ERP Correlates of Perceptual Reversal During Binocular Rivalry: A No-Report
Paradigm

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Abstract

Binocular rivalry is a phenomenon which occurs when competing images are presented to each eye. One image is perceived (dominant stimulus), and the other is invisible (suppressed stimulus). The viewer's visual experience spontaneously alternates between the two images, with either stimulus maintaining dominance for several seconds before the other takes over, in a process called perceptual reversal. Perceptual reversals constitute robust changes in visual experience with no change in physical input, making them an ideal tool for studying the neural correlates of consciousness (NCCs). Perceptual reversals can be systematically triggered by probing the suppressed image with a brief modulation in stimulus strength. Event-related potentials (ERPs) evoked by these suppressed probes are thus representative of perceptual reversal-related activity when compared to ERPs evoked by dominant probes (which do not trigger perceptual reversals).

Previous research has shown that, compared to dominant probes, suppressed probes evoke a prominent late positivity similar in distribution to the P3 component. The P3 component, once thought to be a promising NCC candidate, has more recently been shown to be associated with task performance (e.g., reporting one's perception), rather than perception itself, at least in certain paradigms. This interpretation of the P3 is consistent with its presence in perceptual reversal-related activity when participants are instructed to hold down a button corresponding to the stimulus currently dominating their perception and to switch buttons when their perception changes.

The present study aimed to determine whether this P3 is related to the perceptual reversal itself or merely the act of reporting the perceptual reversal. To this end, moving stimuli were utilized in order to elicit reflexive motion-tracking eye movements called optokinetic nystagmus (OKN) which have been

shown to closely correlate with subjective perception (that is, the eye always follow the motion of the currently dominant stimulus). Using eye-tracking simultaneously with EEG recording, OKN was decoded to determine which of two stimuli dominated participants' perception in the absence of report. This allowed for the separation of probe presentations into dominant and suppressed categories, so that average ERPs could be calculated for each, with the suppressed minus dominant difference corresponding to perceptual reversal-related brain activity. Preliminary ERP results suggested that the previously observed P3 was partially generated by report-related processes, particularly the frontally distributed subcomponent of the P3, however a smaller late positivity with a parietal scalp distribution remained evident even in the absence of report. These results tentatively support a model of binocular rivalry where competition between images is resolved by distributed higher-order processes such as attention.

I want to dedicate this to my dad, at the end of the day whatever I do for myself I'm really doing for him.

Introduction

I: Purpose

A growing area of cognitive neuroscience research is concerned with identifying neural correlates of consciousness (NCCs). The generally-accepted definition of an NCC is a "minimal neuronal mechanisms jointly sufficient for one specific conscious percept" (Blake et al., 2014). There is more nuance to this definition than meets the eye though, for instance, it does not distinguish between consciousness itself and the *content* of consciousness. By comparing awake brains and brains in REM sleep (the stage of sleep associated with dreaming) to sedated, vegetative and dreamlessly sleeping brains, evidence suggests that differences in functional connectivity within thalamo-cortical networks affecting electrophysiological markers like rhythmic brain waves and the propagation of electrical perturbations are a key signature distinguishing a conscious brain from an unconscious brain (Massimini et al., 2012). It is a much more challenging task to look for neural events related to contents of conscious experience. It has been suggested that, theoretically, neuroscientists should attempt to identify an isomorphism between some neural activity pattern and the conscious experience. That is, a given feature or change in conscious experience should correspond to a specific feature or change in some subset of neuronal activity.

The simplest approach for trying to find such a neural activity pattern may be an experiment where, say, a participant is presented with some visual stimulus, and then the experimenter changes some feature of the stimulus, and measures brain activity evoked by that change. The issue with such an approach is that it does not isolate consciousness, because changes to the stimulus will cause changes in parts of the visual system which are not necessarily related to

consciousness (e.g., photoreceptor activity in the retinae, subcortical activity in the superior colliculus). In fact, in the phenomenon of blindsight, individuals can react to visual stimuli while reporting that they are completely blind. This is evidence that processing of visual stimuli, and even motor behavior associated with that processing, dissociates from visual experience. This dissociation is two-sided. In dreams, for instance, visual experience changes with no change in visual stimulation. This means that neural activity associated with features of dreams is theoretically closer to an isolation of content NCCs than neural activity associated with features of stimuli in waking experience (Nir and Tononi, 2010). However, dreams are unpredictable, and it is impossible from an outside point-of-view to know how the features of a dream are changing with precise timing. For this reason, visual perception researchers often use carefully designed stimuli and paradigms which allow for the dissociation of visual experience and physical stimulus. In some visual illusions for example, there may be features of the viewer's visual experience which do not correspond to any feature of the physical stimulus. The present study is concerned with so-called bistable images. This is a general term for a type of visual stimulus which may be experienced in either of two ways, think here of the well-known "duck-rabbit" image (see Figure 1). Either experience is "stable" in that it doesn't seem to be ambiguous in itself. The viewer can see one version or the other during a given moment of time, and is often able to switch between the two percepts every few seconds, but they can never see both images at once. The advantage of this type of stimulus is that the viewer experiences a change in their percept while physical input remains the same.
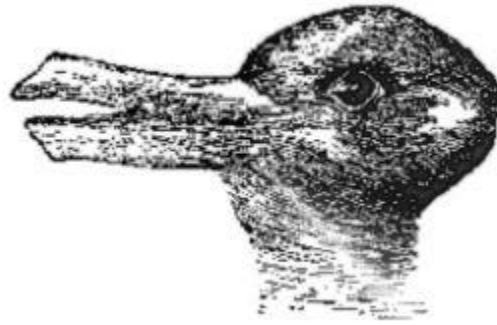
Figure 1

The figure can be Interpreted as a rabbit facing to the right, or as a duck facing to the left. (Image from Jensen and Mathewson 2011)

Binocular rivalry (BR) is a sort of visual bistability that occurs when incompatible visual stimuli are presented to each eye (dichoptic presentation). Depending on the type of stimuli presented dichoptically, the resulting percept may take a number of forms. It may have a mixture of features from both stimuli (*binocular fusion*), it may look like one stimulus in some areas of the field of view, and like the other in other areas (*patchwork* or *piecemeal rivalry*), or one stimulus may dominate the other, so that the viewer sees only one stimulus at a time (*complete dominance*). The typical percept of a particular display depends on a number of physical factors of the stimuli, including color contrast, luminance contrast and motion. In particular, when the two stimuli are roughly equivalent in physical strength, but highly distinct visually, typically one stimulus completely dominates at any given time, but the dominant stimulus switches every few seconds (*spontaneous perceptual reversal*) (Alais and Melcher, 2007).

The underlying dynamics producing BR may provide insight which is useful to the development of an NCC framework. If the minimal neural events responsible for perceptual reversal can be identified, some subset of those events is related to the production of conscious visual experience from sensory information from the eyes. Reversal-related events are events related to changes in the sensory source material for perceptual awareness. In the global workspace

theory of consciousness, for instance, they are changes in what is broadcasted to the dynamical workspace which generates conscious experience. It is appropriate then, to discuss what is known about the neural basis of BR, to get a better understanding of what is happening in the brain during dominance and especially during reversals.

II: Binocular rivalry, models and experimental evidence

BR has been the subject of extensive study going back to the nineteenth century, capturing the interests of Gestalt psychologists and other early psychophysicists. Still, there is controversy regarding models of rivalry mechanisms. To simplify the storied history of these models, we will lump them into two broad categories. First, there is the local model, which suggests that rivalry is resolved within low-level visual circuits by competition between signals from each eye. The underlying mechanism described by this model is *reciprocal interocular inhibition*, where the neural pathway associated with the dominant visual signal suppresses its laterally opposite counterpart and eliminates it from higher-level processing. Spontaneous reversals are caused by the effect of neural exhaustion or adaptation in the dominant pathway. Typically, the firing rate of the laterally inhibitory neuron is thought to decrease over the course of a dominance period, steadily reducing the stability of the dominant percept, until the opposite pathway takes over (Stollenwork and Bode, 2003). A characteristic of BR that this view has struggled to account for is the stochasticity of dominance periods. This is because dominance periods are *sequentially independent*, that is, the length of a given dominance period is not correlated with the length of the previous dominance period (Blake, 1990). If dominance was produced by an adaptation effect, one would expect that a longer dominance

period would lead to a larger, more lasting change in signal strength of its corresponding visual pathway, thus a relatively long dominance period would be followed by another relatively long dominance period, but this is not born out experimentally.

The second main category, global models, emphasize the role of higher-level processes like selective attention, task-based motivation and voluntary control in perceptual reversals. Although the effect of voluntary control on reversals has been doubted in the past, it is now generally accepted that an observer can affect the length of their BR dominance periods voluntarily, either by trying to keep the currently dominant percept in focus for as long as possible, by trying to switch their percept as quickly as possible, or by trying to keep one of the two stimuli in focus and suppress the other, although it appears to be impossible to completely abolish perceptual reversals by voluntary control (Marx and Einhäuser, 2015). BR shares this characteristic with other bistable visual stimuli (van Ee et al., 2005). For instance, look at the Necker cube below and you can probably convince yourself that you can experience a perceptual reversal by "trying to see the cube the other way" (try to see the "far" face as the "near" face and vice-versa). Furthermore, you may notice that the longer you look at it, the easier it becomes to induce a reversal. In this sense, affecting perceptual reversals is a skill influenced by practice.
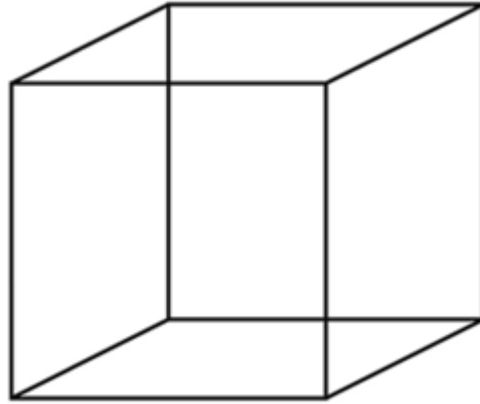
Figure 2

The Necker Cube is a multistable image whose 3-D effect can be perceived as viewed "from-below" or "from-above". (Image from Loued-Khenissi and Preuschoff, 2020)

