Sampling Motion in Time: The Neural and Cognitive Mechanisms of the Fröhlich Effect

by

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A dissertation accepted and approved in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy
in Psychology

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Fall 2025

DISSERTATION ABSTRACT

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Neural oscillations in the alpha-band frequency are purported to gate perception through alternating states of neural excitation and inhibition, shaping our visual sampling rate and modulating outcomes such as target detection thresholds (Mathewson et al., 2012). Does this mechanism extend to the ability to localize moving targets? The magnitude of the Fröhlich effect (where an observer mislocalizes the starting location of a moving object in the direction of motion) could be modulated by variance in this sampling rate.

Across three experiments, participants judged the starting location of a moving target. In Experiment 1, alpha entrainment at two frequencies modulated perceptual sampling, and behavioral responses were densely sampled for rhythmic signatures (Ronconi et al., 2017). Illusion magnitude was reduced under fast entrainment, suggesting alpha frequency affects processing speed and perceived onset. However, Fast Fourier transform analysis revealed no frequency-specific peaks in the time series, implying an influence of alpha frequency but at a level that is not detectable with more rigorous tests such as phase alignment. Experiment 2 found no relationship between illusion magnitude and any reaction time component, arguing against early sensory gating. Experiment 3 replicated the null entrainment effect by comparing the behavioral time series of a Fröhlich task with a two-flash fusion task (a phenomenon that has been shown to reveal an effect of entrainment).

Our results provide some evidence that the Fröhlich effect is influenced by entrainment frequency but not in a way that is detectable by phase alignment. It is possible that the illusion is partly the result of visual sampling delays driven by the alpha rhythm, but that this effect is diluted by additional mechanisms that have their effects in higher levels of perceptual processing (e.g., motion extrapolation).

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ACKNOWLEDGMENTS

I wish to express my sincere admiration and respect for Professor Dassonville for his incredible patience and insight in the preparation of this manuscript and series of experiments. This could not have been done without his help. In addition, I'd like to thank my loved ones (both family and friends) as their support through the highs and lows of embarking on this nearly decade long adventure have kept me sane, aware, and most of all, hopeful. I've met so many amazing people in this community throughout this journey and my gratitude cannot be expressed for the piece of their selves that they left with me, no matter how short or long our time together.

"I cannot remember the book I've read any more than the meals I've eaten; even so, they've made me."

- Ralph Waldo Emerson

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CHAPTER I

THE ARCHITECTURE OF TEMPORAL PERCEPTION

In the field of sensation and perception, the question of *where..?* has dominated inquiry – *where* do different visual stimuli fall on the retina? *Where* are various environmental stimuli processed in the brain? *Where* do we perceive ourselves in space at any given moment? *Where* in the world can we find the answers to all these questions? But the *when* is just as fundamental and intrinsically linked to the *where*. Despite the impression of immediacy, perception is not instantaneous. Neural transmission takes time, and our perceptual experience of the world is constructed through the restrictive lens of our own biology. As a result, our perception shifts with each pulse of neural information, unfolding across time yet forever consigned to the past.

Time and space are not independent dimensions in motion perception; they are tightly coupled processes integral to the interaction between us and our dynamically changing environment. To navigate such an environment, we ourselves must be as dynamic, quickly and flexibly changing to its demands in a type of closed-loop system. Of course, we cannot completely surrender our sensory systems to the onslaught of available stimuli without being overwhelmed by the sheer amount of information, so a strategy must be employed. A strategy of rhythmic gating, fluctuating between states of excitation and inhibition, to filter irrelevant noise and amplify meaningful signals (Busch et al., 2009; Mathewson et al., 2011). This allows our sensory systems to selectively

sample from our environment, striking a balance between accumulation of relevant environmental information and the limits of our neural economy.

Discrete and Continuous Perception

The exact nature of the brain's gating mechanism has been a topic of much debate in perception science. The evolution of our conscious perception following stimulus presentation appears to be fluid and continuous when going about our day-to-day lives, but delay is an inherent consequence of the mechanism by which neuronal communication operates. Thus, the question is asked – is the flow of visual information processed in snapshots that align to our neuronal communication structure (rhythmic pulses of action potentials), or in a continuous stream that aligns more closely with our lived experience of the world?

Although simpler and more intuitive, the continuous model of perception cannot successfully explain a large body of psychophysical data. In contrast, the discrete perception hypothesis proposes that perception unfolds through "snapshots" of sensory input, akin to the frames of a film where information is integrated (VanRullen, 2016). A recent wave of literature has provided substantial support for this view, indicating that our fluid perceptual experience is constructed from a rhythmically sampled construction of reality (VanRullen & Koch, 2003; Milton et al., 2016; Schneider, 2018; Cravo et al., 2015; Chota & VanRullen, 2019; Ruzzoli et al., 2019; Samaha & Postle, 2015). However, even this expansive research on the subject has its shortcomings.

Psychophysicists have focused on bistable percept tasks to explore discrete perception and the factors contributing to differences in human perception even when stimuli remain constant. For example, Ronconi and colleagues (2017) found that in the

two-flash fusion phenomenon, when observers are shown two flashes in quick succession (one flash about 40ms after the other), they report seeing two flashes in about half of the trials while only one flash is reported in the other half. Since the parameters of the stimuli remain constant, then the driving force behind these varying percepts must be at the physiological level.

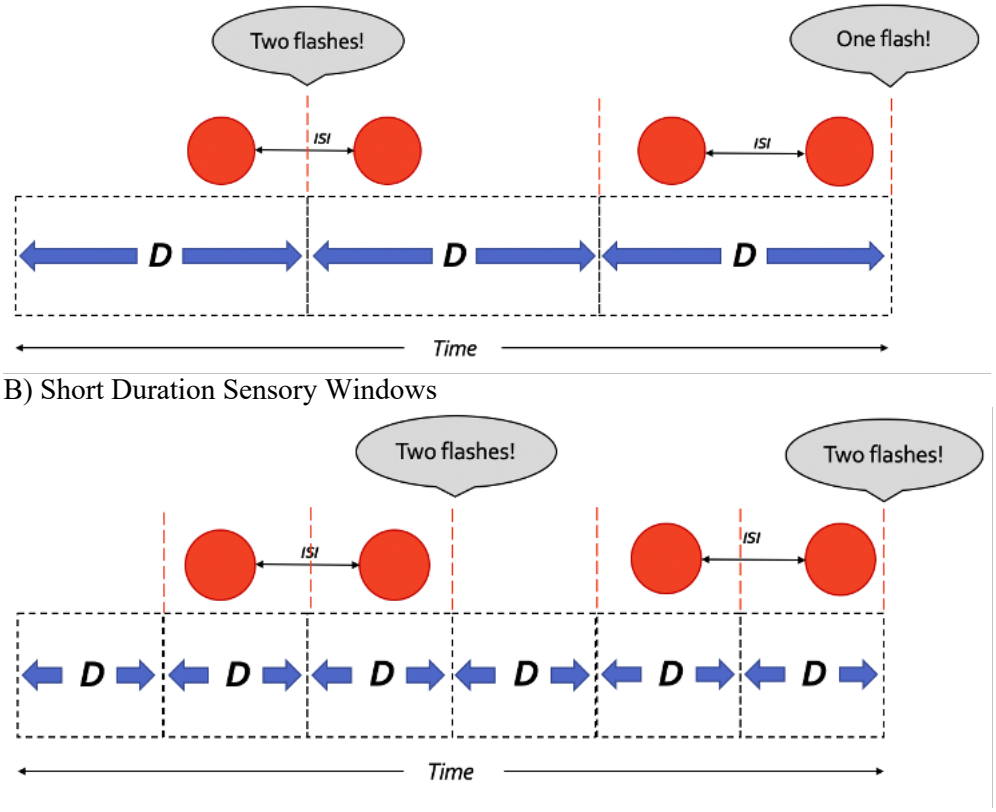


Fig. 1.1. (A, B) Theorized effect of sensory window duration (***D***) on perceptual report. (A) Upon presentation of two subsequent visual flashes with a constant inter-stimulus interval (ISI), the perceptual report (one flash vs. two flashes) will change dependent on timing of stimulus onset with respect to the sensory window. Flashes occurring in two separate sensory windows are perceived as two (distinct), while flashes occurring in the same sensory window are perceived as one (fused). (B) Decreasing the duration of sensory windows increases temporal resolution of the sampling system, allowing for flashes to more readily fall into discrete sensory windows. *Time axis not shown to scale

Discrete perception suggests that although the changes in the environment are continuous, our cognitive updating seems to be rhythmic, where the time interval

between stimuli influences their perceptual properties. This critical time interval between visual stimuli has been described as a sensory window of processing. Within this window of time, information is accumulated and averaged, resulting in a final fused percept; in contrast, stimuli falling between sensory windows will be perceived as sequential (Schneider, 2018). The report of two flashes fused into a single event is a result of the sampling mechanism failing to resolve two discrete events as the timing of sensory inputs is outside its temporal resolution (Ronconi et al., 2017). If two flashes happen to fall into two separate processing windows, two flashes are perceived; however, if they fall into the same window, the brain suppresses information until the end and averages across, resulting in the perception of only a single flash (Fig. 1.1). Specifically, the probability of perceiving one vs two flashes is linked to the temporal resolution of our visual sampling mechanism, where longer windows increase the chance that both flashes fall within the same window, resulting in a fused-flash percept (Ro, 2019; Wutz et al., 2016). This raises the question: what neural mechanism underlies the sampling rate of our visual system and can it be externally manipulated?

Visual Sampling Rate and Neural Oscillations

In the last decade or so, interest in identifying the neural mechanisms behind some of the phenomena identified by discrete perception research has increased, specifically the question of how identical stimuli can result in multiple distinct percepts in a variety of different tasks, such as stimulus detection (Ergenoglu et al., 2004; Busch et al., 2009; Mathewson et al., 2010), segregation/integration (Gulbinaite et al., 2017; Wutz et al., 2018), temporal order judgment tasks (Chota et al., 2020), and localization illusions (Hogendoorn et al., 2015; Chota et al., 2019). Such findings suggest that bistable

perception of identical stimulus arrays must lie in dynamic internal processes. One proposed mechanism involves the fluctuation between excitatory and inhibitory states of neuronal assemblies processing sensory input, which are posited to be coordinated by neurophysiological rhythms of the EEG (Haegens et al., 2011; Minami, 2017; Sokoliuk, 2016; Sauseng & Klimesch, 2008; Van Kerkoerle et al., 2014; Keitel, 2019; Taylor, 2005; VanRullen & McDonald, 2012; Lozano, 2019; Mercier, 2013; Hohaia, 2020; Shinomori, 2003; Mathewson, 2011; Lorincz, 2009).

