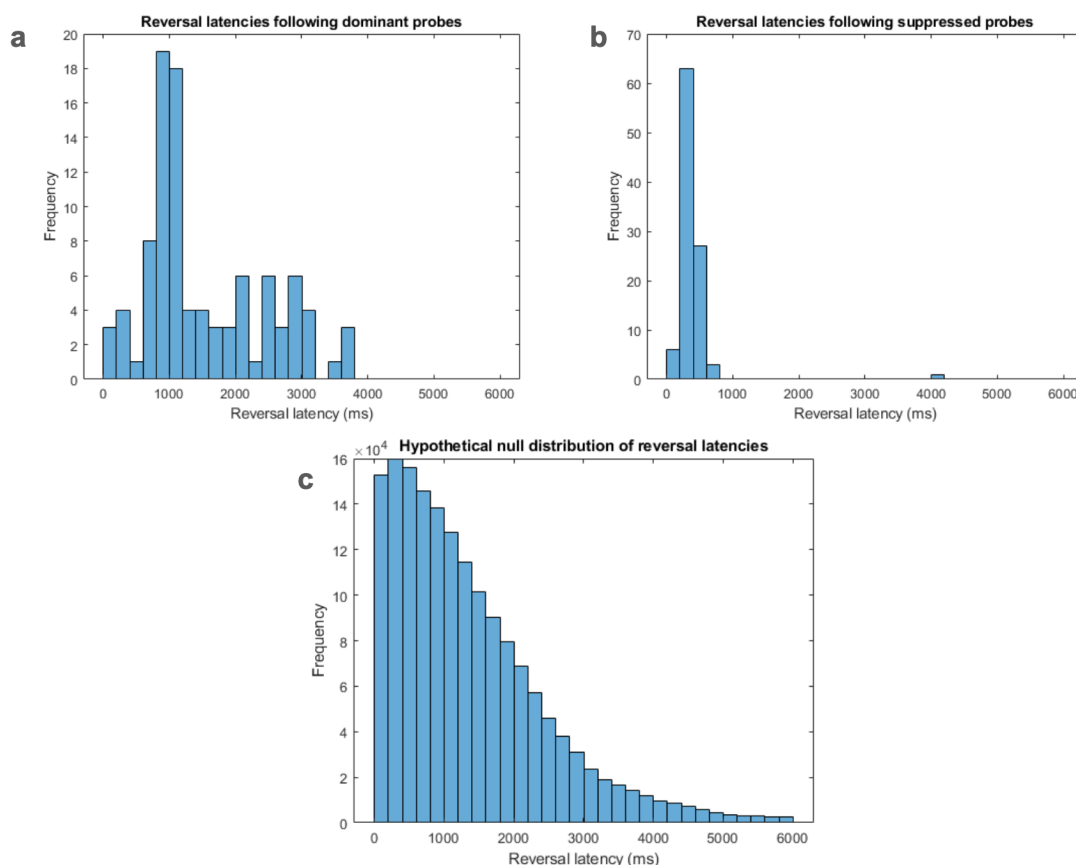


Figure 8. Example reversal latency distributions (from one of the sessions for Subject 0).

Reversal latencies following probes for the **a.** dominant eye and **b.** suppressed eye, and **c.** the null distribution if the probes did not have any effect. These distributions are from Subject 0, session 4, in the report task condition. Reversal latency distributions for this subject across sessions and task conditions were nearly identical to this one.

3.2 Statistical analysis

Because of the experimental approach (small number of subjects, multiple sessions per subject), inferential statistics were suboptimal, but are reported here

in multiple ways to provide a general idea of how the results would likely turn out if this study was repeated on a typical 20-30 subject sample. 2x2 ANOVAs with the factors perception (stable, reversal) and task (report, no-report) yielded several statistically significant main effects and interactions consistent with the ERPs and scalp distributions but was likely over-estimating the effects due to treating the dataset as coming from 15 individual subjects (i.e., variability was artificially lower because 3 subjects repeated the experiment 5 times each and there was extremely high consistency in the ERPs across sessions within each subject). Alternatively, 2x2x5 ANOVAs (perception x task x session) took into account that there were 3 subjects with 5 sessions each, but because the effects of interest (the 2x2) involved collapsing across the 5 sessions, $N=3$, which yielded little to no statistical significance simply due to the small sample size, thus under-estimating the true effects. We chose to report the results of both of the suboptimal analyses, the 2x2 and 2x2x5, as both were imperfect but together might present a balanced overview of the results that can help provide a decent estimate for how the effects might be inferred to a larger population.

3.3 ERPs

In the statistical analyses, the individual ERP amplitudes from the ERP-relevant electrodes from each session and participant was used. To get the ERPs used in data visualization, the grand average across all five sessions across all three participants was taken. Difference waves were generated by subtracting stable trials (stable following probe presented to dominant eye) from reversal trials (reversal following probe presented to suppressed eye) for the report and no report task conditions. ERPs did not appear to be significantly different between the average (of all channels) and mastoid (average of left and right mastoid) references, so the mastoid reference was chosen for both statistics and data visualization.

3.3.1 N1

Occurring from 180-220 ms and centered on electrode 43, the amplitude of the N1 was strongly impacted by perception, with task having little to no influence. We found that the N1 amplitude was significantly attenuated in the reversal condition compared to the stable condition (Fig. 9).

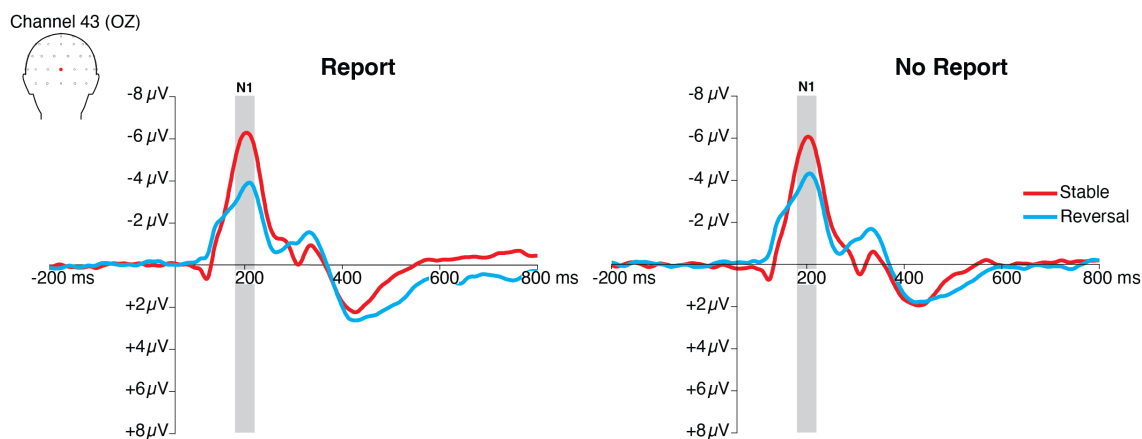


Figure 9: N1 ERPs in stable vs. reversal segments

ERPs from both the report (left) and no report (right) task conditions. ERPs are from the grand average of all 15 sessions and are located on electrode 43 (OZ).

The N1 for both perceptions was quantified by the mean amplitude across 180-220 ms (time window indicated by grey box).

Given that the N1 is associated with early visual processing, it makes sense that the amplitude would be significantly larger when the probe is presented to the dominant eye compared to the smaller amplitude seen when the probe is presented to the suppressed eye.

The difference in N1 amplitude seen in the ERPs is also seen in the scalp map distributions occurring in the same timeframe (Fig. 10).

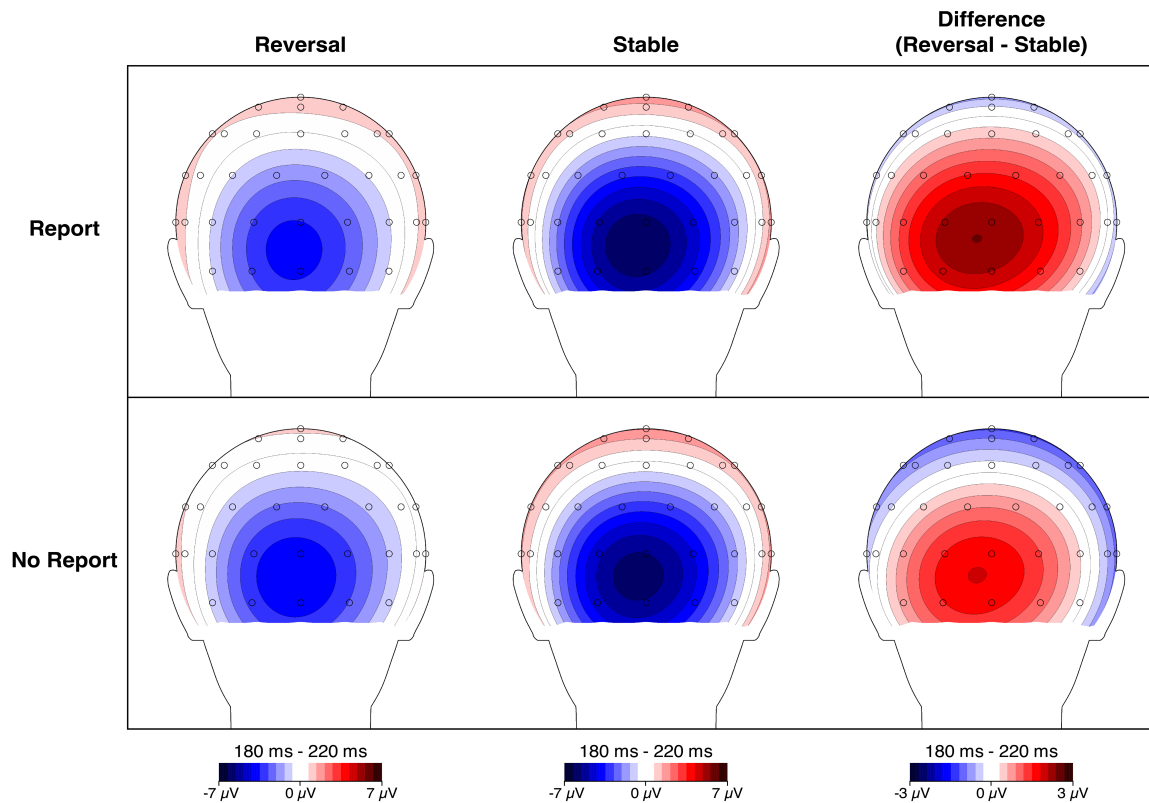


Figure 10: N1 scalp distributions

N1 scalp distributions for reversal (left) and stable (middle) perceptions, as well as the difference (right), in both report (top) and no report (bottom) task conditions in the timeframe of 180-220 ms.