This aspect of BR is what primarily led Logothetis and Leopold (1999) to reconceptualize perceptual reversals as *behavior*. They compare the stochastic temporal nature of perceptual reversal to that of saccadic eye movements and propose that these may be two different types of *exploratory behavior*. Whereas saccadic eye movements sample different points in an observer's field of view, perceptual reversals sample different possible interpretations, or what they call "perceptual organizations," of the same visual information. By iteratively sampling possible interpretations, the visual system is able to discern meaningful and relevant structure from ambiguous visual information, even when that structure is not picked out at first pass. In the images below, it may take a few seconds to realize the object hidden within the noise, but once you see it, you can't "unsee" it. That organization or interpretation of the visual information is then inseparable from your perception of the object.
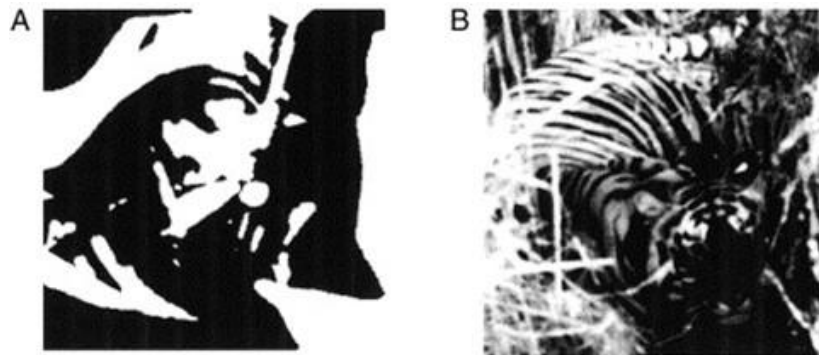
Figure 2

A: Contrast thresholding transforms recognizable images into seemingly random patterns. Discerning meaningful structure from this image may take several seconds of inspection, to allow for iterative reinterpretaion of retinal information. Notice that the process is made easier by high-level conceptual knowledge about the hidden pattern, such as the clue "Star Wars". B: Demonstrates the potential evolutionary adaptive function of isolating hidden images within seemingly ambiguous patterns. (Image from Leopold and Logothetis, 1999)

A consequence of Leopold and Logothetis's (1999) view is that it is not the two eyes which compete with each other, but the two images themselves. There is some brain imaging evidence to support this. With spatially precise imaging techniques like fMRI and single-cell recording, we can investigate what areas of the brain exhibit differential activity based on dominant percept. That is, neurons in the visual system which fire equally regardless of whether the left or right image is perceptially dominant are probably more related to physical input, not the dynamics of BR. The other way to think about this is that those neurons likely appear in a part of the visual pathway which precedes the resolution of rivalry. In single-cell recording studies performed by Leopold and Logothetis (1989, 1996), monkeys were trained to report their dominant percept while viewing BR stimuli. The researchers found that only about 20% of neurons in V1 and V2 showed patterns of firing which correlated with perceptual dominance, and in a similar study by Lehky and Maunsell (1996), none of the neurons in the lateral

geniculate nucleus (LGN) showed the expected BR modulation. These results suggest that rivalry is not resolved in early visual areas, challenging local models of BR. On the other hand, Logothetis' lab found about 40% of neurons in V4, in the middle temporal area (MT), and in the medial superior temporal sulcus (MST) showed BR modulation. Finally, the proportion of BR modulated neurons reached 90% in the inferotemporal cortex (IT) and superior temporal sulcus (STS). These results provide good reason to believe that rivalry is not entirely resolved until visual information reaches higher-level temporal visual processing areas, and, contrary to local views, both dominant and suppressed patterns are significantly represented in low-level occipital sensory processing. They do seem to suggest, however, that BR is likely resolved before visual information reaches fronto-parietal areas. Still, it is possible that fronto-parietal areas are involved in driving perceptual reversals through feedback into lower levels of the visual hierarchy.

In an fMRI study by Lumer et al. (1998) in humans, results suggested an association between activity in fronto-parietal areas and perceptual reversals; however this study and others like it have been criticized by Blake (2014) for their imperfect "replay" comparison condition. In the Lumer et al. study, fMRI data from participants undergoing BR and reporting their perception is compared to fMRI data from the same participants watching a video stimulus which attempts to "replay" what the participant saw during the BR condition, without actually inducing rivalry. Researchers present the same pair of stimuli, fading in one or the other intermittently. They use the timing of button presses obtained during BR to determine when to fade from one stimulus to the other, attempting to produce percepts which approximate the percepts observed during BR. fMRI readouts from replay trials were subtracted from BR trials, the resulting difference supposedly representing brain activity specific to the resolution of competing stimuli. Blake (2014) points out that the replay condition did not accurately recreate the unpredictable and strange percepts produced

during transition periods. Between periods of perceptual dominance, during perceptual reversals, BR viewers typically experience a transition period of mixed dominance where stimuli appear superimposed or the two stimuli each take up different parts of the visual field. Many viewers also report a "traveling wave", where the suppressed stimulus appears in one corner of the visual field and appears to sweep over the previously dominant stimulus until it fills the visual field (Blake, 2014; Stollenwork and Bode, 2003). For this reason, increased fronto-parietal activation during BR may have been related to the participant's uncertainty about whether or not a reversal was occurring during a transition period and thus how they decide to report their percept. On the other hand transitions were likely much more clear-cut in the replay condition, which led to less activation in decision-making areas. This issue of report and other non-perceptual processing generating confounds in frontal brain activity will be addressed in detail later (see also the discussion of Kapoor et al. (2022) in the next section), but it already poses a problem as well for the single-cell recording studies described above, particularly when Leopold and Logothetis (1999) points to fronto-parietal activation during perceptual reversals as evidence that decision-making systems are responsible for affecting reversals, when we already know that decision-making systems are responsible for reporting reversals.

Other interesting evidence regarding the role of frontal brain regions in perceptual reversals comes from Windmann et al.'s (2006) work with humans who had undergone lesions of the prefrontal cortex (PFC) due to brain tumors. This work showed that baseline reversal rate was not consistently different between lesion patients and control participants, nor was reversal rate consistently different between the two groups when participants were instructed to control their perception so as to sustain dominance periods for as long as possible. However, when participants were instructed to switch their perception as many times as possible within a 60-second viewing period, lesion patients

were largely incapable of affecting their reversal rate in this direction as compared to baseline, whereas control participants were consistently able to increase their reversal rate significantly. This study suggests that the neural bases for spontaneous and voluntary shifts in perception, as well as the neural bases for sustaining percepts and switching between them, may be differently localized, and that the PFC specifically is involved in driving voluntary perceptual reversals, but perhaps not spontaneous ones.

Understanding the role of attention in BR is also essential to understanding its relationship to NCCs. Leopold and Logothetis (1999) compared perceptual reversal to selective attention in terms of function, but more recently significant evidence has been brought forward that the two might be essentially equivalent, that is, attentional shifts invariably underly perceptual reversals. In work which will be discussed in more detail later, Britz and Pitts (2011) demonstrated that there are compelling physical similarities between electroencephalography (EEG) signatures for perceptual reversals and shifts in selective attention. Behavioral evidence also supports a crucial role of attention in influencing BR dynamics. In an ingenious experimental design, Brascamp and Blake (2012) demonstrated that the predictable patterns of BR perceptual reversals are interrupted when attention is diverted away from the rivalrous stimulus, in an article titled "Inattention abolishes binocular rivalry". In their control (attended) condition, a Gabor patch stimulus was presented to only one eye during Phase I (one half of a BR stimulus), then in Phase II a rivalrous Gabor patch was presented to the other eye in the same position. Since novel stimuli nearly always dominate BR, at the onset of this stimulus, control participants predictably perceived the novel stimulus as dominant. For the duration of Phase II, control participants tracked the BR stimulus and reported dominant percept, meanwhile, a rapid serial visual presentation (RSVP) of alphabetic characters appeared in the center of the screen as well as some distractor Gabor patches. Finally, in Phase III, only the BR stimulus was present, as participants continued

to report dominant percept. Since BR dominance periods obey a unimodal distribution (specifically, a gamma distribution), and since the initially dominant stimulus was predictably the novel one, the likelihood across trials that the original or novel stimulus is perceived at a given time point in Phase II and III is not truly random. Instead, averaging over many trials, stochastic variation in dominance periods produces a pattern of steady fluctuation (a *temporal autocorrelation curve*). In comparison, participants in the unattended condition were instructed to attend to the central RSVP and count the number of red k's and blue j's that appeared during Phase II while the rivalry stimulus remained on the screen just in the periphery. When participants returned their attention to the BR stimulus at the onset of Phase III, the likelihood that they perceived either the original or novel stimulus was entirely random. In fact, the results for the unattended condition are indistinguishable from the results when there was no BR stimulus present during Phase II (absent condition).
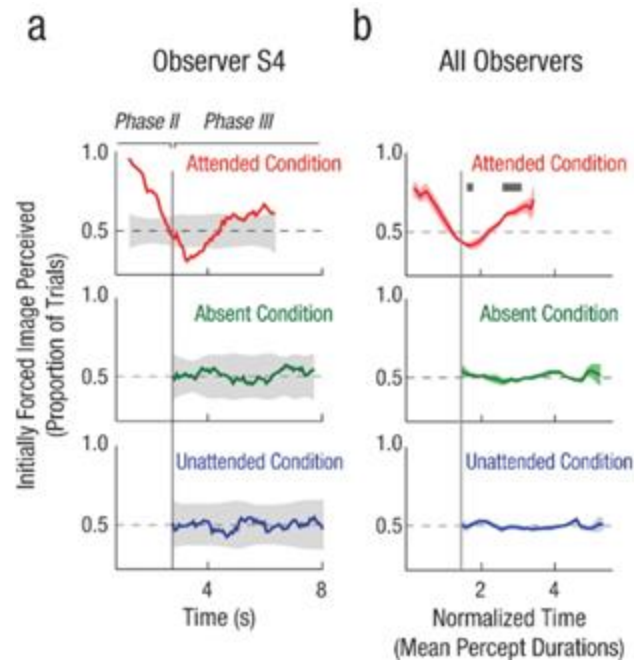
Figure 3

Results demonstrate that BR dynamics are interrupted when attention is withdrawn from BR stimuli. A) Perceptual dynamics from exemplar participant, x-axis is in absolute time. B) Mean perceptual dynamics from all participants. Time was normalized for each participant and condition by dividing elapsed time by mean dominance period (Brascamp and Blake, 2012).

It should be noted that these results cannot be explained by claiming that inattention merely influences the distribution of dominance periods, because *any* unimodal distribution of dominance periods would produce some sort of pattern of dominance. One could also try to explain the results by pointing out that in the attended condition, the retinal position of the BR stimulus is held constant, while in the unattended condition BR is occurring in the periphery during Phase II and at fixation in Phase III, and perhaps BR dynamics at different retinal positions are independent of one another. Brascamp and Blake (2012) accounted for this by demonstrating in an additional control condition that brief saccades from BR stimuli to fixation and back do not "reset" BR dominance states. Furthermore, many studies have used the fact that when BR stimuli are displayed and removed from display intermittently, dynamics are not "reset" between each

presentation. Rather, in many paradigms, observers tend to experience one percept multiple times in a row before experiencing a reversal on the next presentation (Britz and Pitts, 2011). Thus, under the correct attentional conditions, BR stimuli do not have to be continuously displayed to a specific retinal location to achieve continuous BR. Brascamp and Blake's (2012) results strongly suggest that BR simply remains unresolved outside of attention, thus each stimulus is equally represented in the visual system. This begs the question what participants actually see at the location of the BR stimulus in the unattended condition, and suggests a sparse view of visual experience. Also interesting is that Dieter et al. (2016) adapted the Brascamp and Blake (2012) paradigm for a bistable phenomenon called motion-induced blindness (MIB), and their results suggested that attention is unnecessary for perceptual reversals to occur in MIB. They conclude that BR may be fundamentally different from other bistable phenomena in that it requires attention while other forms of bistability do not, which may have to do with the extra processing that goes into resolving interocular conflict. Results like these should be brought into consideration when generalizing results from BR paradigms to other bistable phenomena.