Recently, research into the rhythmic characteristics of discrete perception has correlated characteristics of the alpha rhythm with perception and subsequent task performance. The frequency of the individual alpha rhythm upon stimulus onset has been shown to correlate with the maximum inter-stimulus time interval required for segregation versus integration, demonstrating a possible modulation of the duration of these sensory windows of processing and suggesting a speed of the sampling rate of our visual system (Cecere et al., 2015; Samaha & Postle, 2015; Ronconi et al., 2017; Ronconi et al., 2018; Romei et al., 2008).

The phase of alpha oscillations has been shown to modulate detection of perithreshold visual stimuli (Mathewson et al., 2009; Dugue et al., 2011; Busch et al., 2009; Ergenoglu et al., 2004) and impact evoked neural activity (Hanslmayr et al., 2013; Ro et al., 2003; Ro, 2019). These effects have led to the theory that alpha oscillations may be playing a bigger role in conscious perception than originally believed (VanRullen & Koch, 2003; Chakravarthi & VanRullen, 2012; Wutz et al., 2016; Palva et al., 2011); however, several important questions still remain.

The present series of experiments seeks to explore the interplay between the temporal and spatial factors in shaping perception, using a mislocalization effect known as the Fröhlich effect (FE) as a model system. The temporal dynamics involved in our perceptual systems could potentially give rise to spatial distortions in perceived location. Through these experiments, we aim to contribute to the literature on neural mechanisms underlying discrete perception and to clarify their role in shaping localization abilities.

Oscillatory Characteristics of Perception

Neural rhythms in different EEG frequency bands have been associated with distinct perceptual and cognitive processes. However, this paper focuses on the alpha frequency band of the EEG, thought to serve as the mechanism for perceptual gating through the suppression of irrelevant sensory information (Klimesch, 2012), its involvement in discrete perception, the mechanisms by which it operates, and the outputs of its modulation, particularly in the context of motion-induced mislocalization effects.

Frequency

Recently, more literature has been dedicated to understanding the link between the speed of neural oscillations and the temporal resolution of perception (Cecere, et al., 2015; Samaha & Postle, 2015). Oscillatory activity in neuronal populations, measurable through local field potentials (LFPs) and scalp EEG, has been theorized to correlate with the timing of processing within cortex (Haegens et al., 2011). Specifically, in occipital cortex, LFPs of neuronal populations tend to modulate within the alpha frequency, suggesting that alpha brain oscillations may be correlated with different aspects of our visual perception. Specifically, an individual's peak alpha frequency (IAF) has been proposed as a marker of temporal resolution, influencing how quickly (or how slowly)

the visual system can sample information by modulating the duration of sensory processing windows. If our perception occurs in discrete samples from the environment, then the frequency of alpha may be modulating the rate of sampling (VanRullen & Koch, 2003; Schneider, 2018; Samaha & Postle, 2015; Chota & VanRullen, 2019; VanRullen, 2016; Cravo et al., 2015; Chakravarthi & VanRullen, 2012). Even small differences in frequency within occipital alpha oscillations can either increase or decrease the rate at which our visual system accumulates and processes information.

Many recent studies have sought to investigate the depth of this correlation between alpha frequency and the timing of perception. For example, reaction time has been highly correlated with the frequency of the alpha rhythm (Surwillo, 1963). Despite this correlation, periodicities in reaction time are found to be even faster than 100ms (the average period of the alpha cycle), with underlying modulations at a 40 Hz rhythm in the gamma-band, perhaps suggesting an interaction between frequencies affecting motor decisions and behavior (VanRullen & Koch, 2003b).

Research suggests that the visual system integrates visual stimuli into single percepts when both fall within the same alpha cycle (8 – 12 Hz). Ronconi and colleagues (2017) posit that the exact frequency of the observer's alpha rhythm may be influencing the duration of these sensory windows and our ability to segregate stimuli, specifically in the two-flash fusion effect. As the frequency of occipital alpha oscillations increases, the interval between flashes required to produce a fused percept decreases. As a result, these individuals are more likely to be able to distinguish two stimuli in their perception (Cecere et al., 2015; Samaha & Postle, 2015). This finding supports the idea that the alpha frequency may be rhythmically modulating perceptual processing.

Ro (2019) conducted a metacontrast masking experiment using transcranial magnetic stimulation (TMS) to examine the relationship between an individual's IAF and the temporal dynamics of processing in visual cortex. Participants had to report the detection of a circular target followed by a metacontrast mask at varying latencies, followed by a TMS pulse on occipital areas near early visual cortex at varying latencies. A strong negative correlation was found between peak IAF and peak TMS suppression latency, suggesting that higher alpha oscillation frequencies correspond to shorter time intervals between processing windows and an earlier peak in TMS-induced suppression. These results suggest that not only is the alpha frequency correlated with the processing speed of the visual system, but also that it may be following a type of rhythmic oscillatory pattern with moments primed for processing, theorized to correlate with the phase of these oscillations.

Cecere and colleagues (2015) used transcranial alternating current stimulation (tACS) at different frequencies within the alpha band in order to observe the relationship between the IAF and processing speeds of sensory windows, and found that when two beeps are presented in the same 100ms window as a single visual flash, a second flash is erroneously perceived in a "sound-induced double-flash illusion". This finding provides additional support that the alpha frequency may be responsible for gating stimuli to perceptual awareness and may play a role in cross-modal integration processing as well. One explanation of this effect suggests that the presentation of the auditory beep causes a phase-reset of alpha oscillations in visual cortex, resulting in the interruption of the sensory window and resulting in a phase re-alignment of ongoing alpha activity in visual cortical neurons (Lakatos, et al., 2008; Diederich et al., 2012). This illusory perceived

flash may be a result of the sudden change in excitability induced by the auditory stimuli, increasing the likelihood that sensory neurons once again reach the excitability threshold necessary for the flash to reach perceptual awareness (Romei, et al., 2012; Mercier, et al., 2013). Another account proposes that when two stimuli fall within a shared integration window, they are fused into a single percept that contains properties or stimulus features of both (Schneider, 2018). Alternatively, one stimulus may coincide with a phase that is unfavorable to cognitive processing and fail to reach awareness, while the second flash falls in time with a favorable processing state and continues on to be processed and perceived (Fries, 2005; 2015).

Entrainment of Alpha Frequency

Some findings have demonstrated a distinction between endogenous oscillatory activity and evoked activity by a visual stimulus, opening the possibility for manipulation of neural activity through entrainment of oscillations with a rhythmic sensory stimulus (Gulbinaite et al., 2017; Ronconi et al., 2018; Sokoliuk et al., 2016; Calderone et al., 2014; Chota et al., 2019; Zauner et al., 2012). Previous research has found that visual stimuli can influence cortical excitability and create stimulus-evoked responses in ongoing alpha oscillations (Busch et al., 2009; Mathewson et al., 2009; Fiebelkorn et al., 2013), making it possible to see carryover effects from a sensory stimulus in the form of reverberations in oscillatory cortical excitability.

TMS and sensory entrainment have been used by a variety of studies in the literature to examine the effects of alpha frequency and phase on visual perception (Mathewson et al., 2012; Zauner et al., 2012; Chota et al., 2019), somatosensation (Haegens, et al., 2014; Ai & Ro, 2014), and auditory perception (Fiebelkorn et al., 2011;

Calderone et al., 2014; Henry et al., 2014; Hickok et al., 2015). While TMS is a more direct way of stimulating the excitability of neuronal assemblies to a desired frequency or phase, relevant neuronal groups also respond to rhythmic sensory stimuli with oscillating fluctuations in excitability levels. By presenting a salient rhythmic sensory stimulus, relevant neuronal groups fire in response to that stimulus, causing the local field potentials within that area to fluctuate at that rhythm as well (Crick, 1994; Haegens et al., 2011; Mathewson et al., 2012).

Given the support for the correlation between the alpha frequency and the temporal resolution of our visual perception, recent literature has attempted to use rhythmic neural entrainment as a way to manipulate the durations of sensory windows and thus our temporal resolution (Ronconi et al., 2018). If the alpha frequency acts as a mechanism for segmenting sensory information into discrete frames, then altering this frequency should allow us to shift the boundaries of these sensory windows. Wutz and colleagues (2016) found a correlation between the inter-stimulus interval between two displays and performance on a segregation versus integration task. This correlation is believed to occur due to the position of each display within the observer's sensory window – either the ISI is long and the displays are segregated into two distinct sensory windows, or the ISI is short enough for both displays to be combined into the duration of one sensory window.

Ronconi and colleagues (2018) sought to expand on the experiment by Wutz and colleagues (2016) by taking this next step and manipulating the duration of the sensory window itself instead of manipulating the ISI of the stimulus. If the effect documented by Wutz and colleagues was indeed due to the timing of stimuli within the observer's

sensory window, modulating the duration of the window should also show a significant difference in task performance (Fig. 1.2A, B). Rhythmic auditory stimuli were used to entrain alpha oscillations to a frequency 2 Hz above or below each participant's inherent alpha frequency. As a result, performance on both tasks was modulated at the entrained alpha frequency, providing evidence that faster frequencies are associated with shorter sensory windows (resulting in higher likelihood that the two arrays fall into temporally distinct sensory windows, enhancing segregation and impeding integration), while slower frequencies are associated with longer sensory windows (resulting in a higher likelihood that the two arrays fall into the same sensory window, enhancing integration and impeding segregation). Based on these results, entrainment of alpha oscillations to higher or slower frequencies can have an impact on the temporal resolution of our visual system and our subsequent perception.