In both no report and report conditions, the N1 originates posteriorly and appears to be clearly attenuated for suppressed eye probes compared to dominant eye probes (note the difference in scale between reversal and stable).

Statistical analysis of the N1 was done using the amplitude of electrode 43 and the electrodes immediately surrounding it: 42, 44, 54, 55, and 56. The 2x2 ANOVA showed a main effect of perception ($p < 0.001$, $F = 145.85$) and a perception*task interaction ($p = 0.004$, $F = 11.42$) and no main effect of task ($p = 0.685$, $F = 0.172$). Despite the ANOVA showing some significance for the interaction between perception and task, a Tukey's post-hoc test revealed that there was no significant difference between the report vs. no-report tasks for the dominant eye probes ($t = -1.538$, $p = 0.431$) or the suppressed eye probes ($t = 2.225$, $p = 0.144$). The 2x2x5 ANOVA yielded a main effect of perception ($p = 0.026$, $F = 36.65$) and no main effect of task ($p = 0.702$, $F = 0.19$) or perception*task

interaction ($p=0.138$, $F=5.80$). The raincloud plots below provide a visual representation of the main effect being from perception and not task (Fig. 11).

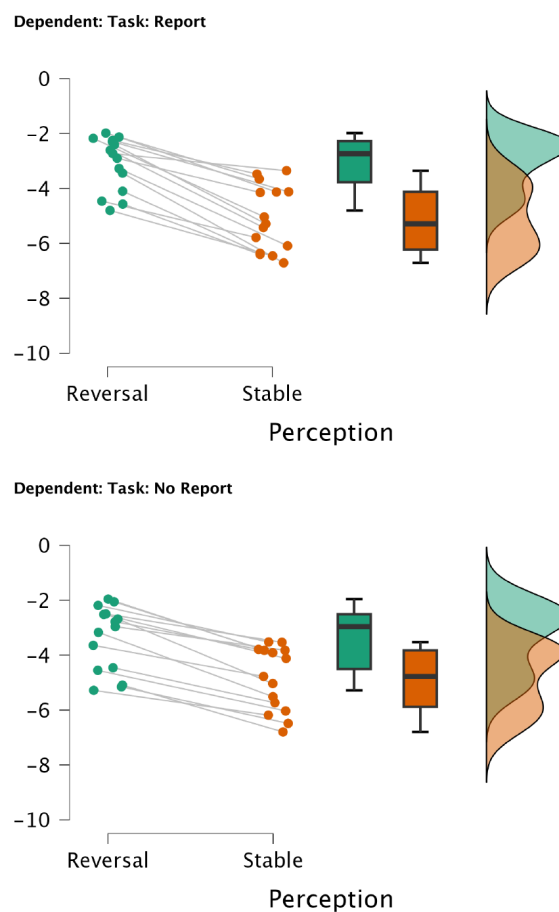


Figure 11: N1 raincloud plot

Raincloud plots of all sessions for both report (top) and no report (bottom) conditions. The X-axis of these plots show perception, and the Y-axis shows the average amplitude (μV) of the N1 ERP from channels 42, 43, 44, 54, 55, and 56 spanning from 180-220 ms. Each dot is a single subject, single session. The boxes represent the interquartile range, the horizontal lines within each box show the median, and the bars depict the minimum and maximum amplitudes of each perceptual state. Distributions are shown on the right.

3.3.2 RN

RN took place between 300-340ms and was centered on electrode 43. Like N1, the amplitude of RN seems to be impacted by perception with task having

no effect. The ERPs show a small negative peak found in reversal trials in both report and no report conditions that is much smaller in stable trials (Fig. 12).

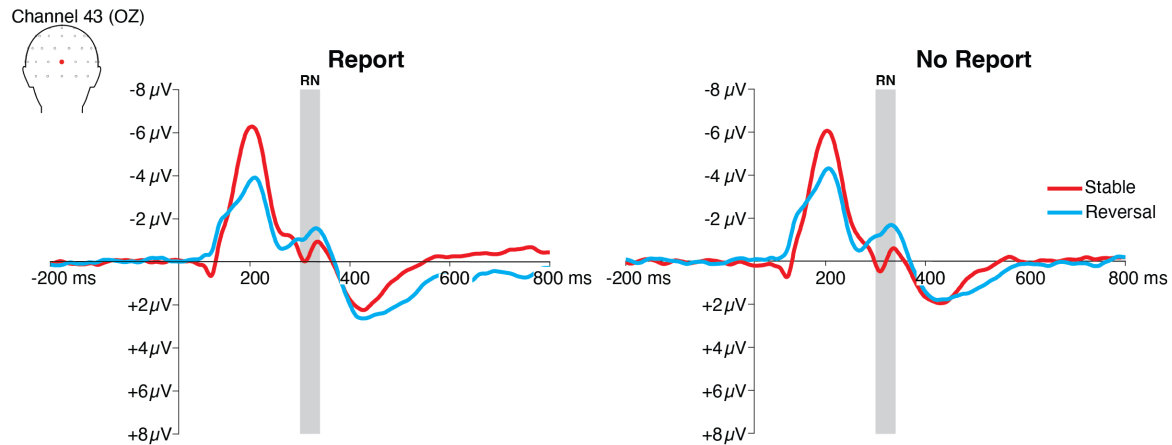


Figure 12: RN ERPs in stable vs. reversal segments

ERPs from both the report (left) and no report (right) conditions. ERPs are from the grand average of all 15 sessions and are located on electrode 43 (OZ). RN for both perceptions was quantified by the mean amplitude across 300-340 ms (time window indicated by grey box).

Unlike the other ERPs, RN is a unique signal superimposed on the sensory-evoked ERPs as the RN distribution does not necessarily match the signals seen at that point in time. The scalp distribution of RN is best seen as the difference when the signals of the stable trials are subtracted from those of the reversal trials, but the posterior negativity can be seen in the reversal trials alone as well (Fig. 13).

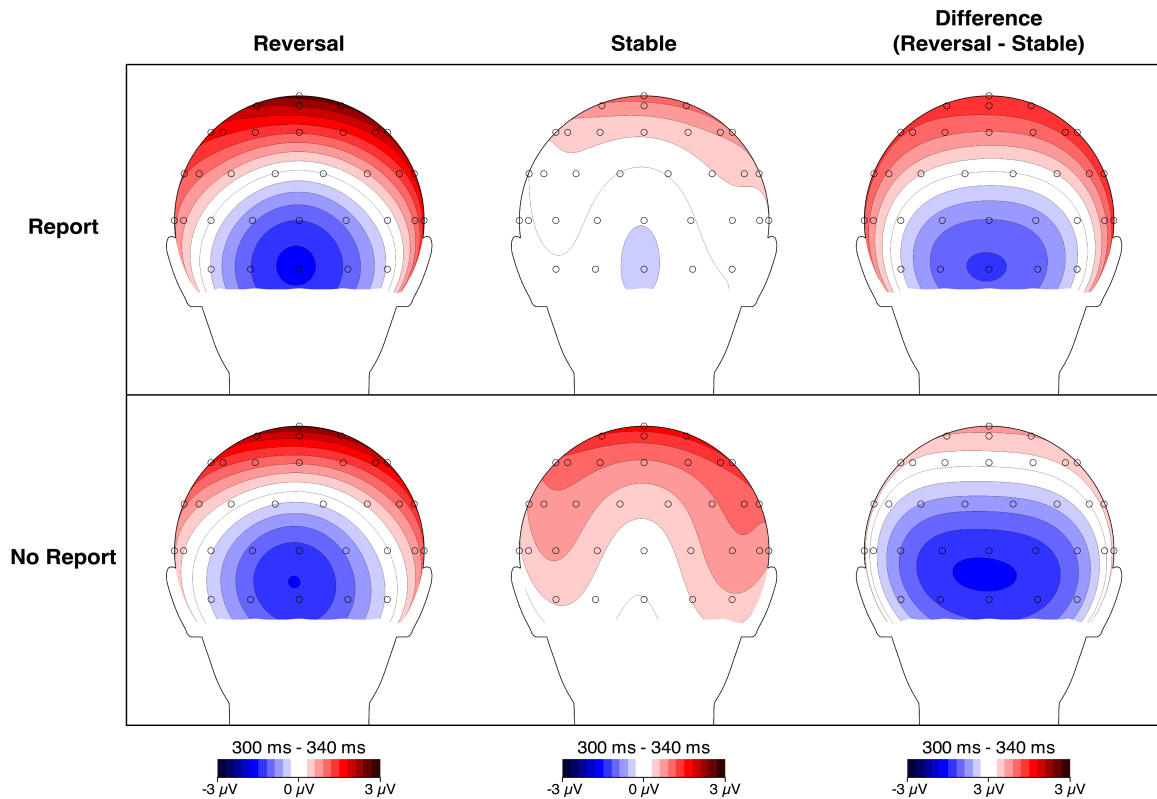


Figure 13: RN scalp distributions

RN scalp distributions for reversal (left) and stable (middle) perceptions, as well as the difference (right), in both report (top) and no report (bottom) conditions in the timeframe of 300-340 ms.

Unsurprisingly, RN is not seen in any significant capacity in the scalp distributions of stable trials.

Statistical analysis of RN was done using the amplitude of electrode 43 and the electrodes immediately surrounding it: 42, 44, 54, 55, and 56. The 2x2 ANOVA showed a main effect of perception ($p < 0.001$, $F = 32.14$) and no effect of task ($p = 0.057$, $F = 4.31$) or perception*task ($p = 0.121$, $F = 2.73$). Post-hoc comparisons of perception*task further confirm that RN is solely dependent on perception with significance being seen between reversal and stable perceptions in both report ($p = 0.003$, $T = -3.975$) and no report ($p < 0.001$, $T = -5.699$). The 2x2x5 ANOVA showed no significance of task ($p = 0.171$, $F = 4.38$), perception ($p = 0.101$, $F = 8.45$), or task*perception ($p = 0.126$, $F = 6.44$) – likely a result of having a small sample size and the small amplitude of RN. The raincloud plot below demonstrates the data across all 15 sessions (Fig. 14).