Since it will be significant later, note that previous work has demonstrated that the dynamics of BR can be influenced by briefly changing or adding to (probing) one of the dichoptic stimuli. In particular, sufficiently salient probes to the suppressed field will trigger a perceptual reversal (probe-mediated reversal) (Blake et al., 1990). This finding is consistent with an adaptation-based or an attention-like model of perceptual rivalry. In the former, visual patterns which were not previously present on the retina are stronger in early sensory processing due to the lack of adaptation. In the latter, pattern changes in suppressed stimuli force themselves into perception in the same way that suddenly appearing images outside of explicit awareness exogenously capture attention.

III: Eye-movements as an objective measure of perception

Research dating back to 1963 by Paul Enoksson has shown that when BR stimuli are bar gratings moving in opposite directions, the pattern of an observer's microscopic reflexive eye movements correspond to their current percept. The eyes track the movement of the currently dominant grating stimulus across the screen (smooth pursuit), then quickly shift back (saccade) in the opposite direction, then repeat. This eye-movement pattern is called optokinetic nystagmus (OKN), and is also observed when viewing moving stimuli on a screen monocularly. Infrared camera eye-tracking allows researchers to differentiate between, and determine the direction of, smooth pursuit phases and saccades. This means that they can determine the current percept of an observer "objectively" during BR, instead of depending on the observer's subjective report. Thus, another advantage of studying BR is that in this particular contrived perceptual situation, aspects of the observer's subjective experience are *externally observable*, which circumvents the need for introspection and report which have been a methodological limitation for visual awareness studies according to Tsuchiya et al. (2015). OKN analysis is then an example of *decoding*, it is a technique which allows researchers to infer (decode) mental states from physiological states.

Tsuchiya et al. (2015) made the case for the development of what they called "no-report paradigms" to pursue NCCs. They proposed that typical visual awareness studies where, for instance, participants report whether or not they were aware of a particular stimulus, tend to *overestimate* NCCs. This is because when aware and unaware trials are compared, the difference does not only consist of the neural events which constitute awareness, since it includes the various pre- and post-processing events that also systematically vary within

those two groups of trials. Subjective report tasks are an excellent example of this. Report tasks lead to brain activity associated with the introspective process of discerning aware from unaware trials, the task-biased attention to target percepts, the encoding of target percepts into working memory, and the preparation and execution of a motor response, which only occur in aware trials, and thus confounds any claim about NCCs made based on neural events during such an experiment. Tsuchiya et al. (2015) suggests that researchers should pursue paradigms that allow researchers to determine a participant's percept in the absence of a report task, such as the BR eye-tracking paradigm described above.

Such a paradigm was implemented by Frässle et al. (2014) utilizing eye-tracking with simultaneous fMRI. They used red-and-black and green-and-black grating stimuli drifting in opposite directions during BR to evoke percept-dependent OKN. Their results suggest that a significant amount of the activity in middle-parietal and prefrontal areas thought to be associated with rivalry by the likes of Lumer et al. (1998) may be an effect of introspection and report. However, their experimental design used an imperfect "replay" control condition, which is problematic for reasons brought up by Blake (2014) discussed in the previous section. They compared fMRI-recorded activity which was present in BR but not in replay for both report and no-report conditions. However, uncertainty in reversal report may be responsible for much of the differential prefrontal activation observed in the report condition, so their comparison may exaggerate the differences between report and no-report. In other words, the differential frontal activation observed in the no-report condition (there was some, just significantly less than the report condition) may be more significant than the authors' interpretation of the results would make them seem. That said, these results provide reason to believe that the role of fronto-parietal areas in BR may have been previously overstated.

In another experiment, Kapoor et al. (2022) paired OKN decoding with single-cell recording in monkeys to determine whether perceptual dominance was represented in the PFC. In similar fashion to Leopold and Logothetis (1989, 1996), these researchers established a subset of neurons which responded differentially to physical stimulus traits (in this case, downward- or upward-moving bar gratings). They then induced BR between a downward- and an upward-moving bar grating, decoded dominant stimulus in the absence of report using OKN, and compared neural responses when either stimulus was dominant. They found that neurons in the PFC consistently responded to the dominant stimulus, and that the suppressed stimulus was not neuronally represented in the PFC. Although these results suggest that representations of visual information in the PFC agree with the BR percept even in the absence of report, it is hard to use these results to determine the role of the PFC in BR resolution. If anything, they show that the representation of the visual field which reaches the PFC is a post-BR-resolution representation, therefore being perfectly in line with the proposition that BR is resolved during earlier processing. In order to determine the dynamics responsible for BR resolution, future studies using OKN decoding paired with single-cell recording across multiple brain areas should examine the precise temporal dynamics of neural responses during perceptual reversals.

The use of no-report paradigms has also been fruitful in advancing the hunt for NCCs in EEG experiments. Pitts et al. (2014) demonstrated that a neural event detectable by EEG called the P3 or P3b is likely associated with report, effectively ruling it out as an NCC. A P3 is almost invariably elicited by any visual detection or discrimination task where participants are instructed to report their perception of some target stimulus. Specifically, it is elicited in trials where the target stimulus is presented and perceived, and not in trials where some other stimulus is presented, or trials where the target stimulus is presented but not perceived. As such, the P3 has long been considered a candidate for NCC

status, indicative of something like "noticing," or "context-updating". This claim, however, is challenged by Pitts et al.'s (2014) results. The researchers used a backward masking paradigm in which awareness of a stimulus could be effectively "manipulated" by altering the time between presentation of a stimulus and replacement of the stimulus with a randomly generated mask stimulus (stimulus-onset asynchrony or SOA). The hallmark of backward masking experiments is that likelihood that a participant will detect a stimulus increases as SOA increases. Backward masking is appealing to NCC researchers because identical stimuli can be perceived or not perceived depending on SOA, similar to how bistable images are single stimuli which can be perceived in different ways. Although differential SOAs technically produce differential sensory input, researchers can use the fact that mask-evoked brain activity is similar regardless of SOA to control for low-level sensory effects of mask onset. Pitts et al. (2014) first used a report task to demonstrate that, in trials with an SOA of 300 ms, the stimulus is always perceived, and with an SOA of 16.67 ms the stimulus is virtually never perceived. In their EEG experiment, they achieved no-report by using either of these two SOAs, which allowed them to differentiate between aware and unaware trials by assuming observers were not aware of the stimulus when the SOA was short and that they were aware of the stimulus when the SOA was long. Using both task-relevant and task-irrelevant stimuli, their results predictably showed that perceived, task-relevant stimuli evoked a robust P3, but they also showed that perceived, task-irrelevant, but still salient stimuli evoked a P3 which was no larger than that evoked by a random pattern, suggesting that the P3 is not directly related to perception, but rather task-related post-perceptual processing. This result was replicated with a similar masking paradigm by Cohen et al. (2020).

IV: Technical background

In order to investigate brain activity, scientists have developed a number of imaging technologies which allow us to measure degrees of activity at a given location in the brain at a given point in time. This study will use electroencephalography (EEG), which takes advantage of the fact that when large populations of similarly-oriented neurons are activated at once, their collective post-synaptic potentials (PSPs) produce an electrical dipole which is detectable by electrodes on the exterior of the scalp (Luck, 2014). Compared to other imaging technologies such as fMRI, EEG has particularly strong temporal resolution. That is, activity can be pinpointed to a particularly precise point in time, with sampling rates in the order of milliseconds. One of the weaknesses of EEG, however, is its poor spatial resolution, making it difficult to localize brain activity to specific areas. Another weakness is that EEG data is particularly noisy. Single-trial EEG data typically looks jagged and is difficult to interpret, because the resting brain produces oscillatory waves at a variety of frequencies which are not related to the experimental manipulation. For this reason, EEG researchers have developed the event-related potential (ERP) technique. In an ERP study, researchers average brain activity patterns across hundreds of trials by *time-locking* trial data to a particular environmental event, commonly, the onset of some sensory stimulus. The resulting average waveform provides an account of the time-course of neural activity related to cognitive processes evoked by that stimulus, because unrelated brain activity is canceled out by averaging. ERP data has led to the development of a vocabulary to talk about the typical peaks which tend to appear in waveforms related to particular types of stimulus events. These are known as ERP *components*. For instance, this study is concerned with observable differences across conditions within the P1, N1, and P3 components, as described by Luck (2014). The P1 component is a positive peak around 100ms (after stimulus onset) centered around lateral occipital electrode sites. It is

thought to be representative of early visual processing in the lower visual cortex, including V1. We mainly think of this processing as just picking up on the most basic features of the stimulus: color, form, and the like, however, attention has been shown to modulate P1 activity, suggesting top-down control even at the very basic level of stimulus processing. The N1, another early sensory component, is characterized by a negative peak around 100-200ms, and is also modulated by top-down attention. Finally, the P3 or P3b component, which was discussed in the previous section, is a positive peak around 300-450ms. It is localized in more anterior electrodes, and is primarily representative of widespread activity in the parietal, temporal and frontal lobes.

Studies have been conducted in the past to investigate the association between these particular components and BR dynamics. In a study where dichoptic images were presented intermittently, on trials where participants report a different percept from the previous trial, ERP data time-locked to stimulus presentation shows early differences in occipital electrode readout at around 100ms which correspond to a larger P1, followed by a highly robust late positivity at parietal electrodes starting at around 440ms, which roughly corresponds to a P3 difference (Britz and Pitts, 2011). Furthermore, a difference wave analysis, where the average ERP wave of non-reversal trials is subtracted from that of reversal trials, revealed a relative negativity at posterior electrode sites at around 150-300ms. Such a difference in this time range has been observed in other bistable perception paradigms and has been referred to as the reversal negativity (RN). This includes monocular bistable stimuli, for instance one study using intermittent presentation of a Necker cube demonstrated the RN, and further demonstrated that the amplitude of the RN is modulated by top-down voluntary control. That is, when participants were instructed to try to reverse their perception, a larger RN was observed compared to control participants who were given no such instruction (Pitts et al., 2008). This suggests that the RN is related to the influence of top-down control on the resolution of BR in lower-

order sensory processing areas. These results, as well as a rough correspondence in time-scale and localization between the RN and the selection negativity (SN), a similar ERP difference associated with selective attention, further suggest the role of attention in bistability dynamics.