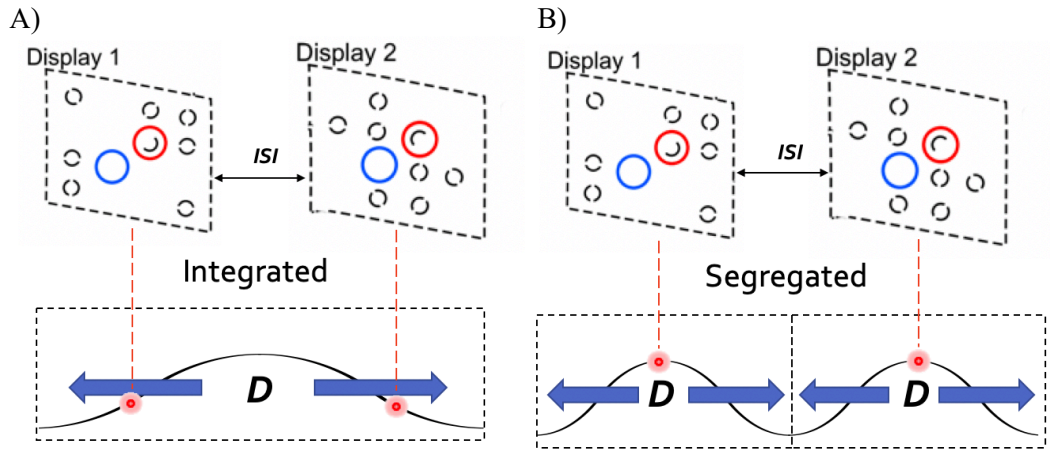


Fig. 1.2 (A, B) Theorized model for the observed dissociation in performance levels between segregation and integration tasks seen in Ronconi et al., 2018. Despite a constant ISI, performance in a segregation or integration task changes dependent on entrainment to a fast alpha rhythm (high temporal resolution) or to a slow alpha rhythm (low temporal resolution). (A) Slow alpha frequency and low temporal resolution. Displays perceived within the duration of a single sensory window are integrated and the integration task becomes easier. (B) Fast alpha frequency and high temporal resolution. Displays perceived within two distinct time windows are processed separately and more easily segregated from one another. Performance on the segregation task increases.

Phase

The phase of ongoing alpha oscillations has been linked to modulations in the voltage of local field potentials of neuronal assemblies, oscillating between states of excitation and inhibition modulating neuronal spiking (Haegens et al., 2011). Haegens and colleagues (2011) recorded from both local field potentials and neuronal spiking in monkey sensorimotor cortex during a somatosensory discrimination task. They found a significant correlation between the alpha-frequency fluctuations in the excitability of local field potentials and neuronal spiking, where firing rates peaked during the downward phase of the alpha cycle and dropped during the upward phase. This modulation has been hypothesized to explain the differing percepts that can arise from identical sensory inputs (Mathewson et al., 2010; Lorincz et al., 2009; Sauseng & Klimesch, 2008; Milton et al., 2016; Jensen & Mazaheri, 2010; Busch et al., 2009; VanRullen, 2016; Ruzzoli et al., 2019).

Building on this framework, Mathewson and colleagues (2011) proposed that the phase of the alpha rhythm could systematically govern whether a stimulus reaches awareness through cyclical modulation of the excitability of task-relevant neuronal assemblies. According to their "pulsed inhibition" hypothesis, alpha oscillations exert periodic inhibitory influences on cortical processing such that at phases of higher excitation, action potentials are more likely to occur; while at inhibitory phases, activity is suppressed. This state of inhibition has been found to impact processing and subsequent perception, where the timing of incoming stimuli relative to the alpha rhythm modulates perception. These findings have been explored further in tasks involving stimulus detection (Busch et al., 2009; Ergenoglu et al., 2004), temporal order judgment

(Chota et al., 2020; Iemi & Busch, 2018; Diederich & Colonius, 2015), and segregation/integration (Ronconi et al., 2018; Wutz et al., 2016).

Busch and colleagues (2009) explored the role of oscillatory phase on perception by using a stimulus detection experiment in non-human primates using a peri-threshold visual stimulus. Despite identical features and saliency, only half of the stimuli were perceived. They found that the instantaneous phase of alpha at stimulus onset significantly influenced whether the stimulus reached perceptual awareness. They measured the concentration of phase angles of LFPs during the task and found that hit trials and missed trials demonstrated significantly different phase angles.

According to the pulsed inhibition hypothesis, this difference arises because hits tend to occur when stimuli fall during favorable phases, whereas misses fall in unfavorable phases. When LFPs of task-relevant cortical neurons are in a phase of the neural oscillation that is unfavorable to processing, then processing will be suppressed and the target has a higher likelihood to be rendered invisible. This result suggests that the neural state *at* stimulus onset plays a critical role in processing and detection probability.

VanRullen and colleagues have described this effect of phase on perception using the pulsed inhibition framework (VanRullen, 2016; Mathewson et al., 2009). At an unfavorable phase associated with greater inhibition, a weak peri-threshold stimulus is not enough to breach the perceptual threshold (Fig. 1.3A). However, the same sensory input can reach perceptual awareness if the pre-stimulus phase-locking angle shifts to one of higher excitability.

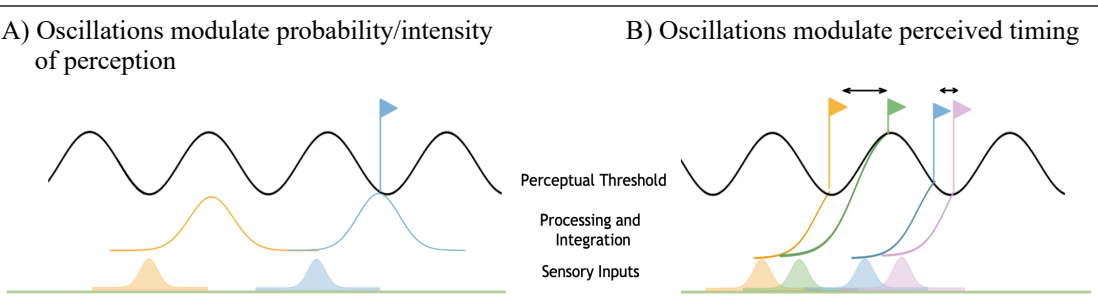


Fig. 1.3. (A, B) Theorized illustration for the alpha rhythm's effect on perceptual threshold. Sensory inputs are processed across receptive neuronal assemblies and the summed output is sent to a higher-level receiving neuronal group. (A) The summed activity of a weak sensory input is not enough to reach the perceptual threshold at an unfavorable phase (yellow) but is sufficient at a favorable phase (blue). At troughs of the alpha rhythm, inhibition is thought to be released and information allowed to flow, decreasing the required strength of the sensory input to reach perceptual threshold. (B) Differences in alpha phase at stimulus onset can also affect the perceived timing of the stimuli. Two temporally adjacent stimuli may seem further apart in perceived time due to the time it takes to reach the oscillating perceptual threshold (yellow/green) or closer together in time due to coinciding with the down-going phase (blue/purple) (Adapted from VanRullen, 2016).

Performance on temporal order judgment (TOJ) tasks may also reflect the influence of alpha phase as a mechanism for discrete perception (Fig. 1.3B). If the visual system employs a rhythmic discrete sampling mechanism that suppresses information until a favorable phase of the oscillation, then temporal order information within these periods of processing will be lost. In this view, differences in oscillatory phase at stimulus onset affect how quickly stimuli reach perceptual threshold. Chota and colleagues (2020) tested this hypothesis by entraining occipital alpha oscillations using TMS. Participants were administered five TMS entrainment pulses at 10 Hz over occipital cortex, followed by the rapid presentation of two differently oriented Gabor patches and a subsequent mask. Participants were asked to report the orientation of the Gabor patch that they perceived as occurring last in time.

To create a time series in which Gabor patches could fall within same or different perceptual windows, the TOJ task was probed at nine different time points, and accuracy

fluctuated based on the ISI (Schneider, 2018). Their results showed that the visual system may be using occipital alpha oscillations as a mechanism to discretize time windows of information within which it discards temporal order information in order to minimize the complexity of visual input.

Several other studies have also demonstrated similar effects of phase on threshold-level stimulus detection and temporal-order judgments (Roberts et al., 2014; Baumgarten et al., 2015; Samaha & Postle, 2015), further supporting the idea that perception operates through alternating periods of high and low excitability that gate the flow of sensory information (Dugue et al., 2011; VanRullen, 2016).

Amplitude/Power

The literature on the role of the amplitude of neural oscillations in perception has been relatively conclusive in favor of the pulsed inhibition hypothesis suggesting that the inhibition of neuronal firing is modulated by the amplitude of alpha fluctuations in membrane potential (Haegens, et al., 2011; Ergenoglu et al., 2004; Gulbinaite et al., 2017; Mathewson et al., 2009, 2011). Physiologically, greater inhibition (reflected in increased amplitude within the alpha rhythm) makes it more difficult for neurons to reach sensory threshold and fire action potentials, whereas conversely, decreases in amplitude during processing release this inhibition and facilitate firing (VanRullen, et al., 2006; Haegens, et al., 2011; Mathewson et al., 2009).

Power and amplitude of these neural oscillations are nearly synonymous, where amplitude refers to the increase in voltage potential of a particular oscillation, and power refers to the voltage across the frequency domain of oscillations. Increases in amplitude lead to increases in power (Basar et al., 1998). However, because power is calculated as a

sum of signal energy in the frequency domain, it can also increase when the voltage of oscillations fluctuate at the same frequency (Ergenoglu et al., 2004).

Ergenoglu and colleagues (2004) found that a participant's ability to detect a peri-threshold visual flash was significantly correlated with alpha amplitude upon stimulus onset. Specifically, perception of the visual stimulus depended on low alpha power at stimulus onset. This resulted in a significant subsequent response in ERP amplitudes, whereas the stimulus was not perceived during periods of high alpha power/amplitude.

This inhibitory role of alpha power has also been observed in the spatial domain. Kelly and colleagues (2006) asked participants to attend to stimuli to either the left or right visual field while ignoring the opposite side. Alpha power increased in the hemisphere contralateral to the ignored stimulus (synonymous with an increase in cortical inhibition) and decreased contralateral to the attended stimulus, corroborating alpha's inhibitory role on cortical processing.

Beyond stimulus detection tasks, a relation between alpha power and perception has also been seen at higher order visual areas as well, such as area MT. Significant differences in the power of oscillations in the alpha frequency were seen in an experiment utilizing the continuous wagon wheel (CWW) illusion and its illusory reversal in direction (Vanrullen et al.,, 2006). Differences in power between real motion and illusory motion in the CWW illusion were observed to be greatest when the wheel rotated at a 13 Hz rate, suggesting that alpha-band activity contributes to motion perception and may even operate at this frequency.