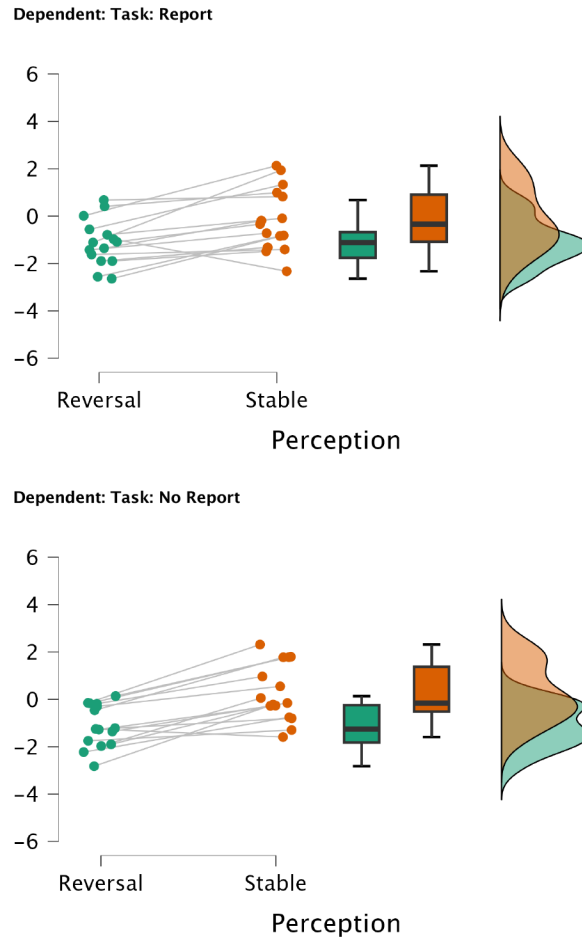


Figure 14: RN raincloud plot

Raincloud plots of all sessions for both report (top) and no report (bottom) conditions. The X-axis of these plots show perception, and the Y-axis shows the average amplitude (μV) of the RN ERP from channels 42, 43, 44, 54, 55, and 56 spanning from 300-340 ms. Each dot is a single subject, single session. The boxes represent the interquartile range, the horizontal lines within each box show the median, and the bars depict the minimum and maximum amplitudes of each perceptual state. Distributions are shown on the right.

3.3.3 P3b

The P3b was centered on electrode 5 and occurred between 400-600ms. Interestingly, the ERPs show that the P3b is slightly negative in the stable segments in both the report and no report conditions. As hypothesized, the P3b appears to be attenuated in the no report condition compared to the report

condition, with the stable and reversal segments in the no report condition being more negative than those of the report condition (Fig. 15).

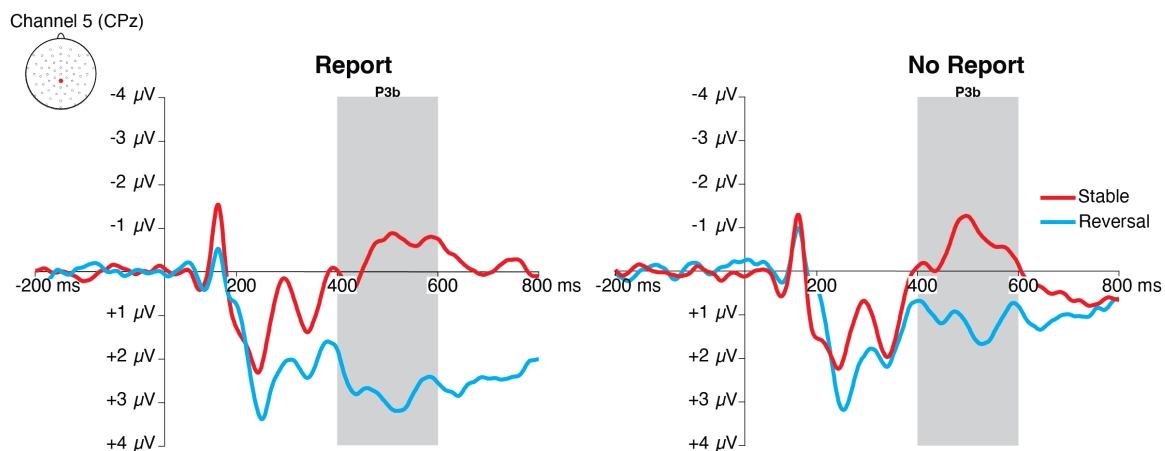


Figure 15: P3b ERPs in stable vs. reversal segments

ERPs from both the report (left) and no report (right) conditions. ERPs are from the grand average of all 15 sessions and are located on electrode 5 (CPz). The P3b for both perceptions was quantified by the mean amplitude across 400-600 ms (time window indicated by grey box).

Despite perception seemingly having an effect, the P3b amplitude seems to be most strongly influenced by task. The scalp distributions help paint a clearer picture as it shows the P3b is clearly attenuated in the no report condition compared to report (Fig. 16).

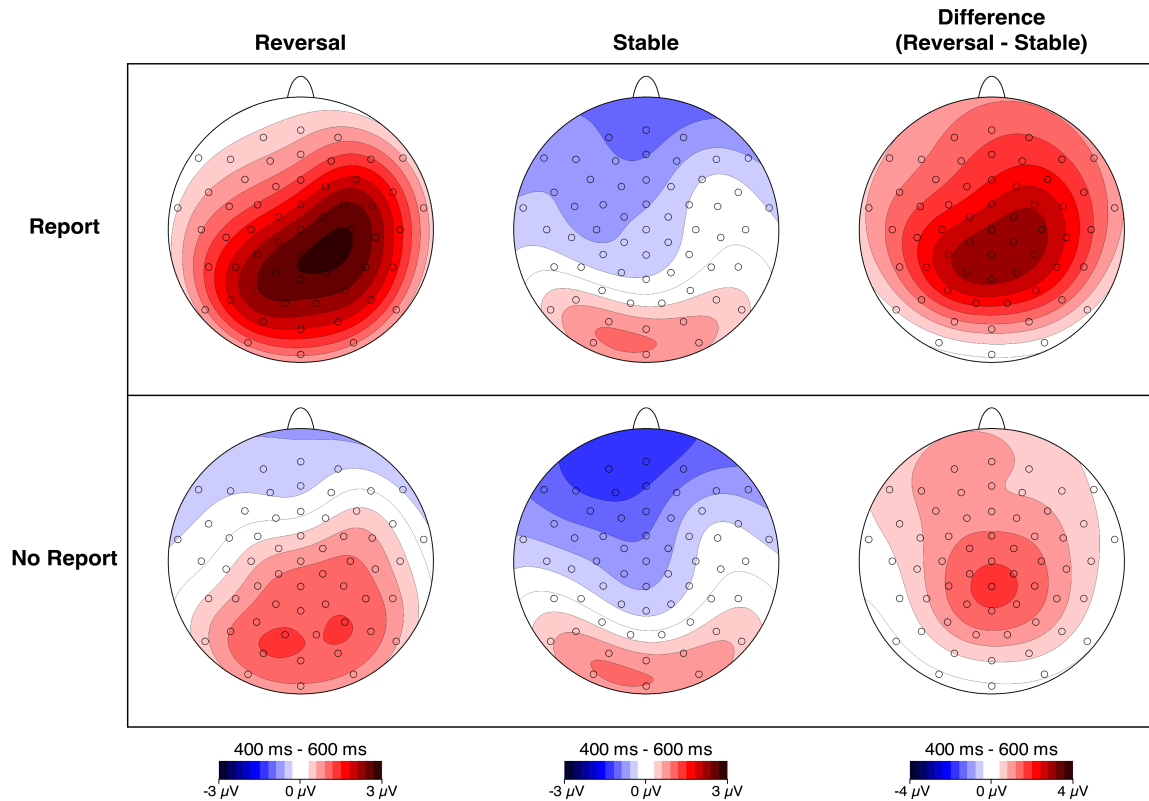


Figure 16: P3b scalp distributions

P3b scalp distributions for reversal (left) and stable (middle) perceptions, as well as the difference (right), in both report (top) and no report (bottom) conditions in the timeframe of 400-600 ms.

Statistical analysis of the P3b was done using the amplitude of electrode 5 and the electrodes immediately surrounding it: 1, 4, 6, 13, 14, and 15. Interestingly, the 2x2 ANOVA showed there was a main effect of task ($p < 0.001$, $F = 19.55$), perception ($p < 0.001$, $F = 34.41$), and the interaction between task*perception ($p < 0.001$, $F = 20.15$). The main effect and interaction of task is primarily driven by perceptual reversals causing a larger P3b during the report condition. This is evidenced by the Tukey's post-hoc test showing no significance for the pairwise comparison between stable, no-report vs. stable, report ($p = 0.950$, $T = 0.535$) despite every other pairwise comparison being significant. The 2x2x5 ANOVA showed a main effect of task ($p = 0.015$, $F = 67.26$) and no significant effect of perception ($p = 0.098$, $F = 8.78$) or task*perception ($p = 0.051$, $F = 18.03$). The raincloud plots illustrate the P3b distributions of the participants between conditions (Fig. 17).