The pattern of reversal-related activity described above, and specifically a large P3, was also observed in Metzger et al. (2017). Instead of intermittent presentation, where the dominant stimulus usually remains the same for the duration of the trial, Metzger used continuous dichoptic presentation to investigate the brain activity associated with perceptual reversal. One issue that must be overcome in an ERP study of continuous rivalry is that there is not an obvious event to which to time lock ERP analysis. In this experiment, dichoptically presented stimuli were randomly probed with briefly presented checkered circles, and researchers time-locked trials to these probes in analysis, while participants continuously reported which of the two stimuli dominated their perception. Using these reports, researchers separated probe presentations into instances where the probe appeared in the current dominant stimulus (dominant-eye trials or non-reversal trials) and instances where the probe appeared in the current suppressed stimulus, and thus triggered a perceptual reversal (suppressed-eye trials or reversal trials).
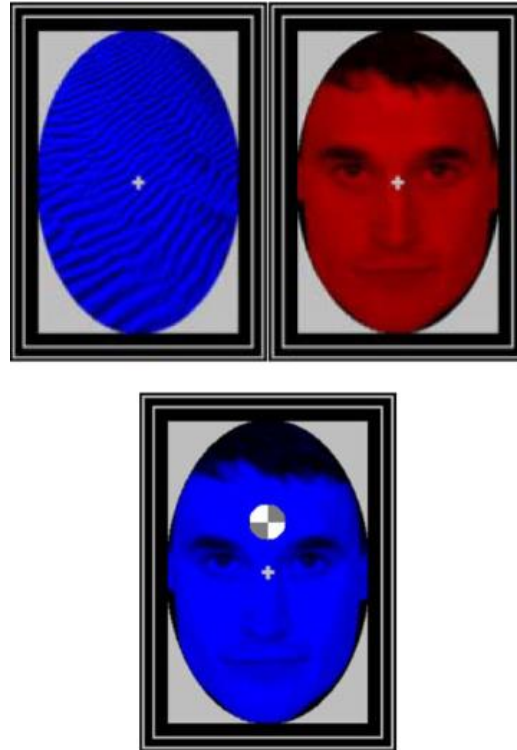
Figure 4

Stimuli from Metzger et al. (2017). Top: Example rivalry stimulus pair, one would be presented to the left eye and one would be presented to the right. Colors and images were selected to achieve high stimulus salience and distinctiveness. Bottom: Example of a stimulus probe, a small circle presented slightly above the fixation point for 200ms.

When ERP analysis was applied to compare reversal and non-reversal trials, similarly to Britz and Pitts (2011), reversal trials were characterized by a slightly larger N1, and a very large late positivity extending from around 350-1000ms. Due to the timing of the onset and the scalp distribution of this positivity, we will call it a P3. This P3 was barely visible on non-reversal trials. Unlike Britz and Pitts (2011), reversal trials on average did not differ from non-reversal trials in P1 amplitude. However, Metzger et al. (2017) further analyzed their data by separating reversal trials into quartiles based on *reversal latency* (RL), that is, the amount of time between the onset of the probe and the subjective report that a reversal has occurred. This analysis showed that *a larger*

P1 is correlated with a quicker reversal. The researchers proposed that this may be because trials where the probe received more low-level processing, and thus were more perceptually salient, are indicated by a large P1. In addition, this RL quartile analysis revealed that P3 latency was linearly related to RL. The peak of the P3 was usually around the same time that the participant pressed the button corresponding to a reversal. This observation, and the presence of a P3 in reversal trials and not in non-reversal trials, is consistent with the possibility that the P3 is related to report and perceptual decision-making, because reversal trials systematically include a shift in perceptual report in Metzger et al.'s (2017) paradigm.
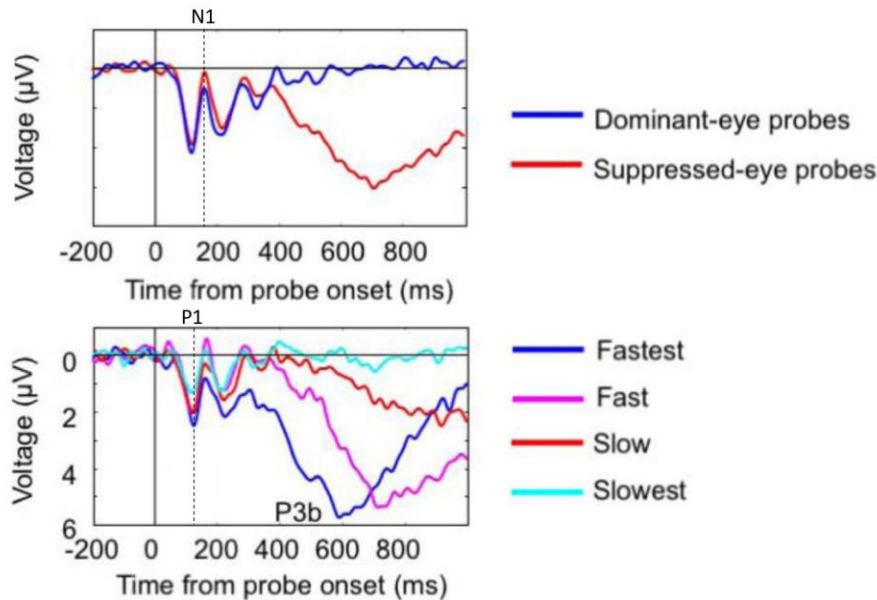

Figure 5

Top: Grand average ERPs for dominant and suppressed-eye probes from Metzger et al. (2017). Note the significant N1 difference and the prominent positivity in suppressed-eye probes after 300ms. Bottom: ERPs for suppressed-eye probes separated into quartiles as a function of reversal latency. Note that there are significant correlations between RL and P3 delay as well as between RL and P1 amplitude.

V: The present study

We will repeat a procedure similar to Metzger et al. (2017), except we will include a no-report condition in addition to their report condition. We will achieve separation of probe presentations into suppressed- and dominant-eye trials within a no-report paradigm by decoding current percept at the onset of each probe using eye-tracking combined with OKN analysis.

We hypothesize that when the Metzger et al. (2017) experiment is reproduced in the absence of report, the P3 will not be robustly represented in ERPs time-locked to suppressed-eye probe presentation compared to dominant-eye probe presentation, similar to the difference between report and no-report conditions observed in Pitts et al. (2014). Results to this effect would provide further evidence that the role of fronto-parietal areas in perceptual reversal has been overestimated due to the confounding brain activity generated by reporting tasks. They may also reveal other NCC-candidate ERP components which were previously obscured by the extremely prominent P3. Furthermore, we expect to see larger RN and P1 components in suppressed-eye trials as reported in Metzger et al. (2017), as we believe the differences in these components that they observed are related to low-level sensory processing, so they should not be affected by the absence of report. The presence of a robust P3 despite the absence of report would lend evidence to anterior, attention-related models of rivalry such as those theorized by Leopold and Logothetis (1999), as these models posit that rivalry is resolved by top-down processes, rather than low-level interocular competition.

Methods

Apparatus

The design of the experimental apparatus is largely based on Qian and Brascamp's (2019) tutorial on building a dichoptic display with simultaneous eye-tracking. The eye-tracker and display were positioned on top of a desk with built-in height adjustability. The display consisted of two identical monitors (60 Hz, 1920x1080pix, 24") arranged on opposite edges of the desk, facing one another. The adjustable chinrest was positioned exactly in the center between the two monitors, affixed to the edge of the desk. The eye-tracker (desk-mounted EyeLink 1000 Plus, sampling rate 1000 Hz) was placed in front of the chinrest at a distance of 45 centimeters. Finally, two infrared-transparent mirrors were mounted on a raised platform designed and 3D printed by Jay Ewing of the Reed College physics department, and positioned directly in front of the chinrest so that the mirrors were level with the participant's eyes when they placed their head in the chinrest. Since the mirrors were transparent to infrared light, but reflected visible light, the eyes could be tracked through the mirrors while the image of each monitor was reflected into each of the participant's eyes. A small amount of red light projected by the eye-tracker was visible to the participant, i.e. there was a grid of faint red dots in the lower right field of view of the participant's right eye. During the experiment, the grid was far in the periphery as the stimuli were small and centered on the screen, so this visual artefact should not be a significant confound to the manipulation of visual awareness in the center of the visual field. Figure 5 shows the main components of the apparatus.
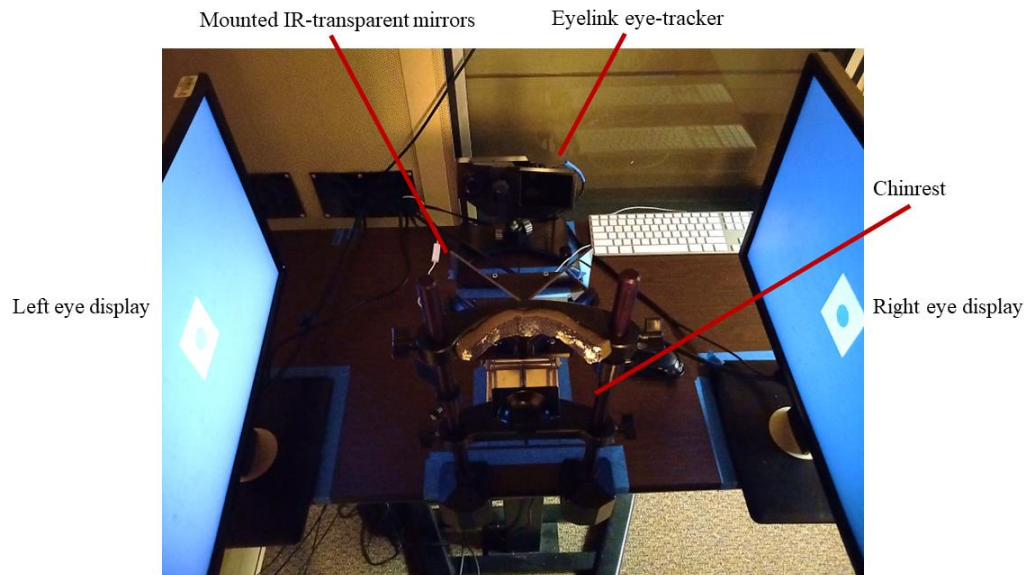
Figure 6

Photo of apparatus in EEG recording room. Stimuli displayed on monitors on either side of participants. Participants viewed stimuli through 45° mirrors positioned in front of chinrest. Eye-tracking is possible through mirrors due to infrared-transparency.