Localizing the Effect of Alpha Oscillations

VanRullen and Macdonald (2012) examined the response properties of visual cortex by correlating visual stimulus luminance levels and the corresponding EEG. When showing an observer a stimulus that oscillated in luminance levels at a 10 Hz rate, their EEG activity mirrored this rhythm, an effect they called a "perceptual echo". This phenomenon demonstrates how visual events continue to influence neural activity even after the stimulus has ended. Topographical mapping localized this 10 Hz response to mainly occipital electrodes, further supporting the correlation between characteristics of the alpha rhythm and visual perception. This is demonstrative of alpha's correlation to iconic memory and the ability to store sensory representations, suggesting that alpha activity supports the temporary storage of sensory information for extended periods of time up to 1 second. However, is alpha directly responsible for the storage of sensory representations, or does it instead facilitate *access* to stored information? Studies have shown that other frequencies, such as gamma, have similar "perceptual echo" properties, reverberating stimulus properties in their own EEG responses (Van Kerkoerle et al., 2014; Landau et al., 2015; Fries, 2015).

Studies have reported a negative correlation between individual alpha frequency and the P2 latency, a component associated with feedback processing (Klimesch, 2011; Thut et al., 2003). These results suggest that alpha may not be modulating the speed of processing at a sensory level, but rather a level of conscious access. This then begs the question: is the modulation seen by changes in the alpha rhythm of the EEG in recent literature occurring at a sensory level or at a level of higher-order access? VanRullen suggests that this modulation may be occurring at a level of the perceptual threshold,

thereby changing the likelihood of perception or perceived timing of a stimulus (Fig. 1.3). However, this effect could also be seen if alpha was modulating the threshold at a very early level of sensation. It then becomes unclear at what level of our cognitive hierarchy is this pulsed inhibition of alpha having an effect; it could be a modulation of a sensory threshold, our perceptual threshold, or a combination of both (Fig. 1.5).

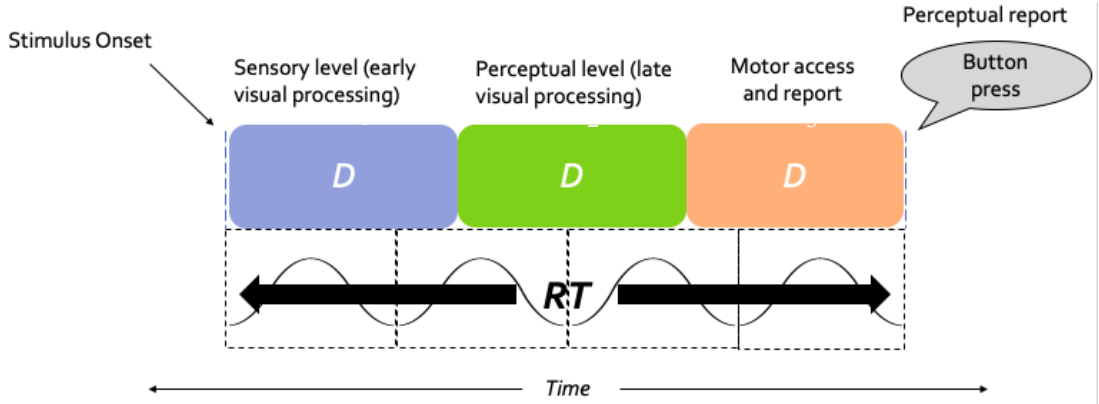


Fig. 1.4. Model depiction of the perceptual process involved in a stimulus detection task. The duration of afferent delays and transmission times of early level sensory information (D_1); the duration of higher-order processing, perceptual awareness of the stimulus, and decision-making areas to initiate a response (D_2); and the duration of transmission times from decision-making areas to motor areas and the efferent delays from motor regions to neuromuscular areas fulfilling the button press (D_3). If faster alpha frequencies shorten the overall reaction time (Surwillo, 1963), any one of D_1, D_2, or D_3 could be shortened and result in the shortening of the overall reaction time duration.

So, is the alpha rhythm an inhibitory mechanism modulating the sensitivity threshold of sensory areas to selectively propagate relevant information, or is it a more complex mechanism that exerts its effect on perception at a higher level? The literature remains unclear on where alpha's role may truly lie.

Take the example from VanRullen (2016) with the theory that neural oscillations modulate the perceptual threshold in a way where the timing of stimulus presentation relative to the observer's perceptual rhythm could influence probability of perception as well as the perceived timing between two stimuli (Fig. 1.3). In this example, an

assumption was made that there is not any modulation occurring at the sensory level – influencing the sensory threshold of incoming information.

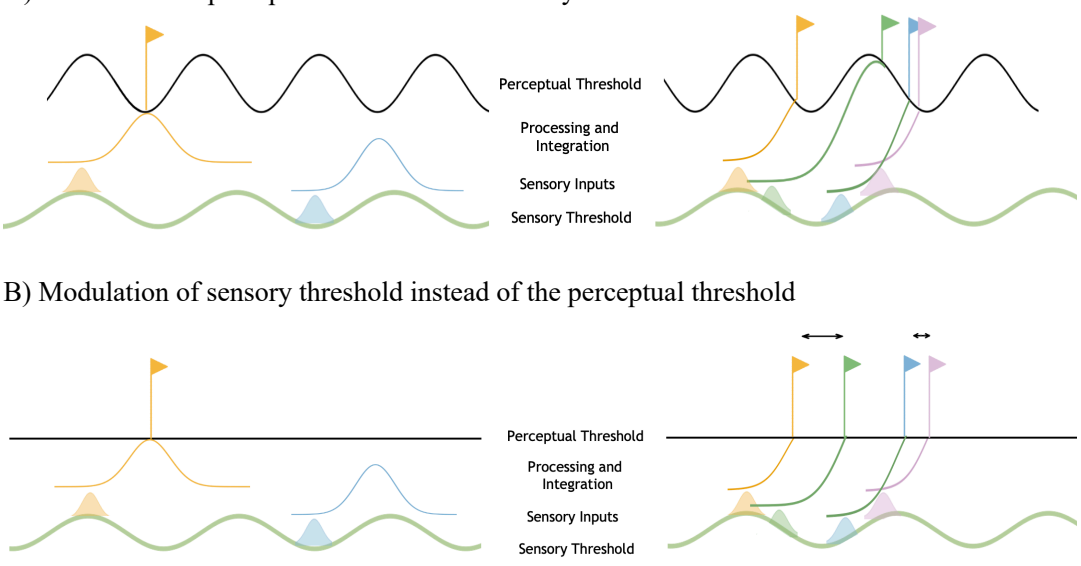


Fig. 1.5. (A, B) Extrapolation of theorized illustration for the alpha rhythm's effect on perception from VanRullen (2016). (A) The combination of a favorable phase in both the oscillation of the perceptual threshold and the sensory threshold allow for summed activity of a sensory input to reach the perceptual threshold (left) but is insufficient at unfavorable phases. The timing of two stimuli with the upward phase of the perceptual threshold and the downward phase of the sensory threshold result in a larger perceived time difference than the alternative (right). (B) Differences in the sensory threshold alone could also result in the modulation in perceptual probability and perceived timing proposed by VanRullen (Adapted from VanRullen, 2016).

The combination of modulations in the perceptual threshold as well as the sensory threshold could magnify the observations proposed by VanRullen. Even modulations at the sensory threshold alone could theoretically explain these differences in perceived timing and probability of perception (Fig. 1.5). However, if alpha is responsible for perceptual gating and maintaining an inhibitory effect on perception – allowing information to flow at periods of low power and increasing threshold at periods of high power – then can alpha have a similar effect at lower-level sensory thresholds? Or is it

the interaction between neural frequencies that shapes the timing and probability of our perception?

Palva and Palva (2007) recognized this discrepancy in the literature and proposed a theory that could reconcile this question: the Active Processing hypothesis. They note that the observations in the literature on alpha power can be interpreted in several ways: as active inhibition of task-irrelevant areas; active processing in task-*relevant* networks; or both. They essentially argue that the role of alpha oscillations in our perception may be more complex than just a pulsed inhibitor and that more research is needed into exploring inter-areal communication in the alpha-band and its role in regulating that communication.

The Active Processing hypothesis goes even further to say that the synchronization of alpha oscillations between regions in the perceptual hierarchies, particularly along the fronto-parietal and occipital regions, may be the interface between frontal and sensory networks (Palva & Palva, 2011; Bonnefond et al., 2017). This suggests that not only are the oscillatory properties of alpha critical to our perception, but how they interact across brain regions may prove to be equally valuable.

Mislocalization Effects and Discrete Perception

The Fröhlich effect (FE) may demonstrate an inherent constraint of the visual system: neural processing lags our perception of the world. When a moving object suddenly appears and darts across an observer's field of vision, they report its perceived starting point to be nudged forward in the direction of motion (Fröhlich, 1925). The question that arises from this observation is – where is this nudge introduced? Is it built in upon early sensory encoding and creation of the representation of the stimulus and its

trajectory? Does it arise later in a higher-order process such as when perception is referred back to for processing of the location judgment?

One category of accounts places the mechanism that causes the bias early in sensation. The speed of temporal sampling has been one suggested theory for the mechanism behind the FE. Activity in the alpha range of the EEG has been correlated with the speed of sampling in segregation/integration tasks (Samaha & Postle, 2015; Wutz et al., 2016), and its phase has been correlated with moment-to-moment excitability in detection tasks (Busch et al., 2009; Mathewson et al., 2010). If the speed of the alpha frequency can be seen to correlate with reaction time, does this also extend to the effect seen in the FE? If observers are able to register the presence of a target more quickly as the speed of alpha frequency increases, it would make sense that they would also be able to perceive the moving target in the FE more quickly and thus earlier along its trajectory. As VanRullen (2016) discusses, modulation of the perceptual threshold can lead to differences in perceived timing determined by the phase of oscillations at the time of the arrival of the sensory signal (Fig. 1.3).

Discrete perception theories can also be used as evidence for the FE being modulated at the early sensory level. If inputs are averaged within perceptual "snapshots", or windows of processing, slower sampling or longer duration windows would pull the apparent onset of the moving target toward the motion's weighted mean (Krekelberg & Lappe, 1999). The "harder" version of this theory supports this outcome as well, in that stimuli landing at unfavorable periods of processing would be delayed until the next window and therefore first detected later in their trajectory (Schneider, 2018).