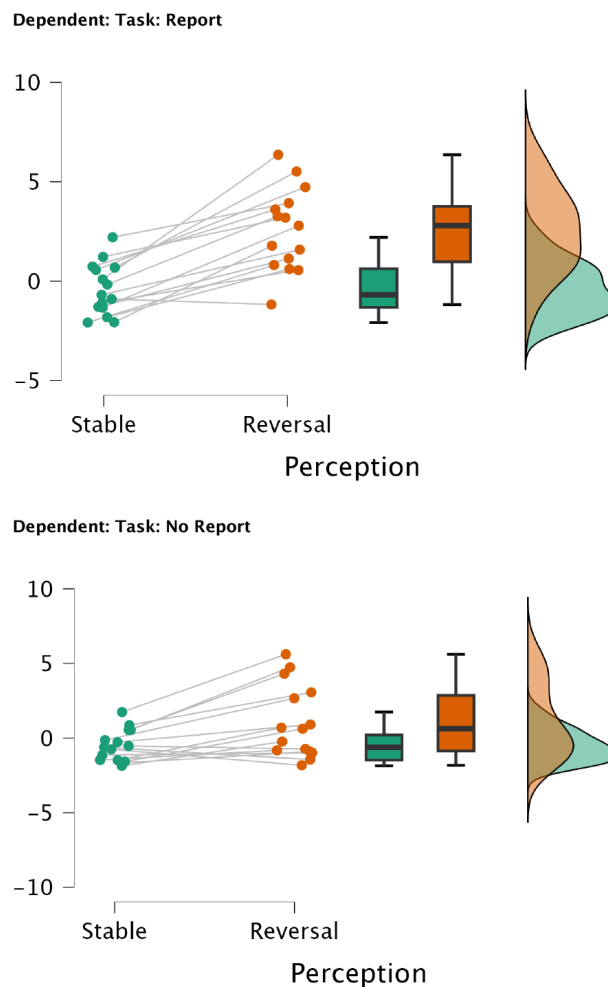


Figure 17: P3b raincloud plot

Raincloud plots of all sessions for both report (top) and no report (bottom) conditions. The X-axis of these plots show perception, and the Y-axis shows the average amplitude (μV) of the P3b ERP from channels 1, 4, 5 (CPz), 6, 13, 14, and 15 spanning from 400-600 ms. Each dot is a single subject, single session. The boxes represent the interquartile range, the horizontal lines within each box show the median, and the bars depict the minimum and maximum amplitudes of each perceptual state. Distributions are shown on the right.

4. Discussion

In this study, we investigated the ERP correlates of probe-mediated perceptual reversals in a no-report binocular rivalry paradigm. More specifically, this study investigated how ERPs differ when probes are presented to the dominant eye vs. the suppressed eye, and how those ERPs differ when a reversal is triggered and when perception remains stable. We also investigated how the task of reporting might impact these ERPs by implementing a no-report paradigm that utilizes eye-tracking and OKN decoding.

4.1 ERP Interpretations

The ERP components we were mainly interested were the N1, RN, and P3b. We found significant changes in N1 and P3b across perception and task respectively, as well as the presence of RN. We identified potentially significant ERPs, as well as the electrodes they're centered on, for data analysis by subtracting the stable segments from the reversal segments.

In this study, we found that N1 amplitude was primarily affected by reversal, with little to no effect of task. The amplitude of N1 was larger when the probe was presented to the dominant eye, suggesting that modulation of the amplitude was indicative of early visual processing. Interestingly, this differs from the findings of the Metzger et al. study, which found that the N1 amplitude was larger when the probe was presented suppressed eye. It's also worth mentioning that the difference in N1 amplitude in their study was much smaller than the difference in the present study. The difference in N1 across studies may be due to the present study using dynamic stimuli, whereas the Metzger et al. study uses static stimuli.

The present study found significant RN in perceptual reversals. This is an important finding as previous studies identifying RN, such as the one by Britz & Pitts (2011), time-lock ERPs to stimulus onset rather than probe-mediated

reversals. The present study is the first to identify RN without stimulus onset, meaning only the participants' perceptions, and not the stimuli, changed. This further supports the idea that RN is unique to perceptual reversals and is not the result of stimulus onset as the stimuli in the present study remained consistent throughout each trial. Furthermore, this is the first study identifying RN in a binocular rivalry study utilizing a no-report paradigm, which further supports RN being a key component of perceptual reversal as our findings suggest that task has little to no impact on RN.

While there is no statistical significance of task in neither the 2x2 nor 2x2x5 ANOVAs, RN does appear to be slightly weaker in scalp distributions in the report condition (Fig. 15). This is likely due to the P3b's strong positivity in the report condition impacting the distribution of RN, since there is spatial-temporal overlap during the end of the RN and beginning of the P3b.

Finally, while the P3b does seem to be affected by perceptual state with it being significantly more negative in the stable perceptual state (Fig. 15), this is likely due to the task of reporting remaining consistent following dominant probe presentation (continue holding down mouse button). When a suppressed probe elicits a reversal, the participant had to make the decision to change their report (translate change in conscious perception to change in report). With this in mind, our most significant finding regarding the P3b was the effect of task.

We found that the P3b was significantly attenuated in the no-report condition compared to the report condition. This is further evidence against the long-held notion that the P3b is a NCC of visual awareness and supports the idea that the P3b is instead most closely correlated with the task of reporting. While this finding supports the findings of the Frassle et al. (2014) study, which found that P3b related activity is not present in no-report binocular rivalry using fMRI and static stimuli, the findings of this study regarding the P3b are slightly more complicated. Subject 0 had little to no attenuation of P3b in the no-report condition, with a strong P3b being present regardless of task. Subject 3 had an attenuated, but still present, P3b in the no-report condition. Subject 7, on the other hand, had almost entirely no P3b in the no-report condition. It's also worth mentioning that Subject 7 was the only completely naïve subject, so it's possible that the presence of the P3b in the no-report conditions of Subjects 0 and 3 were

the result of being more attentive to reversals and/or knowing too much about the no-report methodology and therefore being unable to “not think about a white bear” (Wegner, 1994). It is possible that a repetition of this study with entirely naïve participants could find the absence of the P3b, rather than attenuation, in the no report condition. While we can’t come to a complete conclusion regarding the P3b at this time due to the variation in results across subjects, these findings are promising and could change how we interpret studies regarding visual awareness.

In the Metzger et al. (2017) study, they found that P1 amplitude was closely linked with reversal latency. We did not observe any noticeable differences in the P1 across task or perception and did not do any analyses regarding the interaction between amplitude and reversal latency, thus no conclusions about the P1 can be reached at this time. We saw a small positive peak around 100ms in stable trials that might potentially be a P1, but it was too small to warrant any conclusions.

4.2 Potential Implications

The present study intended to identify the ERP correlates of perceptual reversals in binocular rivalry in the absence of report to provide insight into the models underlying the resolution of visual competition and into the neural correlates of perceptual change more generally. We wanted to know to what extent the perceptual reversals that occurred during rivalry were the result of the low-level (interocular inhibition) and/or high-level models (pattern competition). The N1, which is associated with early visual processing, had a main effect of perception as it was significantly reduced when probes were presented to the suppressed eye. One interpretation of this difference in amplitude would support the low-level model of rivalry, namely the theory of interocular inhibition. In other words, the N1 is attenuated in the suppressed eye due to interocular inhibition of input to that eye, whereas N1 amplitude appears to be more robust in the dominant eye due to there being no inhibition. While

this is the most straight-forward interpretation, the N1 amplitude difference can alternatively be explained by attention.

A secondary interpretation of the N1 difference is the impact of high-level processes affecting low-level visual perception due to the proposed impact attention has on N1 amplitude. This interpretation stems from N1 amplitudes having been seen to be significantly larger in trials in which attention is sustained on a given stimulus compared to an unattended stimulus (Luck et al., 1994). This can be translated to paradigms regarding perceptual bistability, in which attention can be assumed to be sustained in stable trials whereas reversal trials cause a shift in attention (and at least initially, the probe presented to the suppressed eye is on an unattended stimulus). This is not to say that reversal trials are representative of not attending to a stimulus, but rather that reversal trials stem from an initially suppressed stimulus and are indicative of an eventual attentional shift (Pitts et al., 2007). This notion is supported by the differences in N1 amplitude from suppressed vs. dominant eye probes found in the present study. This finding is indicative of top-down visual processing, which supports the notion that high-level processes play a significant role in rivalry as they impact visual perception at low-levels. That said, further studies would be needed to isolate the effects of the probes used in the current study on N1 amplitude.

Perhaps our most notable finding was that of RN. We found significant RN in reversal trials and because the present study is the first to identify RN in the absence of report, the RN component can be more confidently deemed a signal unique to perceptual reversals. This further supports the idea that perceptual reversals are, at least in part, mediated by high-level processes due to the relatively late timing of the RN (here, 300-340ms post-probe-onset). A study by Pitts et al. (2008) investigated the role of top-down voluntary control on RN amplitude. In their study, participants viewed an intermittently presented Necker cube (Fig. 1a) with the instructions to either maintain stable perception, try to initiate perceptual reversal, or passively view the cube with no instruction as to how it should be viewed. They found that RN amplitude was significantly larger in trials in which participants were instructed to try initiating reversals compared to that of the passive condition. The results of that study provide

strong evidence that that RN is mediated by top-down control. Given that RN is significantly influenced by high-level processes, and that RN was identified in the present study in the absence of stimulus onset and report, high-level processes appear to be necessary in the resolution of interocular conflict. This provides further support for the aforementioned theory that top-down visual processing plays a significant role in perceptual reversals.

Finally, given that the N1 and RN had no effect of task, whereas the P3b was significantly attenuated in the no report condition compared to the report condition, the high-level processes mediating perceptual reversals is likely not the result of the neural processes involved in the task of reporting one's current perception. This is to say that since P3b only had a main effect of task (in the 2x2x5 ANOVA), it is irrelevant to testing models about change perception. While we were unable to come to a definite conclusion on the P3b due to the intersubject variability and the present study's small sample size, it is worth noting that the subject with a completely absent P3b (Subject 7) exhibited robust N1 and RN effects. Thus, our results suggest that the high-level processes mediating perceptual reversals can be separated from those related to reporting tasks.

Overall, the present study provides strong evidence for the hybrid of both rivalry theories, which is the idea that both low-level and high-level processes play a role in the resolution of interocular conflict and the dynamics of perceptual switching during rivalry. The N1 might reflect low-level interocular competition, whereas RN could result from high-level pattern competition as it is only seen when a stimulus "wins" the battle for perceptual dominance. This supports the current standing theory that while low-level visual processes are involved in perceptual reversals, they are modulated by high-level processes and are reflective of top-down visual processing. This lends more credibility to RHT and the idea that top-down visual processing is the driving force behind the resolution of interocular conflict. In this framework, the N1 are likely modulated by the feed-forward phase of visual processing, as this phase is modified (but not the result of) attention. This makes sense because if N1 is related to the feedforward sweep, we would expect to see amplitude attenuation when probes are presented to the suppressed eye. Moreover, RN is indicative of the feedback

phase of visual perception, as our data suggest that it is reflective of a change in perception.