Stimulus

Stimuli consisted of moving gratings, such that each eye saw a grating drifting either to the left or the right (left/right motion direction and left/right eye were counterbalanced across mini-blocks of trials). Gratings were viewed through circular apertures and tilted 20° in opposite directions. Also, the gratings presented to the left and right eyes were always opposing in colors to enhance rivalry, one was blue and one was orange-yellow, both with black bars, also counterbalanced across mini-blocks. The exact colors were tuned between participants to achieved equiluminance to prevent stimulus dominance biased by luminance differences. Isoluminant colors were identified using heterochromatic

flicker photometry. Stimuli subtended a visual angle of 4.7 deg, had spatial frequency of 0.94 deg/cycle and drifted at a speed of 8 cycles/sec. Stimuli were displayed against a black background, and each stimulus was framed with an identical random noise pattern to facilitate binocular fusion of the background and to help stabilize ocular vergence. Probes consisted of 200ms periods where the luminance of one of the stimuli was doubled. Probes were presented randomly with equal probability to either stimulus, at intervals which were selected pseudo-randomly from a uniform distribution of 2 to 2.5 seconds.
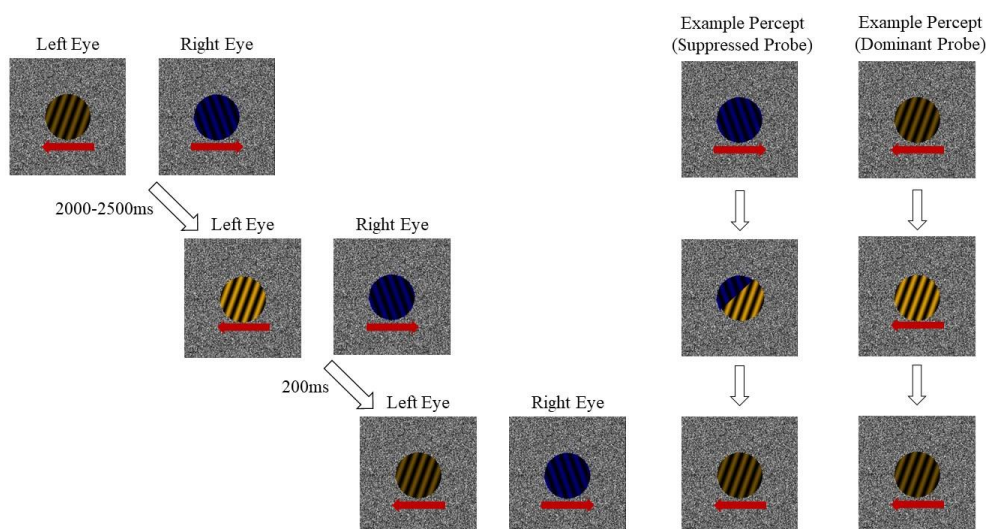

Figure 7

Orange-yellow and blue stimuli drift in opposite directions at a constant rate to induce OKN. Color and direction of movement of stimuli were counter-balanced across mini-blocks. Target and ISI of probes selected pseudo-randomly from a uniform distribution. Example percept shows a probe-mediated reversal, perceived as a "travelling wave" in the direction of motion of the suppressed stimulus.

In order to ensure that each stimulus fell directly in the center of the participant's field of view, monitor positions were aligned manually in a procedure where a white dot in the center of the screen alternated between the left and right monitors, and slight adjustments were made to the position of the monitors on the desk until the dot appeared to remain in the same position with

each alternation. The dot was also framed with a random noise pattern which appeared continuously on both monitors during this procedure to encourage stable vergence.

Behavioral Piloting and Analysis

This study used an OKN analysis algorithm developed and generously made publicly available on Github by Aleshin et al. (2019). This algorithm first isolates segments of smooth pursuit, removing noise and saccades, then it fits the smooth pursuit segments to a continuously differentiable mathematical curve using spline interpolation. The slope of this curve represents the horizontal velocity of eye movements, where a negative velocity represents smooth pursuit to the left, and a positive velocity represents smooth pursuit to the right. Since this method can interpolate across multiple segments of smooth pursuit, unlike previous methods which examined the slope of pursuit segments individually, Aleshin et al. call this method cumulative smooth pursuit (CSP) analysis.

Extensive piloting was conducted to confirm the validity of the OKN analysis method designed by Aleshin et al. and to assess typical behavioral responses to the apparatus, including the stimuli and probes. Participants were Reed College students and faculty. Before attempting eye-tracking, we familiarized each participant with the stimuli and verified by subjective report that they experienced complete dominance of one stimulus over the other and that perception switched between the two stimuli for the majority of the viewing period. In the first pilot study, participants continuously reported the direction of motion of their current perceived stimulus by pressing and holding down the left or right mouse button. During prolonged transition periods or periods of ambiguity, participants were instructed to press neither button. This task was broken into 60-second mini-blocks, and each participant completed 5-10 trials. Mean dominance periods were calculated based on the participants' reports.

Accuracy of the CSP analysis was assessed by comparing OKN-derived percepts (henceforth referred to as the "objective" measure of perception) to button-press-reported percepts (henceforth referred to as the "subjective" measure of perception). Subjectively measured percepts were corrected for reaction time delays by shifting all reports a flat 400ms backwards in time. This initial pilot study was conducted in the absence of probes.

Further pilot studies were then conducted with the inclusion of probes. In order to ensure that perception of the probe itself would not be a confound when we compared suppressed-eye probing trials to dominant-eye probing trials, we verified that probes are perceived even when they are presented to the suppressed eye. To do so, participants were instructed to press the left mouse button each time they perceived a probe. Also, we used the previously verified OKN decoding to assess the distribution of reversal latencies (RLs), that is, the amount of time that elapses between the onset of the probe and the next perceptual reversal when the suppressed eye was probed (compared to that when the dominant eye was probed). We calculated distributions of RL for each session to investigate the effects of probes on BR dynamics, as we wanted to demonstrate probe-mediated reversal. We also collected subjective reports on how suppressed probes were perceived and whether the participant could tell they were causing perceptual reversals.

EEG Data Collection

Participants for the EEG experiment were recruited primarily from Reed College, and were compensated monetarily for their participation ($30 for a 2 to 3 hour session). For each participant, monitors were aligned manually and isoluminant colors were determined. Due to the high level of individual variation in behavioral and perceptual responses to the stimuli upon viewing, participants completed 3-5 x 60-second mini-blocks of training before being fitted

for EEG recording. During this training, eye-tracking was performed, and the presence of consistent OKN was verified by visual inspection. Participants were also asked to report their percept during training mini-blocks to get them used to the task and to make sure they can distinguish dominance periods. After training, participants were asked to describe their percepts. Participants who reported piecemeal or otherwise inconsistent rivalry did not continue with the study. For participants who reported primacy of one color over the other despite flicker photometry-equalized perceived luminance, luminance was adjusted incrementally by hand. Participants were fitted with a 64-electrode EEG cap (EasyCap, Gersching Germany), and EEG readout time-locked to probe onset was recorded to a computer outside of the recording room. EEG data was collected for both report and no-report phases of the experiment from each participant. In the report phase, procedures were similar to those in the first pilot study except with inclusion of probes, and the simultaneous EEG in addition to eye-tracking. Participants were asked to report their dominant percept by pressing and holding the left or right mouse button to indicate left or right perception of movement, regardless of probe activity. The intention of the report phase was to replicate Metzger et al.'s (2014) findings, showing ERP differences for suppressed- vs. dominant-eye probes during perceptual report, using very different stimuli and probes.

In the no-report phase, the report task was taken away. The procedure consisted entirely of simultaneous EEG and eye-tracking while the participant passively viewed the stimuli. Due to the lack of task, participants were encouraged to maintain focus on the stimuli and to take breaks in between trials to prevent exhaustion. The report and no-report conditions each consisted of 30 60-second mini-blocks. After 60 seconds of viewing the stimuli with intermittent probes, the participant was given a break, and the next mini-block began when they pressed either mouse button. After every 6 mini-blocks, eye-tracking drift correction was performed, and the researcher checked in verbally with the

participant. The order of report and no-report conditions was counterbalanced across participants.

At any point, if participants appeared to stop exhibiting OKN, they were told by the researcher between mini-blocks to attempt to increase their focus on the stimuli and to "actively view" the black stripes in the stimuli. If OKN still appeared inconsistent for another mini-block, they were asked to exert a little more effort on focusing on the stimuli. If OKN still appeared inconsistent after this second reminder, they were told to attempt to maintain perception of the currently dominant stimulus for as long as possible. This instruction tends to dramatically improve OKN consistency, but was treated as a last resort as it introduces additional task-relevance to perceptual reversals, which, especially during no-report, could introduce confounding brain activity.

EEG Analysis

Since probe-mediated reversal and percept-related OKN are effects which are pre-requisite for the validity of this study, psychophysical evidence for the consistency of these effects was evaluated before considering a participant for ERP analysis. Due to individual differences in typical OKN speed, CSP analysis parameters and specifically the spline velocity threshold required to classify a reversal were optimized for each participant by iterative analysis of the decoding accuracy of report trials with different parameters. If CSP analysis did not reach 70% accuracy for a given participant in cross-validation with perceptual reports, the participant was excluded from analysis. If reversal latency distribution was not significantly different for dominant and suppressed probes, the participant was excluded for analysis. Using CSP results, dominance periods were calculated for each session to check for abnormalities and to ensure that mean dominance period was not biased in favor of one eye or one stimulus.

Each probe presentation corresponded to one trial segment of the EEG data. Trials where the probe happened to be presented to the dominant eye and a subsequent reversal did not occur within 800ms after stimulus onset were deemed non-reversal trials. Trials where the probe was presented to the suppressed eye and a subsequent reversal occurred within 800ms after stimulus onset were deemed reversal trials. The ERPs for the reversal trials were averaged as were the ERPs for non-reversal trials. A difference wave was calculated by subtracting the mean ERP for non-reversal trials from the mean ERP for reversal trials. This analysis was repeated for the report and no-report conditions, using OKN analysis to determine suppressed and dominant probes in both conditions.

Results

Psychophysics & troubleshooting

Once the apparatus was built, eye-tracking and report data was collected from volunteer participants during apparatus and stimulus design to assess decoding accuracy and psychophysical responses to the stimuli. The original stimuli were red and green, were oriented vertically instead of angled, and were presented on a uniform background rather than being framed by a random noise pattern. Because these stimuli produced incomplete perceptual dominance and very short dominance periods, adjustments were made after this initial piloting phase. One of the aims was to strike a balance between psychophysics (ideal length and completeness of dominance periods) and decodability (accuracy of using OKN to objectively determine percept). Moving stimuli are needed to induce OKN for use as an objective measure of perception, but they tend to produce shorter dominance periods compared to stable stimuli (e.g., Metzger et al. (2017) report median dominance periods above 2.5 seconds with static stimuli, whereas Frässle et al. (2014) report median dominance periods well below 2 seconds with moving stimuli). As dominance periods become shorter, we become less confident in the assertion that probes to the suppressed eye are causing perceptual reversals. Here we report psychometrics and decoding accuracy from 3 pilot participants to give examples of typical results as well as demonstrate between-participant variation.