Attentional lag has also been cited as a potential mechanism for the FE, suggesting that the latency in the shift of attention toward a suddenly appearing stimulus is the cause of the mislocalization. According to a study by Müsseler and Aschersleben (1998), the moving target used in the FE initiates an attentional shift. The object continues along its trajectory during this shift, and the target cannot be fully perceived until that action is complete and consciously accessible. Previous studies have also found that pre-cuing attention to the target's starting location can attenuate the FE (Müsseler & Aschersleben, 1998; Adamian & Cavanagh, 2017). Attentional sampling has been found to be correlated with the alpha rhythm (Landau & Fries, 2012; Calderone et al., 2014; Peylo et al., 2021), so if the FE does emerge from this attention-dependent process, this lends more support toward the hypothesis that the alpha rhythm should modulate the magnitude of the illusion.

Another set of theories attribute the bias to later stages of perception, proposing that motion signals engage higher-order processes to extrapolate object position and compensate for neural delays (Nijhawan, 1994; Baldo & Klein, 1995). Even motion that appears adjacent to a static object has been seen to influence its perceived position (Maus et al., 2013). Motion extrapolation has been supported heavily by the literature but mainly in the context of the flash-lag illusion (Eagleman & Sejnowski, 2007; Hogendoorn, 2020).

Taken together, these ideas suggest that the Fröhlich shift could occur within a number of different stages of processing. If properties of the alpha rhythm correlate with the FE, then we may be able to utilize these two phenomena in conjunction in order to uncover more about their respective mechanisms. It seems that there is a common

question between the Frohlich effect and the alpha rhythm's effect on perception: at what point in the perceptual hierarchy do these mechanisms play a role? Are they after-effects stemming from sensory level modulations that ripple up to higher order perception or do they originate in a top-down fashion such as post-dictive motion extrapolation?

The goal of the following series of experiments is to investigate whether alpha oscillations, which have been widely implicated in the rhythmic structure of perception, contribute to the FE, a mislocalization effect tied to the perception of motion onset. The precise level of the perceptual hierarchy at which either of these phenomenon operate is ambiguous. By analyzing the interaction between these two, we aim to determine whether alpha's modulation on perceptual timing also shapes the mechanisms underlying spatial mislocalization. If a relationship is found, it could offer critical insight for future studies for mapping where discrete sampling and motion perception intermingle and arise in the perceptual hierarchy.

Concluding Thoughts

The literature seems to be unclear on where the alpha rhythm's modulation occurs within the perceptual hierarchy. To better understand this, take a simple reaction time task in which an observer presses a button upon registering the presence of a visual stimulus. As observed by Surwillo and colleagues (1963), the frequency of the alpha rhythm is correlated with the speed of reaction times where faster oscillations lead to faster responses. This reaction time would be made up of several different parts, each with their own duration of processing time (Fig. 1.4): first, afferent delays and transmission times of early level sensory information; next, the time taken for higher-order processing, perceptual awareness of the stimulus, and decision-making areas to

initiate a response; then, transmission times from decision-making areas to motor areas; and finally, the efferent delays from motor regions to neuromuscular areas fulfilling the button press. Although the relationship between alpha oscillations and reaction time has been established, there is no clear indication *where* alpha's modulation could be occurring. It could be early in the reaction time in early sensory areas, facilitating the transmission of information up the cognitive hierarchies – or even at later periods modulating efferent motor delays. Shortening of any of these delays would result in the observation of an overall shortening of the reaction time (Fig. 1.4).

Equally ambiguous is where in the cognitive hierarchy mislocalization effects emerge. Do these effects stem from sensory level or higher level perceptual modulations? Can alpha modulations affect mislocalization phenomena in the same way they affect detection and temporal resolution tasks, or does motion perception operate on a level perpendicular to that of alpha modulation? These are the questions that we seek to answer with the following series of experiments.

- Chapter End -

CHAPTER II

THE ALPHA-BAND OF THE EEG AND THE PERCEIVED LOCATION OF MOVING TARGETS

Discrete perception theory suggests that our view of the world is constructed of easily consumable snapshots of information rather than a constant flood of raw sensory input. Several theories propose neural rhythms as the organizing mechanism for this parsing of information – conducting information like a traffic director through alternating periods of heightened and lowered sensitivity. These oscillations allow the brain to selectively filter information, activating areas involved in the task at hand while temporarily quieting those that aren't (Fries, 2005).

"Endogenous" rhythms are the brain's naturally occurring activity unique to awake, healthy individuals and have been tied to differences in sensory processing speed and temporal resolution (Klimesch, 1999; Samaha & Postle, 2015). The alpha rhythm specifically has been implicated in suppression as well as visual perception (VanRullen, 2016). The alpha phase has been correlated with the brain's ability to suppress information, leading to the theory that alpha may work as a type of gating mechanism to our perceptual awareness (Mathewson et al., 2011; Ronconi, et al., 2018). The alpha rhythm's frequency and phase at stimulus onset have been found to predict performance in detection tasks (Ergenoglu et al., 2004; Mathewson et al., 2010; Spaak et al., 2014) as well as segregation/integration tasks (Wutz et al., 2016; Ronconi et al., 2018).

A slower alpha represents longer integration windows, and therefore more time to merge information across moments but less time to keep them distinct. Faster alpha rhythms represent the opposite, tightening the timing of the perceptual window and making two events easier to isolate in time (Grandy, et al., 2013; Haegens, et al., 2011). The alpha frequency seems to be setting the pace of the visual system's sampling rate, shaping how information is gathered and pieced together over time, where the phase affects the sensitivity of the system.

While much of the work on alpha oscillations has been done in the context of static or briefly presented arrays, the same principles should extend to motion perception. In the case of a moving target, if the processing window increases in duration, the target travels further along its path before being recognized and perceived. Shortening the window should allow for capturing the starting location more quickly with less accumulated motion (Fig. 2.1). This dynamic makes alpha a likely candidate for influencing motion mislocalization effects, shifting the perceived starting position of a moving target in the direction of motion.

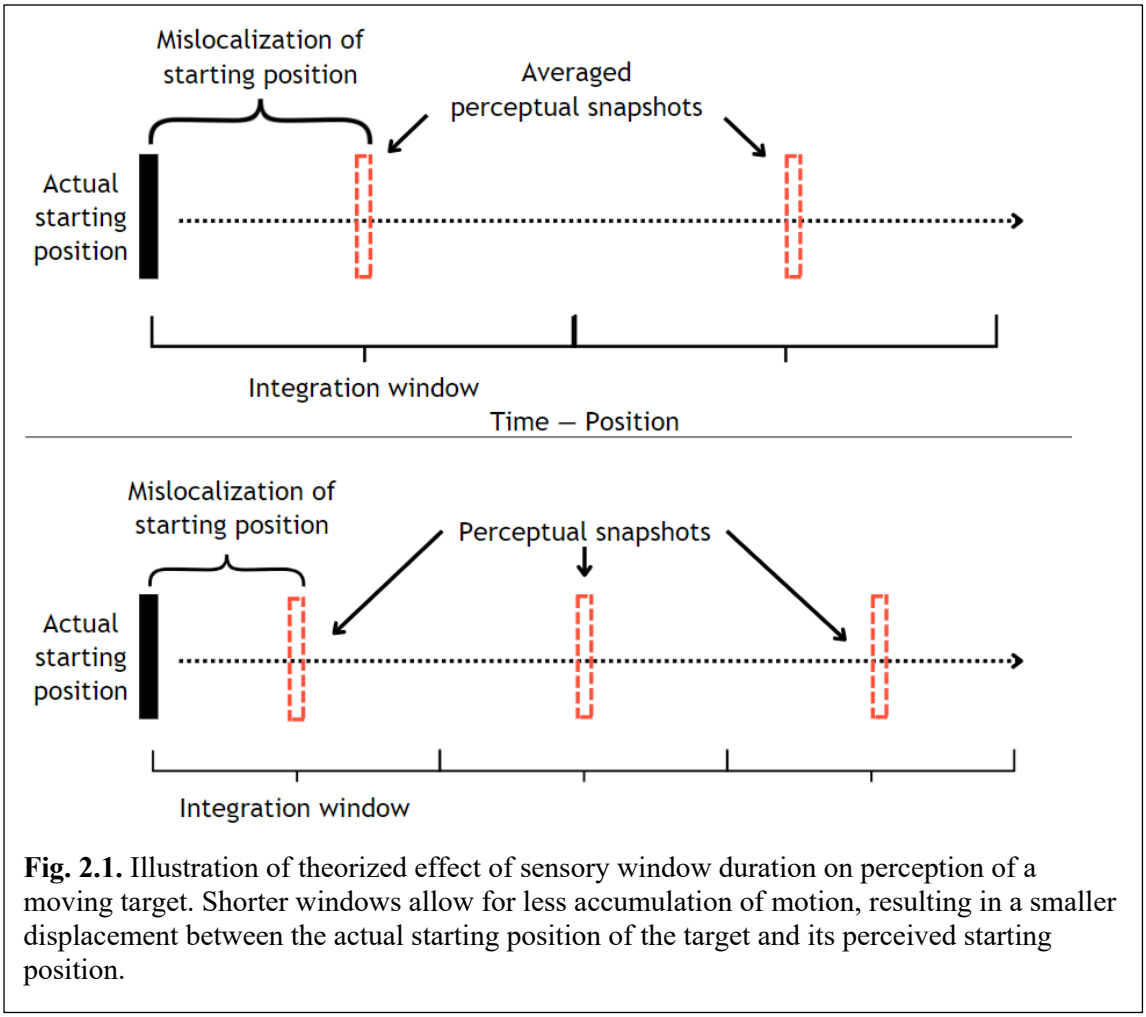


Fig. 2.1. Illustration of theorized effect of sensory window duration on perception of a moving target. Shorter windows allow for less accumulation of motion, resulting in a smaller displacement between the actual starting position of the target and its perceived starting position.

The present study examines the Fröhlich effect (FE), a motion-onset localization illusion in which the perceived starting position of a moving stimulus is shifted in the direction of motion (Fröhlich, 1925). This displacement is thought to stem from a timing mismatch between when the visual system registers the stimulus and the motion that continues during that delay.

Several theories have tried to explain this phenomenon, such as attentional lag (Müsseler and Aschersleben, 1998; Adamian & Cavanagh, 2017), discrete perceptual sampling (Schneider, 2018), and motion extrapolation (Hogendoorn, 2020). If alpha frequency truly sets the pace of visual sampling or the shift of attention, then variations in

alpha should predict the magnitude of the FE. By entraining alpha rhythms and measuring changes in perceived starting position, we can test whether the speed of perception shapes mislocalization.