4.3 Limitations

This study had two main limitations: number of participants and data analysis. As mentioned previously, the original goal of this study was to collect one EEG recording from 20-30 participants. However, the design of this study made it incredibly difficult to find participants who managed to hit all of the necessary criteria. Of the 10 participants that went through prescreening, only 4 passed the necessary psychophysics criteria. Subject 2 was unable to come in for EEG recording, and Subject 4 did not yield clean EEG recordings. Subjects 0 and 3 were the only participants that managed to pass all of the psychophysics criteria and have clean EEG recordings, while Subject 7 did not meet the accuracy threshold but passed in every other measure. Given a larger budget and more time, this would not be as big of an issue. While the results of this study are significant and exciting, it is difficult to draw conclusions that apply to the general population.

The second limitation of this study was data analysis. We chose to include both a 2x2 and 2x2x5 ANOVAs in hopes that together they could paint a clear picture of what is and isn't significant, but it's not the ideal way to analyze our ERPs. Having more participants with one EEG session each would make the 2x2 work better and having more participants with 5 EEG sessions each would make the 2x2x5 work as well. The present data could be better analyzed, but we would need more time to figure out the best analysis. Furthermore, it would be worthwhile to sort and analyze the P1 data by reversal latency in order to compare it to the results of the Metzger et al. (2017) study. We can do this with the current data, but due to time limitations this analysis was not prioritized. The results of this study are promising, but it's too soon to confidently draw conclusions that apply to the population as a whole since both individual differences in a sample size of three can't be ruled out and the data analysis needs more work to be more precise.

4.4 Future Directions

Binocular rivalry with a no report condition opens the doors to several future areas of research. Perhaps the clearest future direction for this study would be a replication with more participants, as well as an analysis of the effect of reversal latency on the elicited ERPs in a similar fashion to the analysis in the Metzger et al. (2017) study. In the Metzger et al. study, there was a significant correlation between P1 amplitude and the speed of perceptual reversal (Fig. 5). However, in the present study, we were unable to identify a clear P1 (besides a small hint of a positive peak prior to the N1 in the stable condition). This may be due to P1 often being more easily elicited by stimulus onset (blank screen, then stimulus appears) rather than constantly present stimuli (that change when the checkerboard probe is added), but an analysis of the present data with ERPs separated by speed of reversals following probe presentation might help us better understand the role of the P1 in no-report probe-mediated perceptual reversals. Additionally, analysis of the present data with ERPs separated by reversal speed could potentially shed more light on RN. If RN is as closely correlated with perceptual reversal as the present data suggest, we would expect to see that the timing and/or amplitude of RN would be impacted by the speed of perceptual reversals.

Another future direction would be to better isolate the ERP correlates of perceptual reversal through an experiment focused on probe saliency. By running a study that decreases probe saliency to the point where it is strong enough to be observed when it is presented to the dominant eye, but not strong enough to be seen or to elicit a perceptual reversal when it is presented to the suppressed eye, the ERPs from dominant (and consciously seen) probes could directly compared to those of suppressed (and unconsciously processed) probes. This would yield an ERP difference that paints a cleaner picture of conscious vs. unconscious processing of a physically identical probe stimulus, without disturbing the ongoing perceptual state. This experiment is similar to the one done by Pitts et al. (2014), in which a 2x2 (task relevance x visual awareness) backwards masking paradigm was used to isolate ERPs. When participants were

able to see the stimulus, they found a posterior ERP negativity from around 200-240 ms, known as visual awareness negativity (VAN), in both task-relevant and task-irrelevant conditions. This component was not present in either of the unseen trials, thus making it a potential NCC candidate as these findings suggest that it is unique to conscious visual perception. A no-report study could be conducted with the setup from the present study in a 2x2 design (probe saliency x task) to potentially isolate VAN and determine if it is truly a NCC, as we would expect it to be present in binocular rivalry if that's the case. Because VAN and N1 overlap somewhat both spatially and temporally, it's possible that the larger N1 amplitude seen in the dominant eye probes could be due to VAN as the probes were more clearly seen in the dominant eye.

Additionally, the potential spatial-temporal overlap of VAN and N1 could be explained by the proportion of probes seen in suppressed vs. dominant eyes. If subjects always saw the probes when they were presented to the dominant eye but didn't always consciously see them when presented to the suppressed eye, this idea would make sense. In the present study, data were not taken regarding the perception of probes in the suppressed eye, but we know that the suppressed probes were at least sometimes perceived. The proportion of suppressed probes perceived is unknown, but if it was less than that of dominant probes, it would likely have resulted in smaller VAN amplitudes. That said, this explanation of the N1 amplitude difference across perception is contingent upon VAN being in the present data, which has not yet been verified. A future study could approach a replication of the present study with a focus on identifying VAN by separating trials by suppressed probes seen vs. unseen. This could potentially be done by monitoring pupil size alongside eye movements (which the EyeLink eyetracker is capable of). Given that probe perception is a shared focus, this future study would benefit by being conducted alongside the previously proposed stimulus saliency study.

Another potential future direction would be to conduct the present study utilizing a different method of data collection. The strength of EEG lies in its ability to provide excellent temporal resolution whilst being noninvasive, and while its spatial resolution is decent, it is not the most precise method as it is on the scale of centimeters. As previously mentioned in the introduction, although

rare, epilepsy patients who receive surgically implanted electrodes for medical treatment are sometimes willing to participate in studies such as the present one. These recordings would provide the most accurate spatial resolution, as they are most comparable to the single-cell recordings from primates seen in the Leopold & Logothetis (1996) study. While recordings from implanted electrodes often lack in spatial coverage, when analyzed alongside the recordings of the present study, the gap between spatial resolution and coverage could be bridged. Ultimately, this would provide the clearest insight into the mechanisms behind probe-mediated perceptual reversals in no-report binocular rivalry.

4.5 Summary

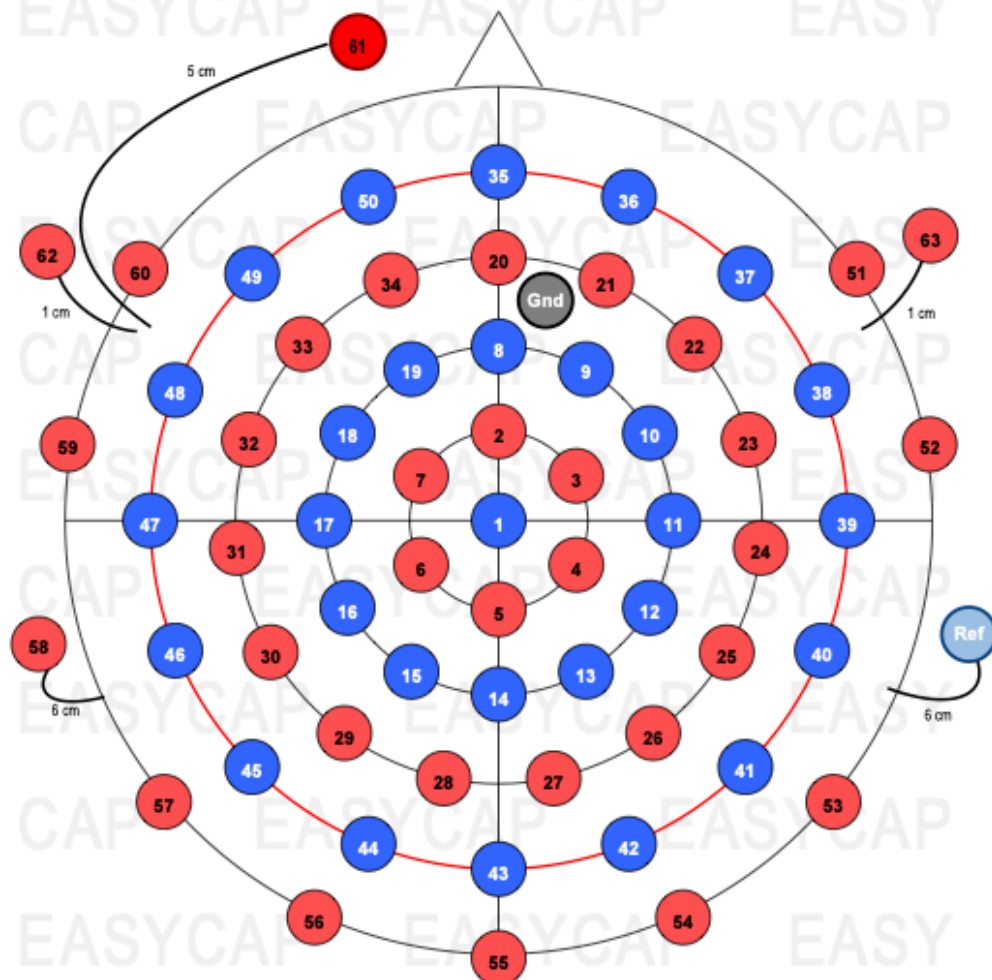
This study aimed to isolate the ERPs of perceptual reversal during binocular rivalry in the absence of report. The experimental setup and OKN analysis were previously validated in Jeff Nestor's 2022 thesis, and data was collected and analyzed in the present thesis. We succeeded in identifying a stronger N1 amplitude in stable segments compared to reversals, the presence of RN, and an attenuated P3b in the absence of report. With more participants and/or more thorough data analysis, the results of this experiment may be able to provide more insight for the mechanisms of binocular rivalry and the neural correlates of consciousness.