Measure	Participant 1	Participant 2	Participant 3
Maximum decoding accuracy	81%	63%	75%
Mean dominance period	1421ms	1494ms	2006ms
Mean suppressed probe RL	1540ms	877ms	1005ms
Mean dominant probe RL	3339ms	1557ms	1090ms

Table 1

Decoding accuracy and psychophysical responses assessed through decoding for
3 pilot participants, each of whom completed 3 90-second viewing periods. None
of these participants have ideal psychophysical attributes, but this data was
collected before the stimuli and procedure were finalized. RL: Reversal latency

There was considerable variation in reported percepts throughout the piloting phase, with some participants reporting consistent and clear perceptual dominance and others reporting consistent mixtures of the two stimuli (piecemeal rivalry), i.e., never seeing complete dominance of one stimulus or the other. Interestingly, many participants reported a training effect, where their initial percept of the stimuli was piecemeal but became less and less so over the course of a few mini-blocks. Anecdotally this was sometimes reflected in OKN analysis by higher decoding accuracy in later mini-blocks than early ones. All participants who experienced complete dominance also reported that they frequently experienced reversals immediately preceded by a probe to the suppressed eye. Suppressed probes were typically perceived as suddenly appearing overlayed on top of the previously dominant stimulus, followed by partial piecemeal rivalry and a "traveling wave" percept, which generally appeared to "travel" in the direction of the suppressed stimulus' motion, as if one grating began sliding over top of the other. Similar traveling waves have been reported and described in previous BR experiments, as well as a similar effect of stimulus motion on traveling wave dynamics (Knapen et al., 2007).

Finally, in separate pilot studies we confirmed that participants saw the probes regardless of whether they were presented to the dominant or suppressed eye. Although on the first couple of viewing periods, participants often missed some probes to the suppressed eye, by the 5th viewing period all participants reported seeing virtually every probe.

Preliminary EEG results

Due to time constraints and the various technical hurdles involved in the piloting phase, a full EEG dataset (~20 participants) was not acquired. Four participants were recruited for the final experiment which involved psychophysics, eye-tracking and EEG all at once. Of these four participants, one was excluded for poor EEG impedance (too much noise in the raw EEG signal), and two more were excluded for poor OKN decodability. The remaining subject displayed ideal psychophysics, crisp OKN and successful EEG recording. Cross-referencing objectively measured percept with perceptual reports revealed a decoding accuracy of 77.6% in the report condition. The participant also had remarkably long dominance periods, meaning spontaneous reversals were less likely to interfere with our study of probe-mediated reversals. In addition, very short RLs induced by suppressed probes suggested that the reversal-mediating effect of these probes was strong and consistent for this individual.

Measure	Report condition	No-report condition
Mean dominance period	2040ms	2174ms
Mean suppressed probe RL	673ms	592ms
Mean dominant probe RL	2934ms	3875ms

Table 2

Typical percept information for selected EEG participant inferred from OKN

decoding in both report and no-report conditions. RL: Reversal latency.

A. Distribution of Suppressed Probe Reversal Latencies

B. Distribution of Dominant Probe Reversal Latencies
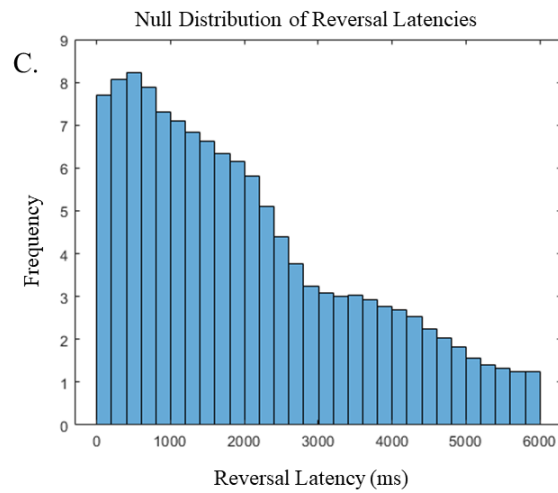
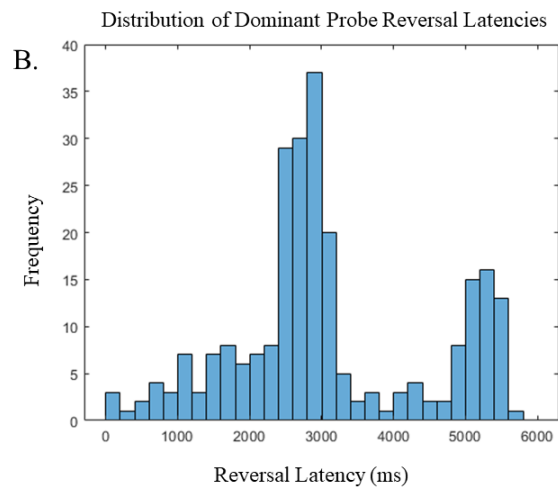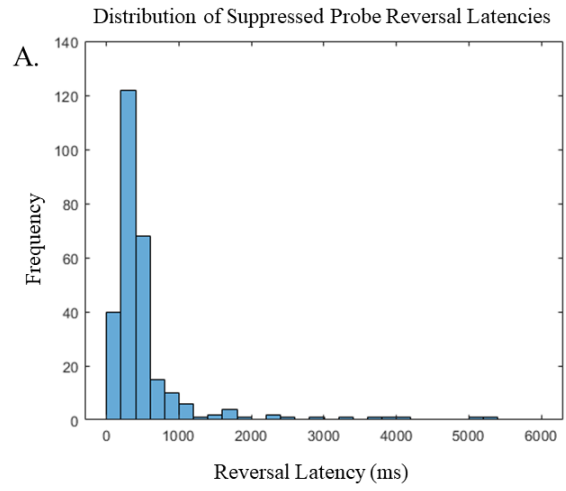**C.** Null Distribution of Reversal Latencies

Figure 8

A: Distribution of reversal latencies to suppressed probes in no-report condition of selected subject. B: Distribution of reversal latencies to dominant probes in no-report condition of selected subject. C: Null distribution of reversal latencies, i.e., the distribution we would be sampling from if timing of reversals was completely independent of timing of probes.

These psychophysical attributes make this individual a very promising participant for the ERP study, since we can be more confident in the consistency of the effects (percept-induced OKN, probe-mediated reversal) which are necessary assumptions to interpret the ERP data. Furthermore, we can demonstrate the validity of OKN decoding by showing the probe ERPs are similar in the report condition whether they are obtained through OKN or through perceptual report (Figure 8).
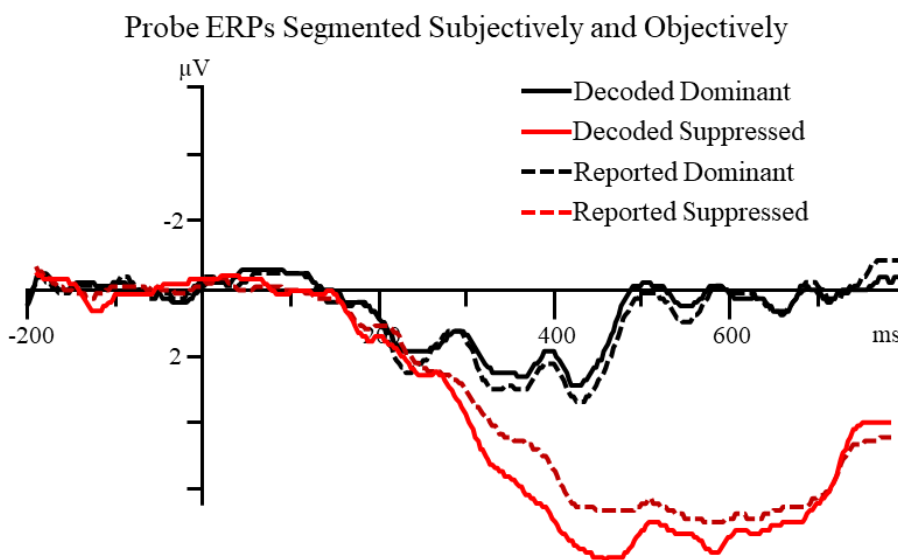

Figure 9

Probe ERPs segmented into dominant (black) and suppressed (red) based on objective OKN decoding (solid) and subjective button-press reports (dashed). The similarity of these waveforms using subjective and objective segmentation help validate the OKN method in the no-report condition.