Alpha's potential role in mislocalization is more than theoretical though, it has been shown that oscillatory phase at stimulus onset can predict the magnitude of the Flash-lag effect (FLE), where a moving object is perceived ahead of a static one (VanRullen, 2016; Chota & VanRullen, 2019) If stimulus presentation happens to occur at an unfavorable phase of processing, its registration may be delayed until a more favorable phase of processing, by which point the moving object has advanced further along its path resulting in an erroneous perception of starting location. Chota and VanRullen (2019) found that entraining neural oscillations at the alpha frequency could modulate the FLE's magnitude, offering evidence that oscillatory timing can causally influence spatial judgments. This same type of modulation may apply to the FE where a suppression of sensory input would result in perceived onset being shifted in the direction of motion.

While alpha has been implicated in mislocalization effects such as the Flash-lag, few studies have tested this directly in the FE. In a study by Morrow and Samaha (2021), they compared modulations in perception in both the FE and the FLE; mislocalization illusions that would, in theory, share the same oscillatory mechanism. Surprisingly, they found no correlation between the magnitude of these illusions, even though they share nearly identical stimulus arrays. This dissociation raises the possibility that the FE and the FLE may be operating with distinct stages of processing. Whether the FE is governed by oscillatory dynamics at all still remains unclear. While it is possible that the use of one

stimulus in the FE versus two in the FLE could explain this dissociation, we also cannot rule out the possibility that they are operating off of separate perceptual mechanisms.

This experiment tests whether the FE can be modulated by neural entrainment of participants' alpha oscillations to specific frequencies using a rhythmic auditory entrainment stimulus to align neural oscillations, then densely sampling localization judgments. If alpha rhythms structure the timing of perception involved in motion onset, changes in entrainment frequency could systematically modulate illusion magnitude. Specifically, if the phase of the entrained alpha oscillation shapes perceptual accessibility to location information, then illusion magnitude should fluctuate rhythmically across a time series of trials producing an observable modulation in the perceived starting location. At unfavorable phases, stimulus processing may be delayed until a more excitable phase, allowing the target more time to travel, thus increasing the apparent spatial shift. Conversely, if no frequency-dependent modulations are observed, it would suggest that the FE may be operating on a level separate from alpha's effect or that perceptual gating does not underlie the FE.

External, rhythmic sensory stimuli, such as a flashing stimulus or a series of auditory clicks, have been found to produce systematic fluctuations in cortical excitability at the frequency of the stimulus, aligning or "entraining" neural rhythms (Mathewson, et al., 2012; Gulbinaite, et al., 2017; Ronconi, et al., 2018). By using entrainment to modulate alpha frequency and phase, we can reduce the variability between individuals and boost the strength of our signal. Researchers have used sensory entrainment to explore how both frequency and phase shape visual perception (Mathewson et al., 2012; Chota & VanRullen, 2019), somatosensation (Haegens, et al., 2011; Ai & Ro, 2014), and

auditory perception (Fiebelkorn et al., 2011; Calderone et al., 2014; Henry et al., 2014; Hickok et al., 2015).

Rhythmic entrainment has been shown to influence perception beyond detection and can more specifically modulate localization illusions (Chota & VanRullen, 2019). When conducting a fast-Fourier transform on behavioral time series data using entrainment, the entrainment frequency can be detected within the behavioral data itself, representing a connection between the modulation of neural rhythms and behavioral outcomes (Spaak, et al., 2014; Fiebelkorn, et al., 2013). Normalizing alpha frequency across participants to a fixed entrainment rate and phase allows control over individual variability and enables a direct test of whether the entrained rhythm is detectable in the behavioral time series of localization responses. The presence of an oscillatory component at the entrainment frequency in this data would supply behavioral evidence for a role of alpha in the FE.

We entrained participants' neural oscillations to either an 8.5 Hz or 11.5 Hz auditory rhythm before presenting a suddenly appearing moving target and measuring the magnitude of the FE on each trial. We then applied an FFT to the behavioral time series to test whether the entrained rhythms were reflected in the perceptual reports. We expected two things to be reflected in our data: (1) If alpha frequency plays a causal role in shaping the temporal snapshots that underlie the FE, we expected to see a significantly higher leftward response rate (and therefore smaller illusion magnitude) in the 11.5 Hz (fast) entrainment condition compared to the 8.5 Hz (slow) condition; and (2) if alpha phase plays a role in modulating the sensitivity threshold and therefore the perceived

onset of the stimulus, we expected to see a detectable oscillatory signature at the entrained frequency in the perceptual reports.

Methods and Procedures

Participants

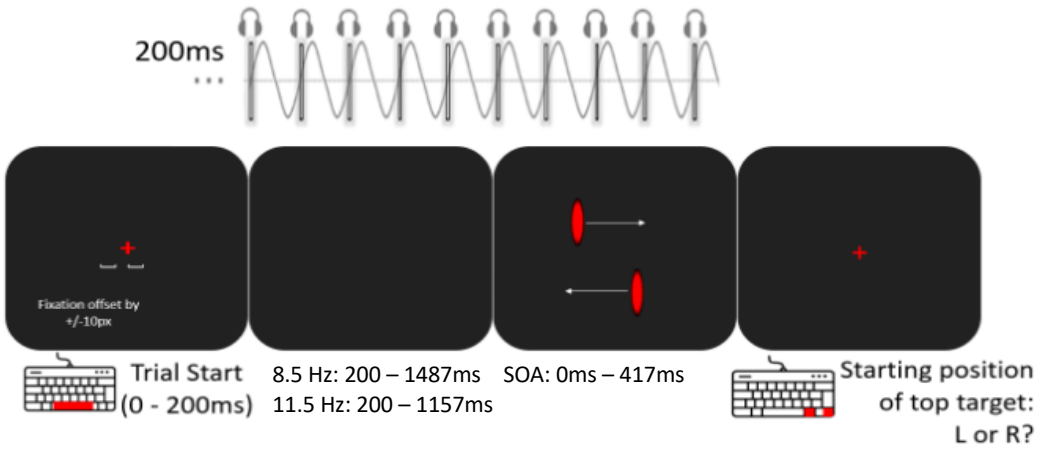


Fig. 2.2. Diagram of Fröhlich task experimental block. Participants began trials by pressing the space bar on the keyboard located in front of them. After 200 ms, an auditory entrainment stimulus (a series of 500 Hz tones of 20 ms duration each, with an 8.5 Hz or 11.5 Hz repetition rate) would begin. The entrainment stimulus continued through stimulus presentation until the participant responded.

Data from 41 participants were collected using the Human Subjects pool at University of Oregon. All participants were given course credit in exchange for participation, provided informed consent and reported normal or corrected-to-normal vision and no history of neurological disorders, epilepsy, or medications that may cause susceptibility to epilepsy. Procedures were approved by the University of Oregon Institutional Review Board. Three participants were dropped from the analysis after applying our exclusion criteria (PSEs beyond 3 SDs of the group mean and/or left response rates > 90%).

Stimuli and Apparatus

Stimulus presentation and response timing were managed by PsychoPy v2024.2.4. For trials in both the Staircasing and Entrainment blocks (see below), visual stimuli were presented on a 24-inch Zowie computer monitor (with a digital image 28 cm wide, 1024x768 resolution, and a 120 Hz refresh rate) located 69cm away from the participant. A central fixation point (0.34° visual angle) remained on screen before, and after each trial but disappeared during stimulus presentation. Target visual stimuli consisted of two Gaussian-blurred ellipses (0.68° wide, 1.70° tall), positioned 1.59° of visual angle above and below the fixation point, moving horizontally in opposite directions to one another at a rate of 50.79°/s for a duration of 500 ms. The target above the fixation point always moved to the right, and the target below the fixation point always moved to the left. Participants were asked to report whether the starting position of the top moving target was left ('F' key) or right ('J' key) of the starting position of the bottom target. Trials in the Entrainment block also included an auditory entrainment stimulus, consisting of a 500 Hz sinusoidal click 20ms long created using Logic Pro.

Procedures

Participants completed the experiment in a completely darkened room using the computer monitor, a chin rest, and a keyboard placed in front of them. Two blocks of the experiment were completed in a fixed order: staircasing block and experimental block. For both blocks, participants were asked to judge the starting location of two suddenly appearing, moving stimuli. Each trial began with a centrally located fixation point, positioned with a random horizontal offset of +/- 0.23° to prevent the fixation from serving as a reference point. The fixation point disappeared upon stimulus onset.

Participants indicated whether the starting position of the top target appeared to begin its trajectory to the left or right of the bottom target, using the 'F' and 'J' keys.

Staircasing Block. In this block, the horizontal displacement between the two targets was adjusted with two interleaved staircases, with initial starting positions ±4.53° left and right of the screen center and an initial step size of 0.18° (decreasing to 0.14°, 0.09° and 0.05° with subsequent reversals). Each staircase completed after 100 trials (200 trials total). The point of subjective equality (PSE) was calculated during the break between the Staircasing and Entrainment Blocks by filtering down to the lowest step size and averaging the starting target locations at those points. This PSE was used as the displacement value for the subsequent Entrainment Block.

Entrainment Block. The Entrainment Block followed the same trial structure as the Staircasing Block, but included an entrainment stimulus, denser sampling array, and the horizontal separation between the top and bottom stimuli was fixed at the participant's PSE as measured in the staircasing block. This was done to approach approximately equal proportions of "left" and "right" responses and examine alpha's modulation around the 50% point.

After beginning a trial and a delay of 200 ms, the entrainment stimulus began playing an auditory tone (lasting 20ms in duration) every 117ms for 1,287 ms (11 beeps in total) for the 8.5 Hz entrainment frequency and every 87 ms for 957 ms (11 beeps in total) for the 11.5 Hz entrainment frequency. The target stimuli were timed with respect to the end of the 11^{th} tone, with one of 51 stimulus onset asynchronies (SOAs) ranging from 0 ms to 417ms in 8.33 ms increments. Entrainment continued through stimulus presentation, and the trial ended when the participant used the keyboard to indicate the

relative starting locations of the upper and lower stimuli. Several control trials were also included, in which no stimulus appeared and participants were required to withhold any response.

There were 51 levels of SOA conditions and 2 control conditions, repeated for 15 trials each at two entrainment frequencies (8.5 Hz and 11.5 Hz), randomly presented (51 SOAs x 15 repetitions x 2 entrainment frequencies + 15 trials x 2 control conditions, 1560 trials in total). Control conditions consisted of an invisible stimulus and the participant was instructed not to respond.