Appendices

A. Electrode Cap Layout

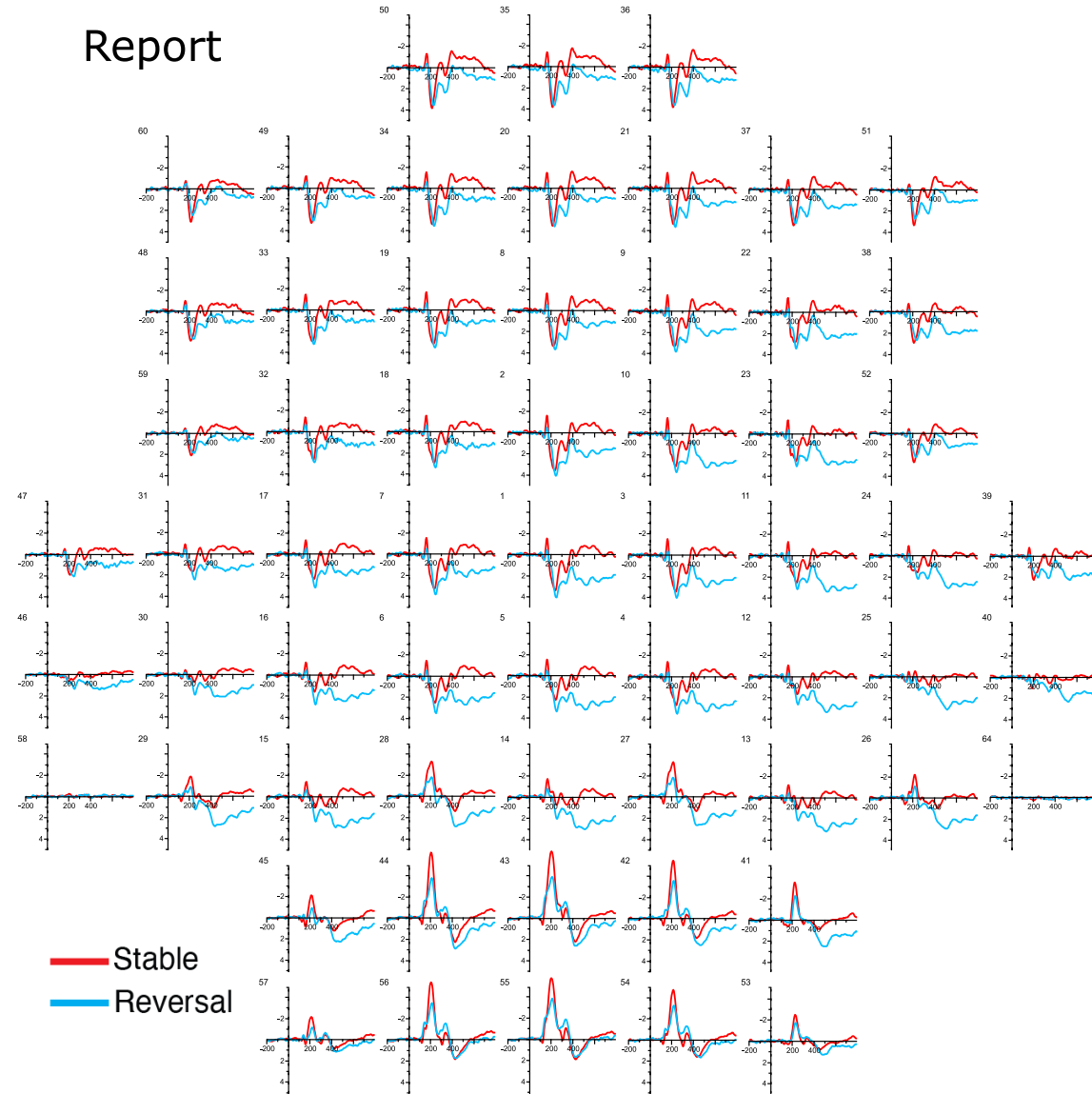
63Ch-BrainCap with Multitrodes,
Equidistant M10, customized for M. Pitts, Portland, December 2014

Electrode Layout and Channel Assignment:

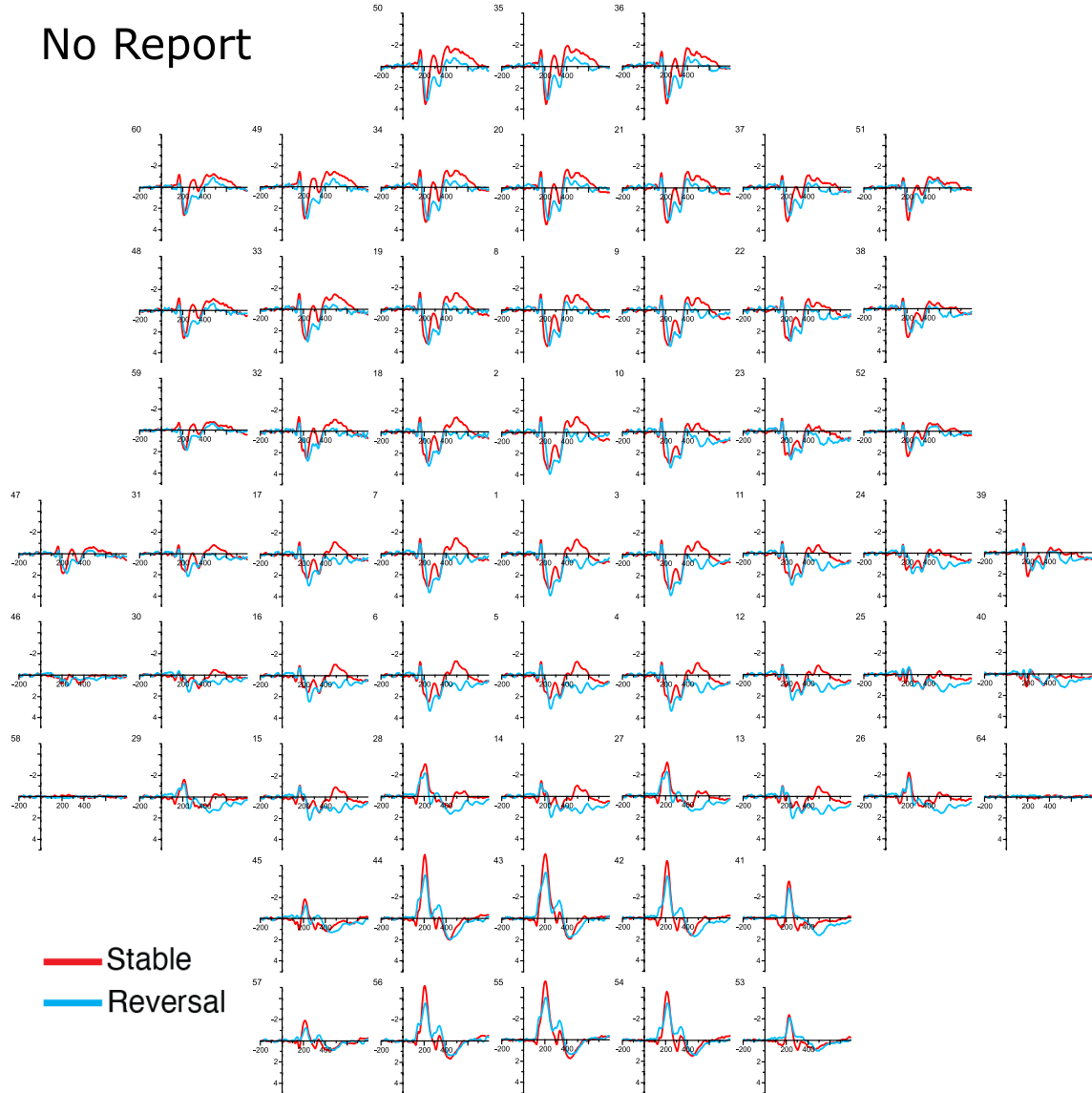


Equidistant M10 places 60 electrode positions in 5 equidistantly spaced concentric rings around Cz. The positions on each ring are also equidistant from each other. The positions on the vertical and horizontal central lines are identical to 10%-positions. The ring marked red is defined as $\Theta = 90^\circ$ and passes through Fpz (35), T8 (39), Oz (43), T7 (47). The outmost ring reaches from the canthii to the Inion. Pos. 61-63 can be used for EOG, pos. 58 and REF can be placed individually on mastoids.

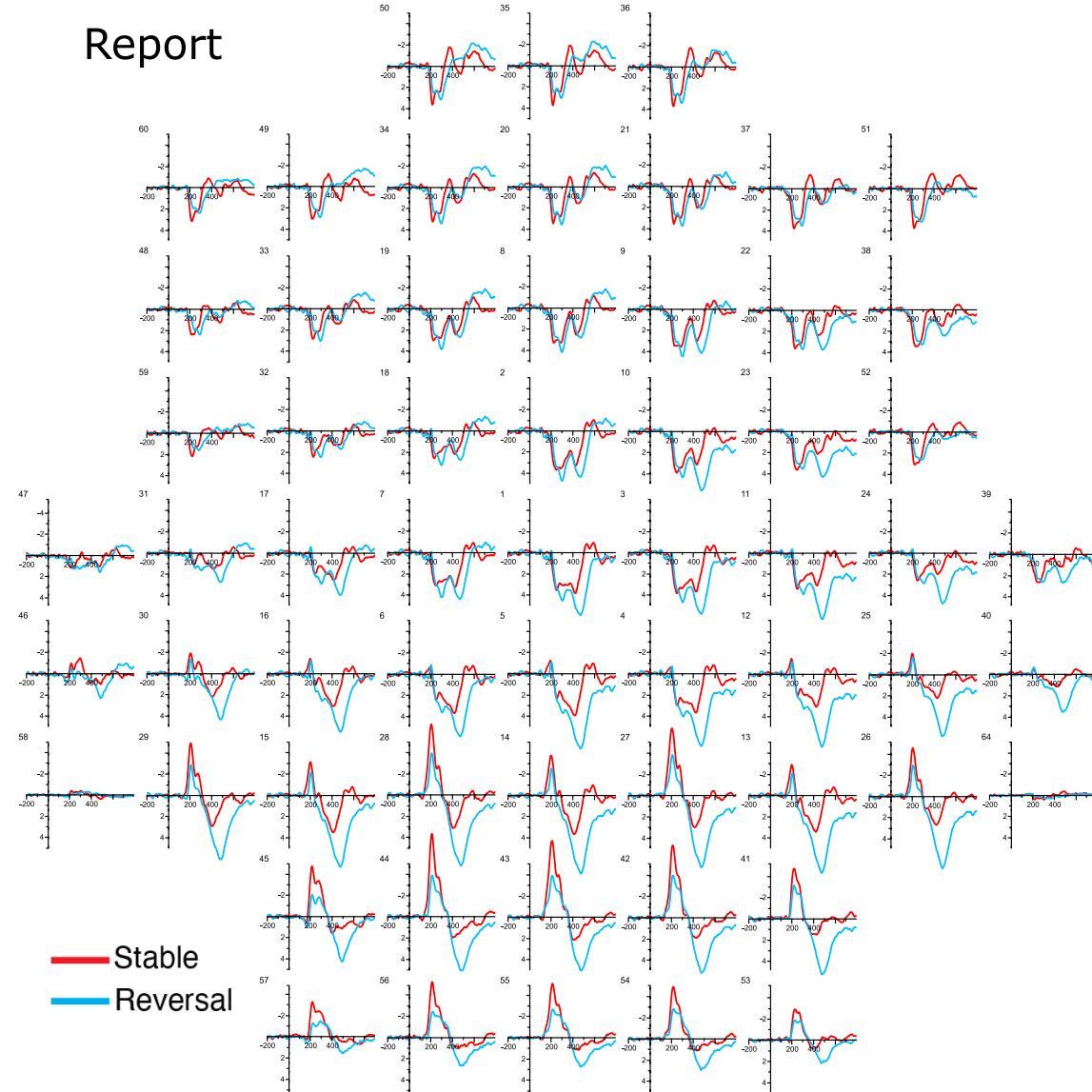
B. Grand Average ERPs Across All Subjects and Sessions (Report)