54

A. Dominant and Suppressed Probe ERPs, Report Condition

B. Dominant and Suppressed Probe ERPs, No-Report Condition
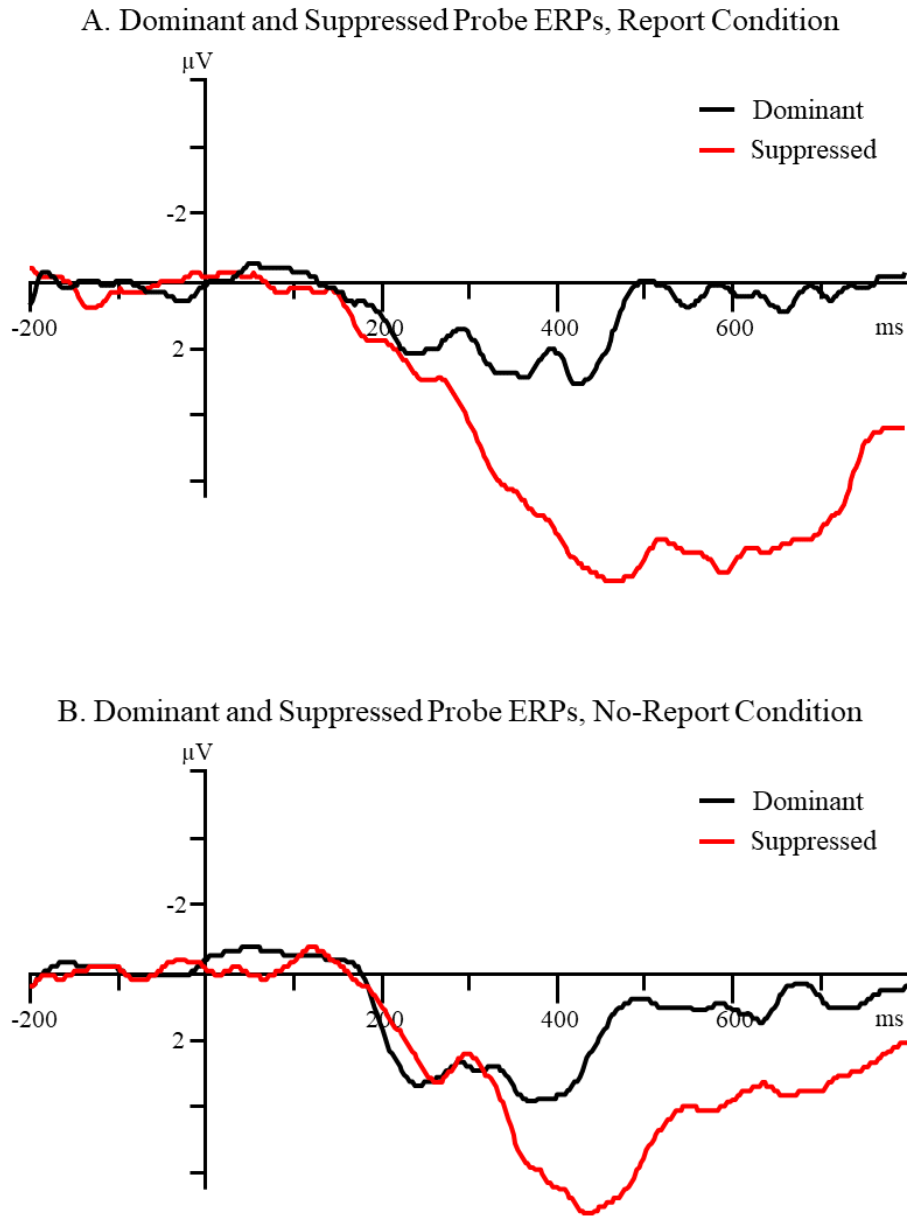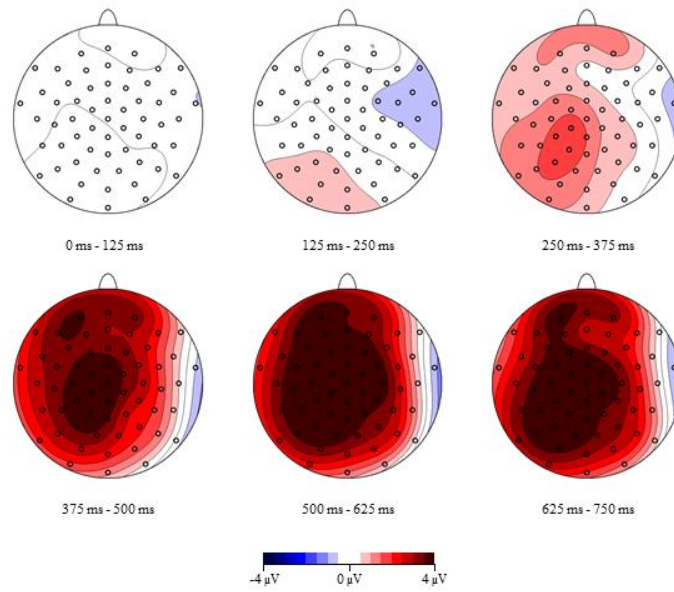

Figure 10

Average ERPs evoked by suppressed (red) and dominant (black) probes in a representative left temporo-parietal electrode closest to CP3. A. Report condition. B. No-report condition. In both conditions, OKN was used to objectively measure the participant's perception.

Although the data is preliminary, the ERPs appeared to show some distinguishable patterns. P1 and N1 activity was difficult to identify in this participant, but the late positivity evoked by suppressed, but not dominant probes, was identifiable in both the report and the no-report conditions. Importantly, this positivity was stronger, and persisted for longer periods, in the report condition. Scalp distribution analysis was applied on the difference wave (suppressed minus dominant) to determine the localization of these distinguishable patterns.

A. Reversal-Related Activity Scalp Distribution, Report Condition

0 ms - 125 ms   125 ms - 250 ms   250 ms - 375 ms

375 ms - 500 ms   500 ms - 625 ms   625 ms - 750 ms

-4 µV   0 µV   4 µV

B. Reversal-Related Activity Scalp Distribution, No-Report Condition

0 ms - 125 ms   125 ms - 250 ms   250 ms - 375 ms

375 ms - 500 ms   500 ms - 625 ms   625 ms - 750 ms
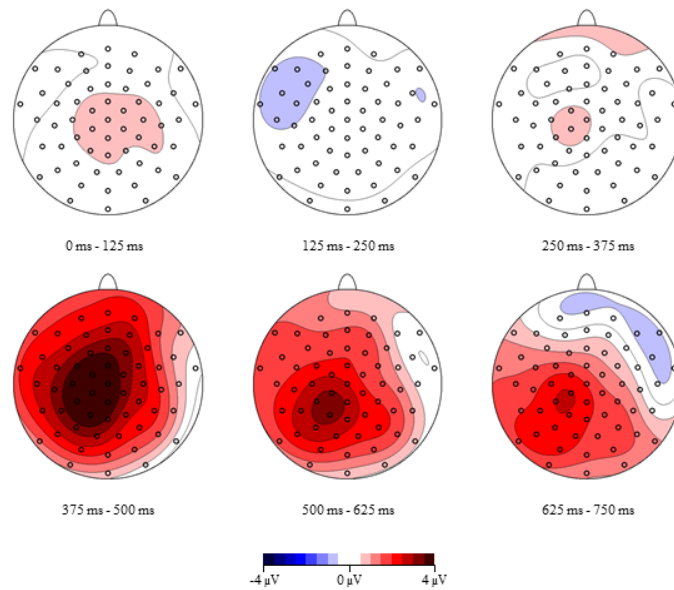
-4 µV   0 µV   4 µV

Figure 11

Spatial distribution of difference wave for ERPs evoked by suppressed minus dominant probes. A. Report condition. B. No-report condition.

In both conditions, the prominent late positivity evoked by suppressed but not dominant probes is widespread across the scalp but centralized over the parietal scalp and left-lateralized, which is typical of the P3 component. Notably, the positivity appears to have a more frontal distribution in the report condition compared to the no-report condition, possibly related to the task-relevance and reporting requirements involved in perceptual reversal in the report condition, which are likely to require networks in the prefrontal cortex. It also appears to peak around 100-150ms later than in the no-report condition.

Discussion

I. ERP Interpretation

This study investigated ERP correlates of probe-mediated perceptual reversals in binocular rivalry using a no-report paradigm. It followed up on Metzger et al. (2017), and in particular, their finding that suppressed-eye, reversal-triggering probes to the visual stimuli evoked a prominent P3-like late positivity in comparison to dominant-eye, non-reversal-triggering probes. We were interested in the possibility that report-related activity might contribute to this positivity, and thus implemented eye-tracking and OKN decoding to segment EEG data into suppressed and dominant probes in the absence of report, to further isolate reversal-related activity.

These preliminary results suggest that the P3 difference between suppressed and dominant probes observed by Metzger et al. (2017) and recapitulated in the report condition of this study may have been largely related to reporting and perceptual decision-making, rather than perceptual reversal itself. However, even in the no-report condition, some P3 activity remained, suggesting that probe-mediated reversal might be a late global effect rather than an early local one, as attention-related models of binocular rivalry would predict. Compared to the no-report condition, the P3 activity in the report condition was of a higher amplitude, peaked later, persisted for longer and was more frontally distributed. It is important to note that what we are calling the P3 refers to the timing and distribution of a widespread pattern of activity, and is not necessarily related to any specific, singular cognitive process. The generators of the P3 activity in the report condition might consist of multiple perception-related

temporo-parietal processes and, separately, task-related prefrontal processes, as the bi-centralized distribution of the activity seems to suggest.

In many ways, these results complement those of Frässle et al. (2014). Using fMRI, those researchers found that nearly all of the frontal activation associated with resolving binocular rivalry observed in their report condition disappeared in their no-report condition. As in the present study, most of the rivalry-related activity that persisted in the no-report condition was localized to the occipital, temporal, and parietal lobes, components of the so-called "posterior hot zone" (Koch, 2016). Interestingly, the rivalry-related activity they found was strongly localized to the right hemisphere, whereas the reversal-related activity in our experiment and in Metzger et al. was slightly left lateralized. It is difficult to compare EEG data to fMRI data spatially, because the location of electrical activity on the scalp does not directly correspond to the location of the originating brain activity. In fact, Bledowski et al. (2004) attempted to identify the generating brain areas of the P3 by combining EEG with fMRI. They found that the scalp distribution of the P3 was bilateral, if not slightly left lateralized, but the fMRI results suggested that inferior temporal activity contributing to P3 activity was strongly right lateralized. With a larger dataset, source analysis can be conducted on the ERP data to attempt to determine which brain areas are truly responsible for generating the scalp distribution. Still, it is important to note the differences between Frässle et al.'s methods and the methods of this study. They attempted to isolate rivalry resolution-related activity by comparing a binocular rivalry condition to a "replay" condition which monocularly recreated a binocular rivalry percept. On the other hand, we attempted to isolate perceptual reversal-related activity by comparing ERPs time-locked to reversal-causing and non-reversal-causing probes. Although both studies attempt to isolate rivalry-related activity, they are investigating two different facets of rivalry processing, and are thus not directly comparable.

Unfortunately, we did not observe any P1, N1, or RN activity in the ERPs for the single participant remaining in the sample. We expect to see P1 and N1 activity as the sample becomes larger, as these components were evident in some of the excluded subjects for the subset of conditions that had enough clean trials. With a larger dataset, we will analyze these components for the effects observed by Metzger et al., that is, a larger N1 amplitude in suppressed-eye probes, and a P1 amplitude which correlates negatively with reversal latency. The RN was not observed in Metzger et al. (2017) but has been observed in other binocular rivalry studies, and would be exciting to identify in these results, as it has not yet been identified in a no-report study.

II. Potential Implications

The discovery that perceptual reversal is correlated with a late signal with a widespread distribution, even in the absence of perceptual report, would lend support to the idea that perceptual reversals are representative of a shift in higher-order visual processing and interpretation of lower-order visual signals, rather than a shift in the lower-order signals themselves. In addition, a lack of noticeable ERP differences during early visual processing in suppressed compared to dominant probes would suggest that early visual processing is not responsible for triggering perceptual reversals. Thus, as Leopold and Logothetis (1999) proposed, it would not be the low-level signals from each eye which compete during BR, but the higher-level representations of each image. In other words, the global model of BR would be supported.