Analysis Plan

By continually presenting target stimuli in the Entrainment Block at the participant's PSE, the participants should report the horizontal starting location of the upper target as being left and right of the lower target's starting location with approximately equal probability. However, if alpha entrainment successfully modulates the magnitude of the FE, these judgments should be modulated with the SOA, with a frequency equal to that of the entrainment stimulus. To test this specifically, we conducted a Fast Fourier-Transform (FFT) on behavioral responses to determine the power at the 8.5 Hz and 11.5 Hz frequencies, respectively.

We organized the leftward response rate time series by SOA and then conducted a real-valued FFT. Before transformation, for each participant, we detrended with a natural cubic spline to mitigate masking effects, isolated alpha components using a second-order Butterworth band-pass filter (4 – 18 Hz), and improved spectral resolution by applying 4x zero-padding. This pipeline was also used to create our null distribution data set where

we created 1000 permutations of the data where SOA labels were randomly shuffled to erase time-dependent patterns.

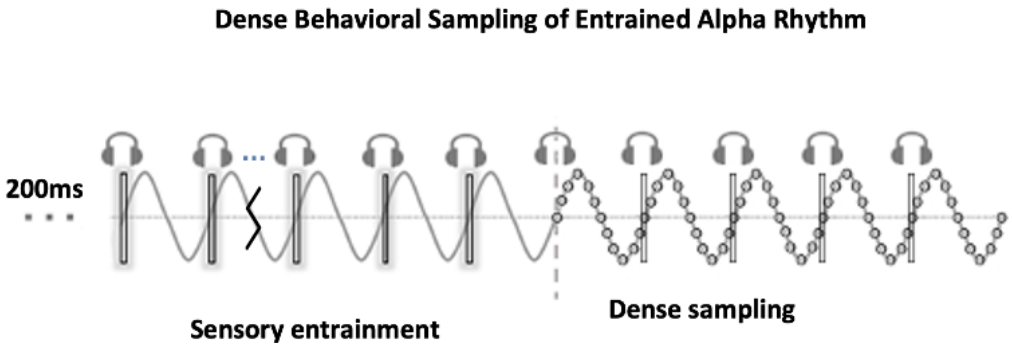


Fig 2.3. Illustration of dense behavioral sampling after 500 ms auditory entrainment period in the entrainment block. After a 200 ms delay from trial initiation, an auditory tone (20 ms duration) was played over headphones at either 8.5 Hz or 11.5 Hz to entrain the participant's neural oscillations to a consistent rhythm.

Results

We computed the leftward response rate (LRR) for all participants to create a time series of LRR across 51 different SOAs (Fig. 2.4) for each entrainment condition. To minimize any masking effects caused by the entrainment stimulus, we detrended each individual time course with natural cubic splines, and then isolated the frequency range of interest by applying a 4 – 18 Hz, second-order IIR Butterworth band-pass filter to the detrended time series (Fig. 2.4B). We found a strong downward deflection present in the data within the first three time points of the aggregate time series. This is likely due to a masking effect between the end of the entrainment stimulus and the presentation of the target stimulus, however, the effect is quite large and clearly not carrying any relevant or interesting oscillatory data. In order to enhance the effectiveness of spline detrending the data, we decided to exclude these data points in our preprocessing stage. We may be

missing data from the first several time points of our time series, but this should strengthen (not weaken) our analysis of the oscillatory patterns present in the data.

After preprocessing, we averaged time courses across participants within SOAs to create the aggregate data set. In order to test the presence of any modulatory effects of entrainment present in the response data, we created a null distribution for each entrainment condition consisting of 1000 permutations of the individual raw time series with shuffled SOA labels to erase the presence of time-dependent effects in this data set. After permuting, individual time series were detrended, filtered, and aggregated to create the null data set.

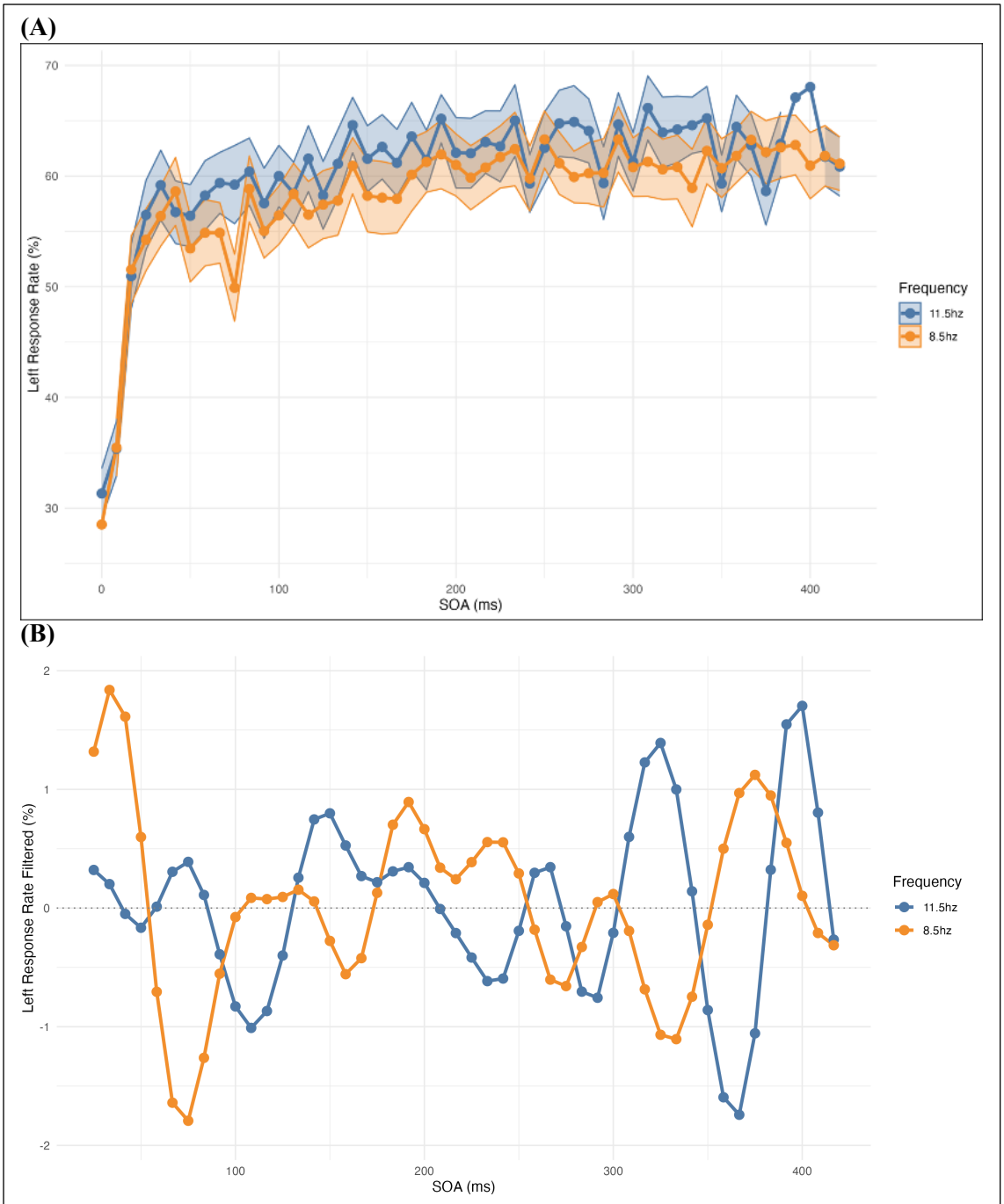


Fig 2.4. Raw (A) versus preprocessed (detrended, filtered; B) group-level time-series of left response rate (%) across SOA (ms) with first three time points removed.

Paired Samples T-test

To address whether entrainment frequency had an effect on the overall illusion magnitude, we conducted a paired samples t-test between the 11.5 Hz and 8.5 Hz entrainment conditions. We found a significantly higher LRR in the 11.5 Hz group compared to the 8.5 Hz group ($\mu_D = 2.34$, $t = 5.32$, $p < .001$), indicating a smaller illusion magnitude with the 11.5 Hz entrainment (Fig. 2.5).

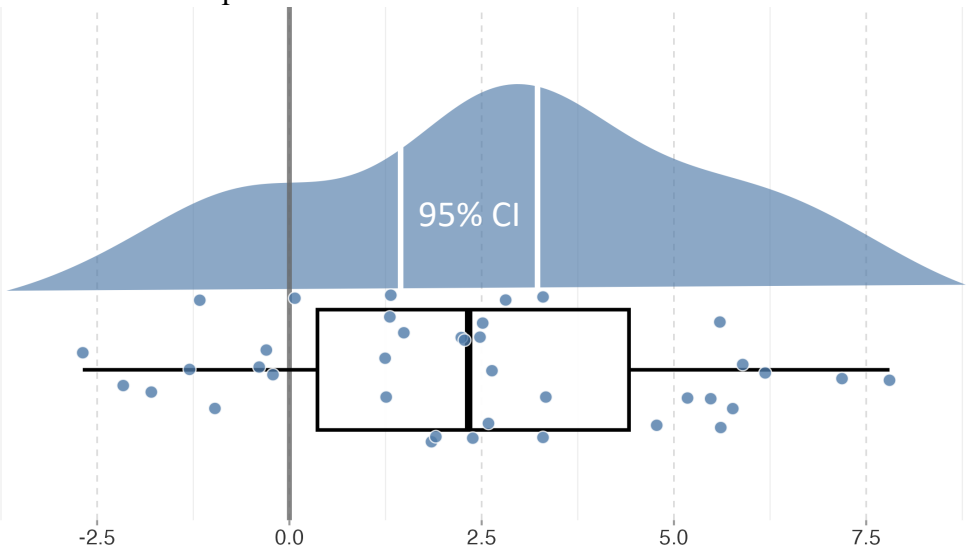


Fig. 2.5. Raincloud plot of mean difference values (11.5 Hz condition – 8.5 Hz condition). Mean difference between conditions ($\mu_D = 2.34$) was significantly greater than zero. The 11.5 Hz entrainment condition exhibited consistently greater LRR and therefore a smaller illusion magnitude.