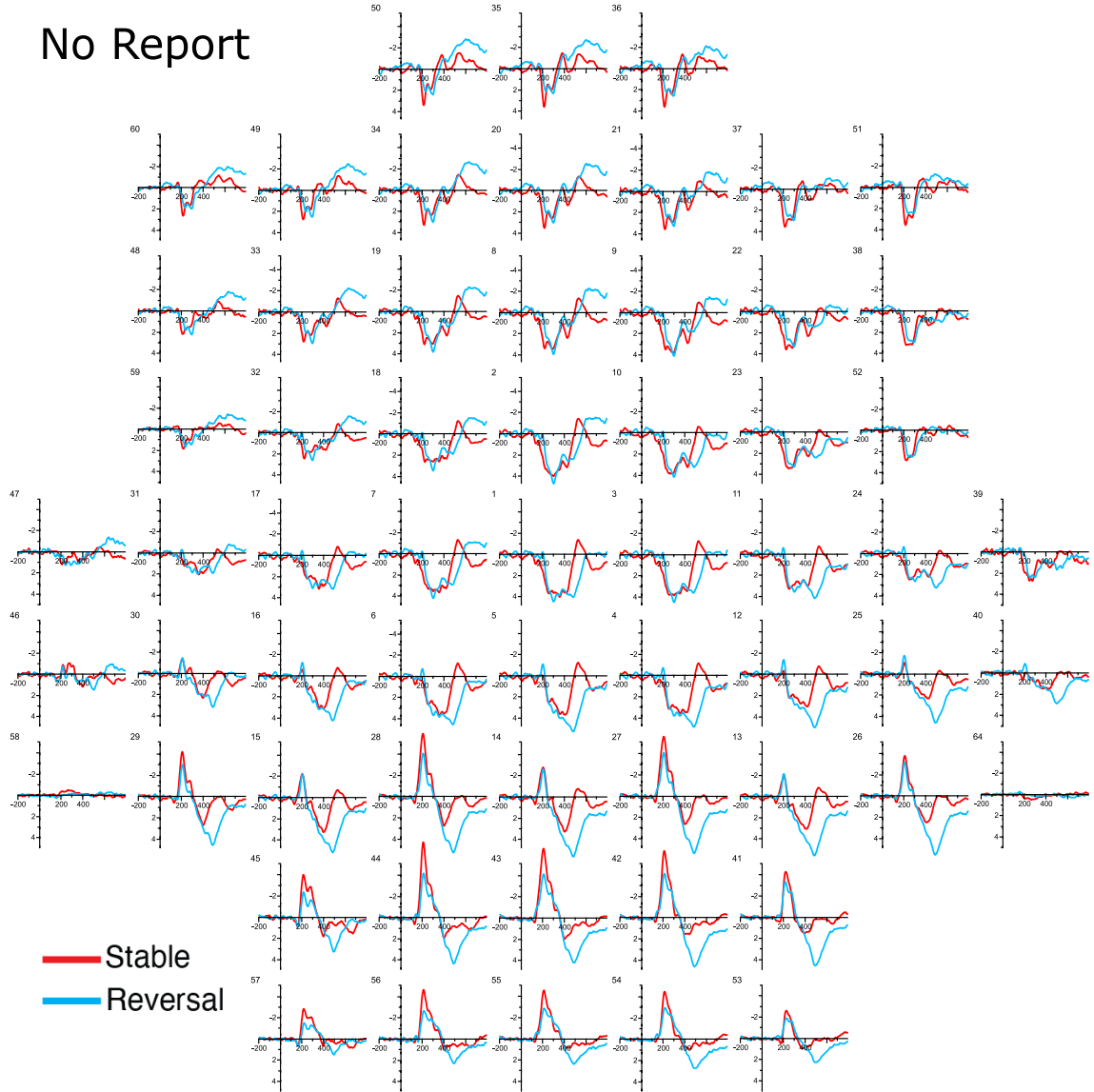
C. Grand Average ERPs Across All Subjects and Sessions (No Report)



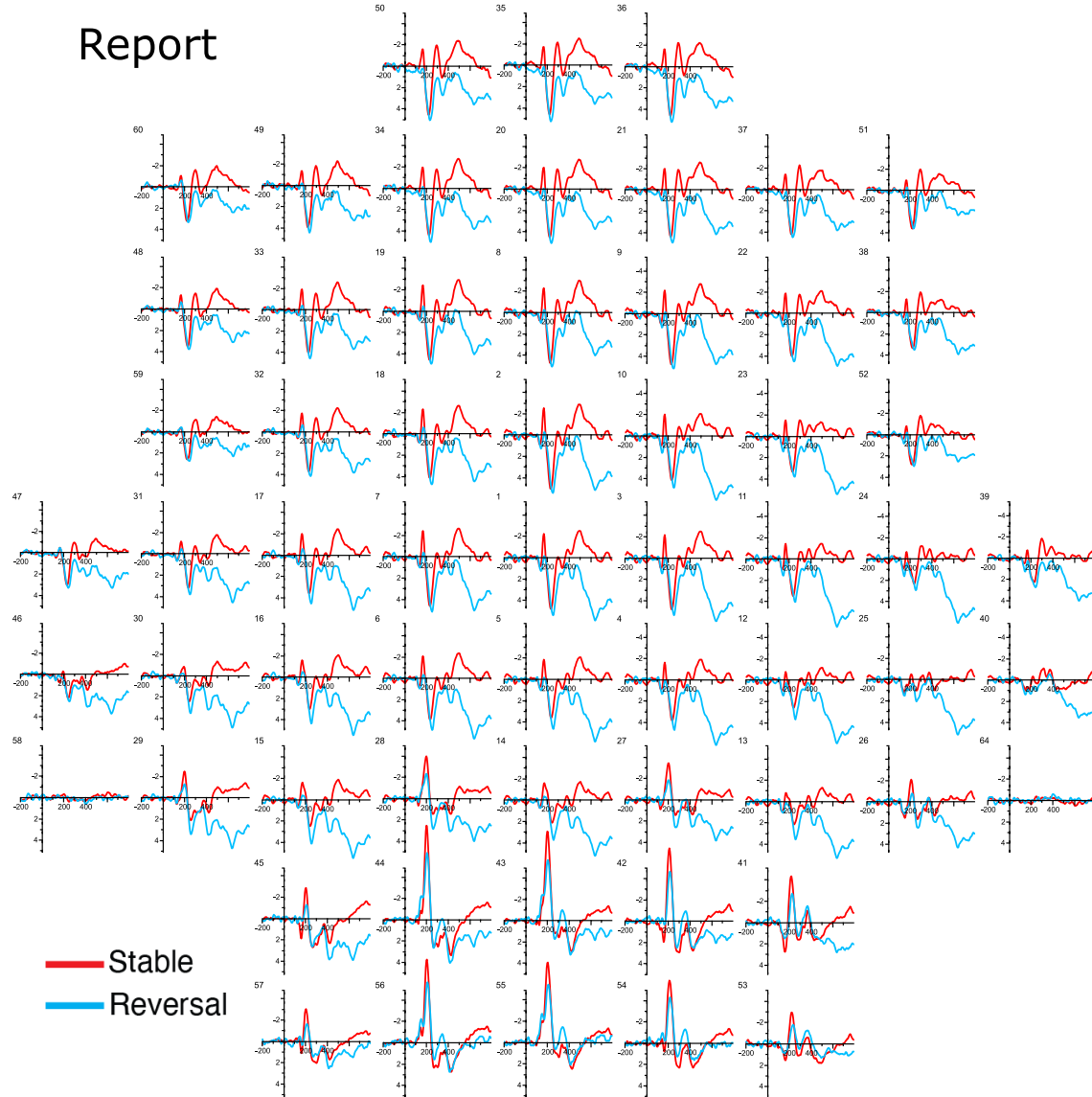
D. Grand Average ERPs Across All Sessions for Subject 0 (Report)