However, local models of BR could account for this result by proposing that the observed late global signal is a downstream outcome of the local shift in ocular dominance within the early stages of the visual hierarchy. This signal may be a result of BR perceptual reversals inherently activating attentional circuits due to their unpredictable nature. In fact, the P3 component is readily activated

by target trials in an "oddball" paradigm, where a string of "typical" non-target stimuli are followed by a sudden "rare" target stimulus (Luck, 2014). Thus, the P3 is elicited by an unexpected change in physical input. However, since the P3 is generated by relatively high-level processing areas, reflected by its distribution and its relatively long delay from stimulus onset, it is not the physical input itself whose changes elicit the P3, but the inputs to these high-level areas. Thus, if perceptual reversal is truly representative of a shift in ocular dominance at an early local level, it would not necessarily be surprising to observe a P3 in perceptual reversal ERPs. These local models would, however, predict some amount of early, occipitally localized activity reflecting a reversal in interocular inhibition at low-level visual processing areas. However, a lack of noticeable activity in an ERP study is not good enough evidence to discount the possibility of such activity existing, as this low-level activity may not appear in ERPs due to its particular neural signature not producing a dipole significant enough to be detected on the scalp. Also, since early local models posit that perceptual reversals involve suppressing the activity related to one eye and augmenting the activity related to the other eye, early reversal-related activity may be lateralized such that positive and negative activity in each hemisphere average each other out when suppressed probes from the left and right eyes are combined. The present study can explore this possibility with a larger dataset by further dividing probes based on target eye. We would then calculate difference waves for suppressed minus dominant probes to the left eye, and for suppressed minus dominant probes to the right eye, thus still controlling for the possibly lateralized low-level processing of the probe itself.

It is important to note that the aim of this study is specifically to isolate neural correlates of perceptual reversal (NCPRs) during BR. This does not necessarily mean that we are isolating neural correlates of consciousness (NCCs). In order to extrapolate these findings to situations outside of the BR paradigm, we must consider what different theories of consciousness would predict the

NCPRs to look like. For instance, local theories of consciousness such as recurrent processing theory (RPT) posit that brain activity entirely localized to the visual system is sufficient to elicit a visual percept (Lamme, 2006). These local theories of consciousness predict local models of BR, because if BR remained unresolved during early visual processing, we would be able to perceive images from both eyes at once. Thus RPT would predict the existence of early, occipitally localized NCPRs, although for reasons already discussed, it would not necessarily rule out the possibility of additional late, widespread NCPRs. On the other hand, global theories of consciousness generally predict global models of BR. Specifically, Leopold and Logothetis (1996) has been cited as supporting global neuronal workspace theory (Promet and Bachmann, 2022), due to the researchers' observation that neuronal activity early in the visual hierarchy tended not to correlate with dominant percept, and the proportion of neurons responding to the dominant percept increased as we move up the visual hierarchy. Both images are represented equally in early visual processing areas, unlike in subjective experience, thus it is up to higher-level processes to determine which image to represent perceptually "in the workspace". The existence of early local NCPRs would most likely be difficult to account for under any global theory of consciousness. Percept-dependent differential activity in the low-level visual areas during passive BR may be contributed to feedback from higher-level areas, but a global theory would predict that a probe-mediated reversal-triggering process would originate as a late, global signal.

III. Limitations and Complications

The current study is harshly limited by its limited sample size. Collecting usable data is very difficult in this paradigm because participants need to experience ideal percepts and display clear OKN throughout the experiment, and EEG recording must have high signal-to-noise ratio. During initial screening

of percept and eye movements, we may have been too lenient in accepting piecemeal percepts, inconsistent probe-mediated reversal, and poor OKN. The excellent participant who remained in the sample was the last participant we ran, and they set the bar higher for our expectations for future participants' psychophysical data. Future data collection will be streamlined by including a longer eye-tracking session before the day of EEG recording, which would allow us to analyze OKN and psychophysics in detail before deciding whether to invite the participant for an EEG session.

Another problematic limitation of the study is the attentional difference between the report and no-report conditions. Unsurprisingly, passively viewing stimuli for extended periods of time with no task except to maintain focus leads to attentional fatigue. Especially given results like Brascamp and Blake (2012), which suggest that BR can remain unresolved when spatial attention is not directed at the rivalrous stimuli, this difference in attention likely led to differences in percept. It is unsurprising, then, that they seemed to also lead to differences in OKN. Our included participant displayed clean OKN in the training section with report, but in the first no-report mini-block, their eye movements were almost entirely still. Their eye movements still did not improve after instructing them to attempt to actively view the stimuli, so they were instructed to attempt to keep the currently dominant stimulus in focus as long as possible. As expected, this led to strong OKN. However, this gives the participant a covert (non-motor) task which systematically changes in response to perceptual reversal. This means that, in addition to reversal-related activity, we are capturing activity related to perceptual decision-making and task response in our ERP comparisons. This calls into question the relevance of the P3-like late positivity observed in this participant evoked by suppressed probes in the no-report condition, as this positivity could be attributed to this covert task-switching.

A promising solution to the attention issue is to introduce a new overt "distractor" task to the no-report condition. Cohen et al. (2020) implemented such a task in their no-report backward masking paradigm. In their experiment, they presented stimuli which were either perceived or not perceived by adjusting the time between the stimulus presentation and the onset of a visual mask. Most stimuli were black line drawings, but occasionally the researchers would present a green circle. Participants were instructed to count how many green circles were presented in each experiment block, and report their count between blocks. Importantly, trials where a green circle was presented were excluded from analysis. Thus, participants exerted task-directed attention towards the stimuli, but since every trial used in the ERP analysis only involved the presentation of a "miss" stimulus, task-related brain activity was controlled for in their ERP comparison. Something similar is possible in this study. The distractor task would have to be attention-demanding, and it would have to not interfere with OKN. A possibility is to occasionally make one stripe on each stimulus briefly turn white, and for the no-report condition instruct participants to count how many times they see a white stripe in each mini-block. This would keep participants' attention on the stimuli and their eye movements tracking the motion of the gratings without introducing confounding task-related brain activity.

Finally, a question that any experiment which uses eye movements as an objective measure of perception will eventually have to grapple with is whether their results are confounded by brain activity related to the eye movements themselves. That is, since we know that perceptual reversal is systematically accompanied by a change in OKN direction, when we try to isolate reversal-related activity we are also capturing the activity related to controlling OKN direction. We are trying to control for decision-making processes, but in doing so we are systematically introducing the process which makes the unconscious "decision" to move the eyes in a particular direction. There is no easy solution to

this problem, as reflexive eye movements are deeply entangled with motion perception. However, one place to start looking for a solution is in the rare situations where eye movements dissociate from motion perception. Examples of such situations are compiled in a review by Spering and Carrasco (2015). For instance, Spering et al. (2011) used a rather convoluted presentation procedure using dichoptic drifting grating stimuli to produce a situation where the direction of perceived motion was constant across trials, but OKN direction varied, and was approximately equally likely to be either congruent or incongruent to the direction of perceived motion. Comparing brain activity in trials where OKN direction was incongruent to perception direction to those where OKN direction was congruent to perception direction would allow us to isolate OKN-related activity from motion perception-related activity. This would provide useful information about how OKN-related activity is localized, however, an ideal paradigm would allow us to do the reverse, isolating motion perception-related activity from OKN-related activity. The development of such a paradigm would be invaluable in controlling for all possible confounds in studies which use OKN as an objective measure of perceptual experience.

IV. Future Directions

Dichoptic presentation with eye-tracking capability opens up many possibilities for visual perception studies. For instance, a similar paradigm might be used to compare seen and unseen stimuli in the absence of report. If saliency of probes can be reduced to the point where they do not cause perceptual reversal, so that they are only visible when presented to the dominant eye, we could attempt to isolate brain activity related to the perception of the probes by subtracting ERPs evoked by dominant probes from ERPs evoked by suppressed probes. This version of the study would be more directly comparable to the no-report backward-masking studies by Pitts et al. (2014) and Cohen et al. (2020).

These studies compared ERPs to the same stimuli when they were visible and when they were rendered invisible by the subsequent presentation of a visual mask. While no P3 was observed in the comparison of seen vs. unseen trials in the no-report conditions of either of these studies, Pitts et al. (2014) did describe an occipital-parietal negativity around 200-300ms which was present in seen, but not unseen trials, even when participants did not report their perception. This negativity has been dubbed the "visual awareness negativity" (VAN). The VAN is considered an NCC candidate for this reason. If it is a true NCC, we would expect it to be present in such a BR probing paradigm.

Another direction would be to further interrogate the role of attention in BR dynamics. Logothetis et al. (1995) attempted to investigate this question. They used OKN as an objective measure of percept to examine changes in BR dominance period length during attentionally demanding distractor tasks, both auditory and visual. They found that these distractor tasks had little to no effect on BR dynamics. This is in stark contrast to the more recent studies by Brascamp and Blake (2012) among others, who have found that attention is necessary for the resolution of rivalry. This difference in results is likely due to Logothetis et al. using insufficiently robust modulations on attention. This is understandable, as in order to consistently elicit OKN, rivalry stimuli had to occupy the center of the display, thus it would be difficult or even impossible to completely divert attention from rivalry stimuli as Brascamp and Blake (2012) did. However, it seems likely given Brascamp and Blake's (2012) results that modulating attention would modulate BR dynamics. Logothetis et al. (1995) was an experiment of low statistical power with only two participants. It would be worthwhile to experiment with a variety of attentionally demanding tasks which can be performed while maintaining fixation on rivalry stimuli to determine if BR dynamics are influenced by moderate levels of inattention.

In another line of BR research, Denison et al. (2011) demonstrated the role of expectations in BR dynamics. When participants are presented with the same

"rotating" sequence of static gratings (i.e., 0º, 45º, 90º and 135º rotated static gratings) to both eyes, when a 90º grating is presented to one eye and a 180º grating to the other, the 180º grating is more likely to be perceptually dominant. Denison et al. (2011) proposes that this is because we expect a rotating object to continue rotating in the same direction, so the 180º grating is the expected next item in the sequence. Thus, BR dynamics are biased towards expected stimuli. Also supporting this interpretation, participants were faster to respond when they perceived the 180º than when they perceived the 90º grating. This suggests that perceptual dominance of expected stimuli is more likely, and possibly that perceptual transitions to these stimuli occur faster, compared to unexpected stimuli. This result has not been recapitulated in a no-report paradigm. It would be interesting to experiment with a probe-mediate reversal paradigm with OKN-eliciting stimuli where the expectancy of probes was manipulated. Based on Denison et al.'s (2011) results, we would expect that higher expectancy probes to the suppressed eye would trigger reversals with higher frequency and quicker reversal latencies compared to lower expectancy probes. Designing probes with different levels of expectancy, but similar stimulus attributes is not simple. One possibility is to instruct participants on what to expect, but Denison et al. (2011) distinguishes between these arbitrary, situation-specific, "attentional expectations" and prior "perceptual expectations", such as the expectation that a moving object will continue to move in the same direction.

V. Summary

This study aimed to isolate perceptual reversal-related brain activity during binocular rivalry using EEG in the absence of report. We validated and implemented the OKN technique for objectively measuring percepts during binocular rivalry, and effectively determined our participants' percepts without button-press reports. We applied the ERP technique to preliminary EEG data,

which showed that the previously observed P3-like late positivity associated with perceptual reversals may be partially, but not entirely, related to perceptual decision-making and volitional report. These findings are promising, and with the addition of more data they may help mediate between early local and late global models of binocular rivalry resolution.

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