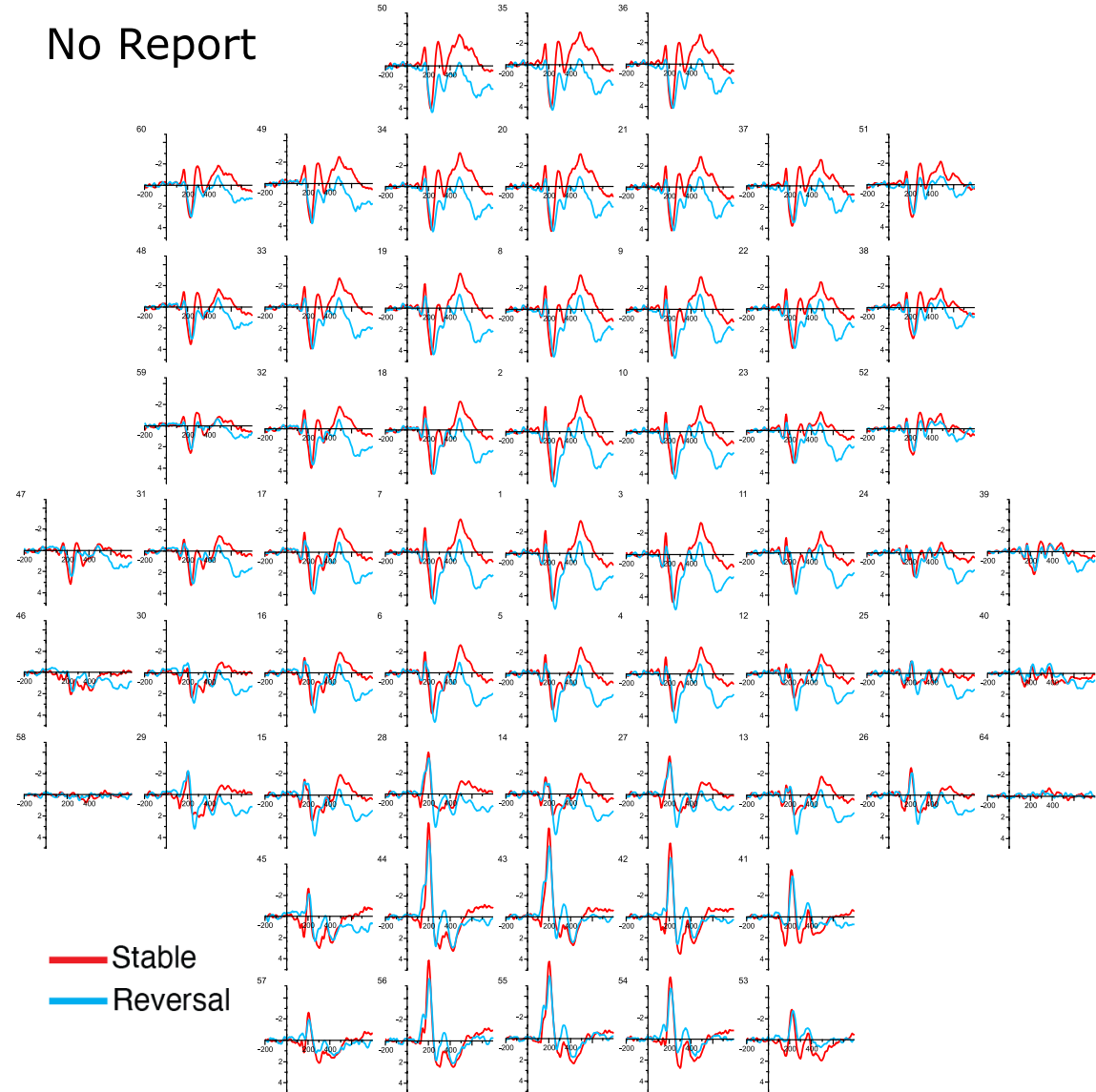
E. Grand Average ERPs Across All Sessions for Subject 0 (No Report)



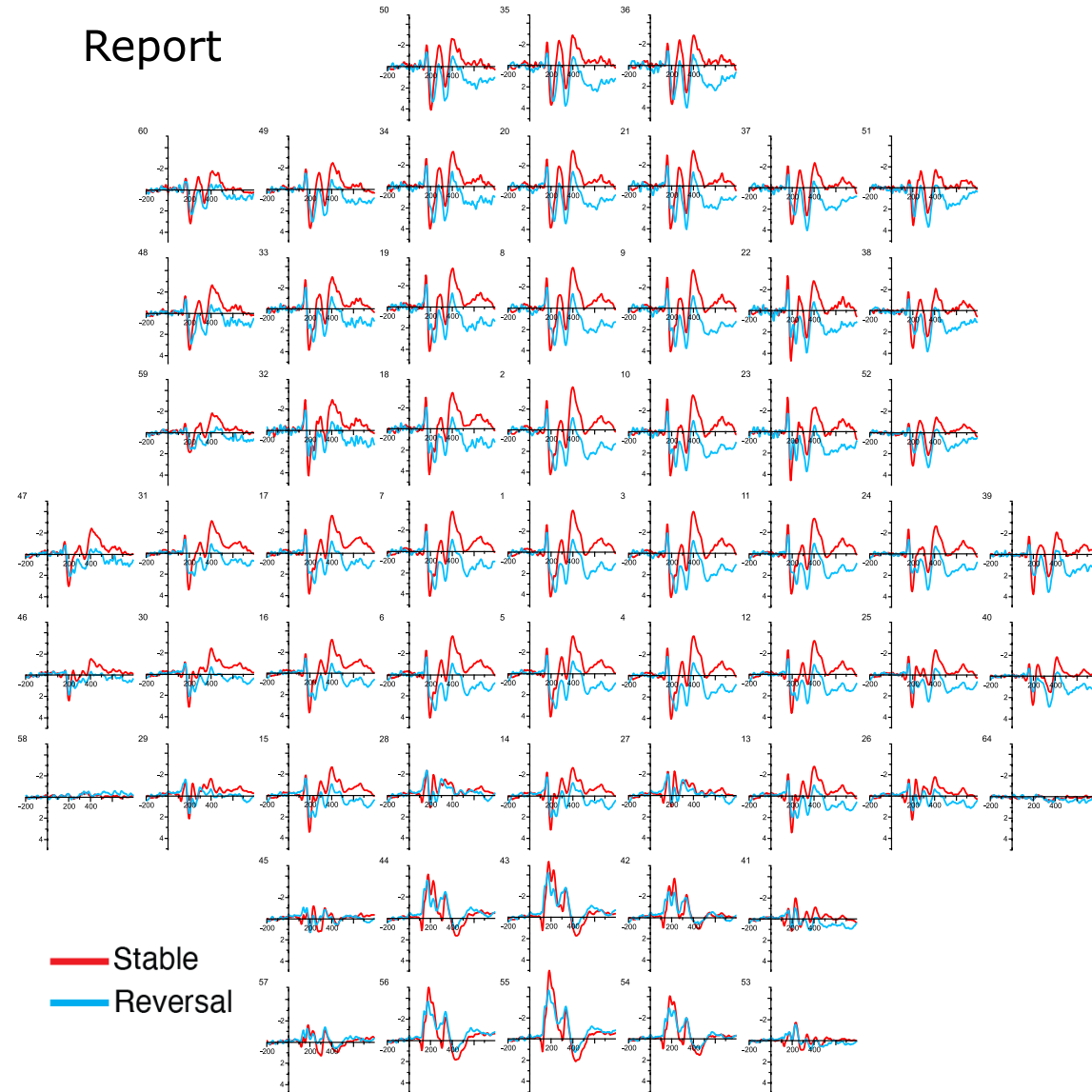
F. Grand Average ERPs Across All Sessions for Subject 3 (Report)



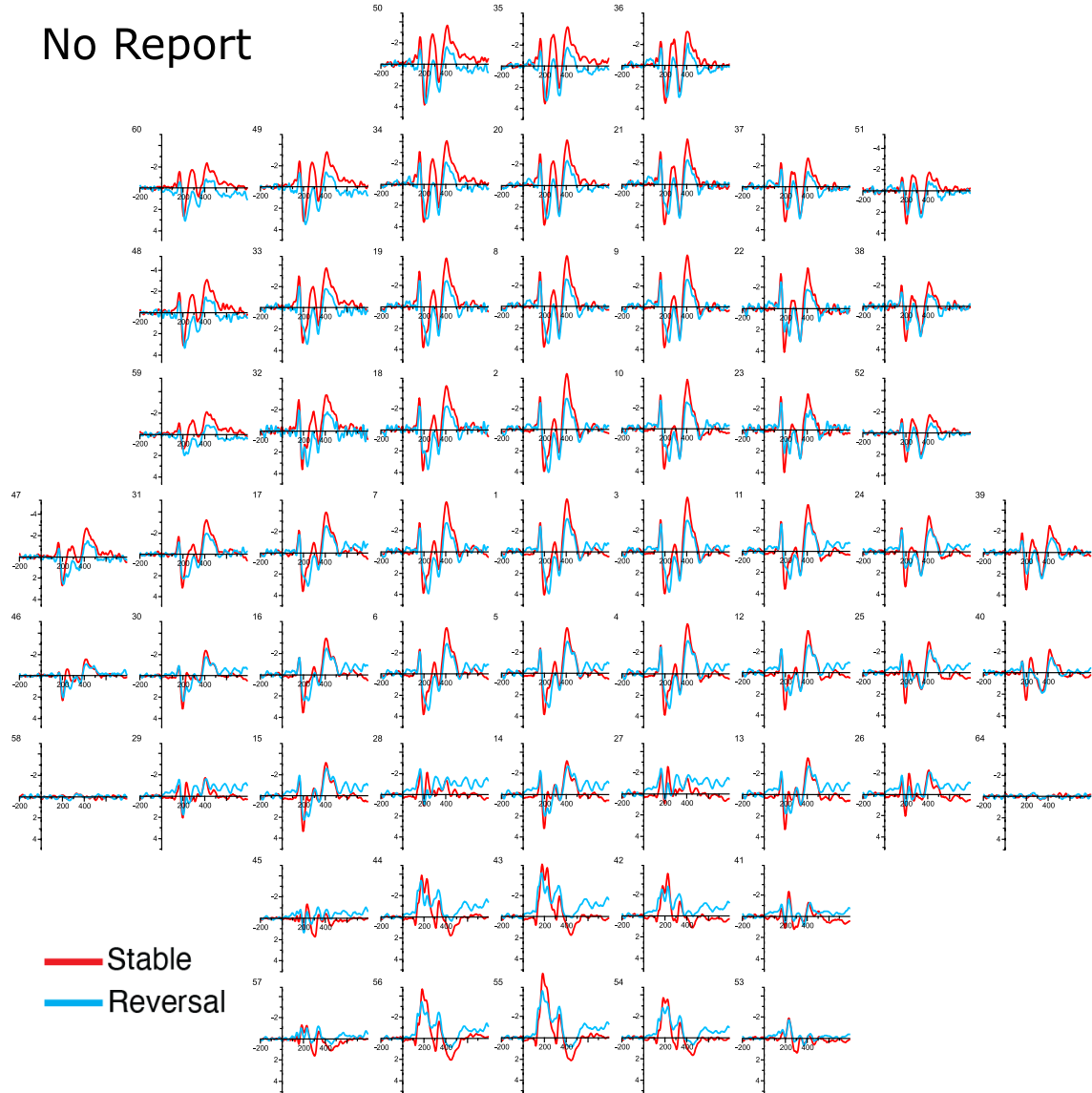
G. Grand Average ERPs Across All Sessions for Subject 3 (No Report)



H. Grand Average ERPs Across All Sessions for Subject 7 (Report)



I. Grand Average ERPs Across All Sessions for Subject 7 (No Report)



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