Sinusoidal-fitting Permutation Analysis

To determine whether or not the entrainment frequency could be reflected in the behavioral response data of the FE by entrainment condition, we fit a sinusoidal model (with a frequency matching the entrainment frequency) to each entrainment condition observed group-level time series (Fig. 2.6). Goodness of fit of this pattern was measured

using the adjusted R^2, comparing the fit of our observed data to fits in the null distribution. Our sinusoidal functions were defined as:

$$y = \mu + a \cdot cos(2\pi fx) + b \cdot sin(2\pi fx)$$

where μ represents the mean response, *a* and *b* represent the cosine and sine coefficients, and *f* is the frequency parameter (8.5 Hz or 11.5 Hz in our observed data). All parameters were allowed to vary freely in the sinusoidal fit of our permutation data. For the fit of our observed data set, frequency was constrained to the entrainment frequency in order to robustly test the presence of our observed oscillatory pattern modulated by the entrainment frequency compared to those created by the null data set.

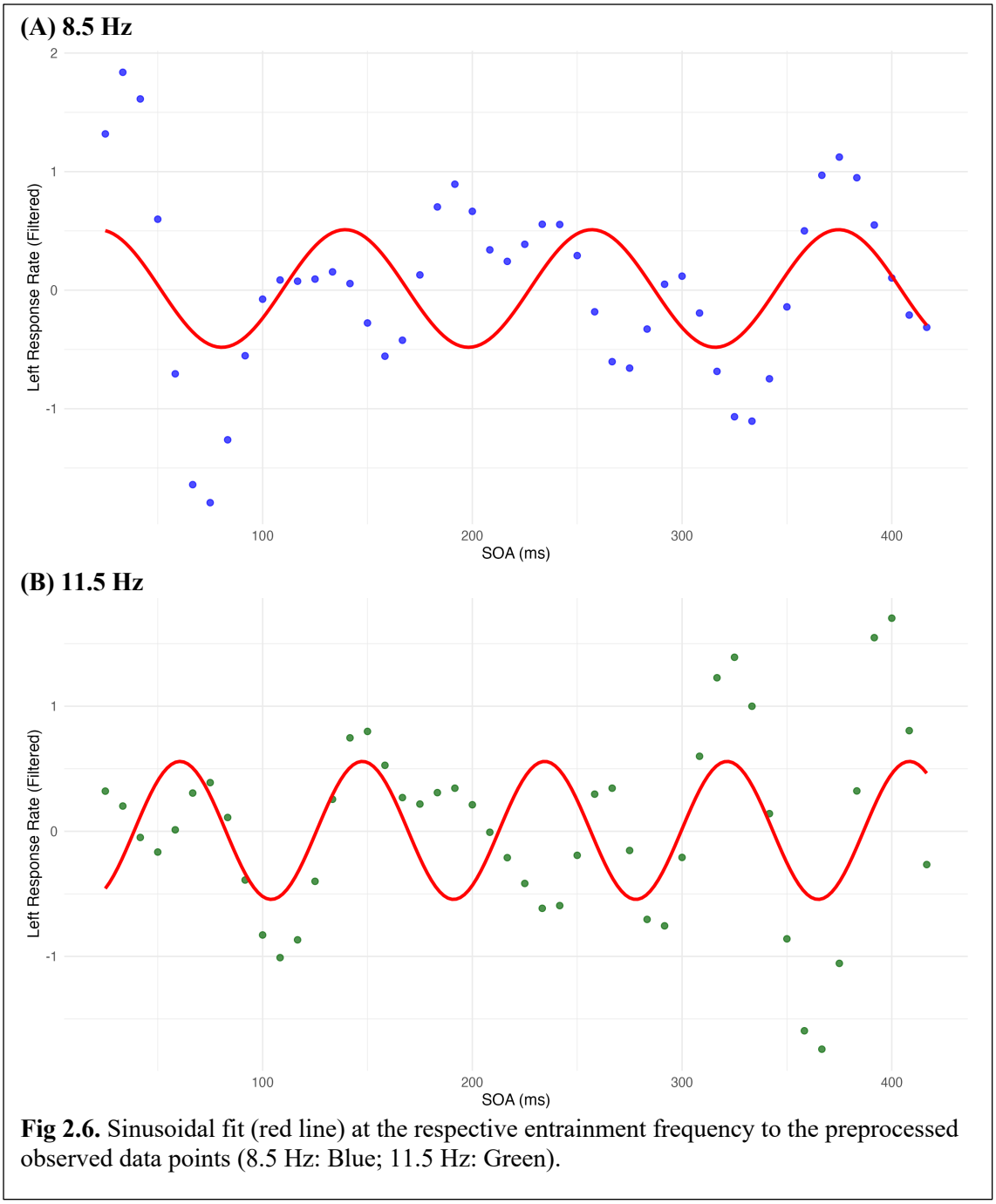


Fig 2.6. Sinusoidal fit (red line) at the respective entrainment frequency to the preprocessed observed data points (8.5 Hz: Blue; 11.5 Hz: Green).

The observed adj-R^2 value was compared relative to the 95th percentile ($\alpha = 0.05$) of the permuted null distribution (Fig. 2.7). The goodness of fit for both entrainment conditions was extremely low as evident by the adj-R^2 value falling below the threshold of the null distribution, (8.5 Hz: adj-R^2 = 0.152, critical value = 0.688, p = 0.998; 11.5

Hz: adj-R^2 = 0.236, critical value = 0.676, p = 0.982). This indicates that our entrainment frequency is not being significantly reflected in the time series of either entrainment condition behavioral data.

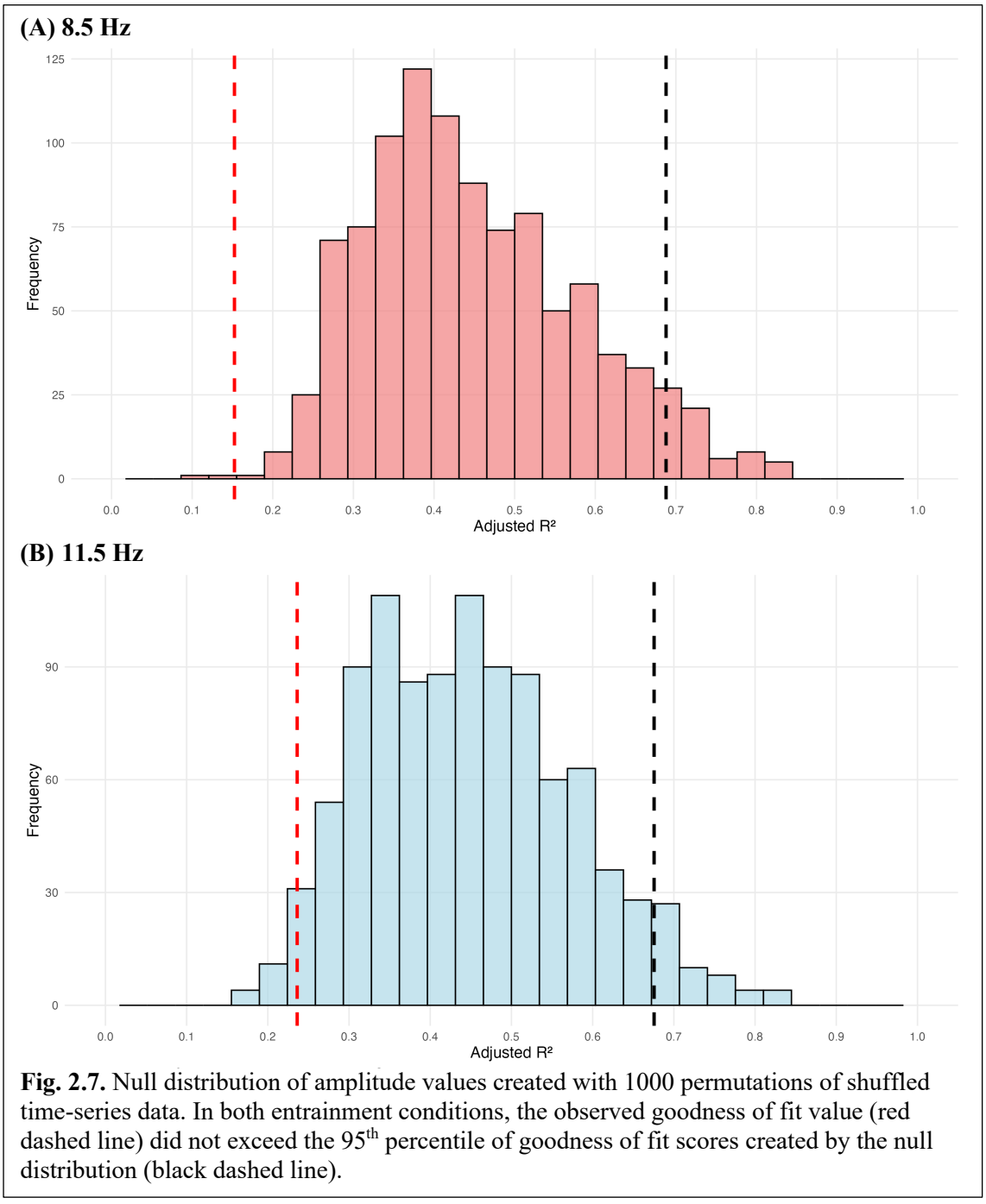


Fig. 2.7. Null distribution of amplitude values created with 1000 permutations of shuffled time-series data. In both entrainment conditions, the observed goodness of fit value (red dashed line) did not exceed the 95th percentile of goodness of fit scores created by the null distribution (black dashed line).

FFT Amplitude Permutation Analysis

To further test the presence of a modulation at the entrainment frequency present in the behavioral data, we performed a real Fast-Fourier transforms (RFFTs) on the preprocessed aggregate time series. The amplitude spectrum was extracted for all frequencies of interest (Fig. 2.8). RFFTs were also conducted on the 1000 permutations of shuffled time series using the same preprocessing as the observed data set. This created a null distribution of amplitude values with which to compare our observed data set across frequencies. For each frequency (bins of 0.5 Hz), we calculated the *p*-value as the percentile rank of the observed amplitude relative to the permuted amplitude distribution, using the 95th percentile boundary as the critical value for significance. None of our observed amplitude values at any frequency exceeded the 95 percent range of the null distribution, further confirming the absence of a modulation at the entrainment frequency in the behavioral data set of either entrainment condition, (8.5 Hz: amplitude = 0.059, critical value = 0.173, $p = 0.722$; 11.5 Hz: amplitude = 0.064, critical value = 0.167, $p = 0.685$).

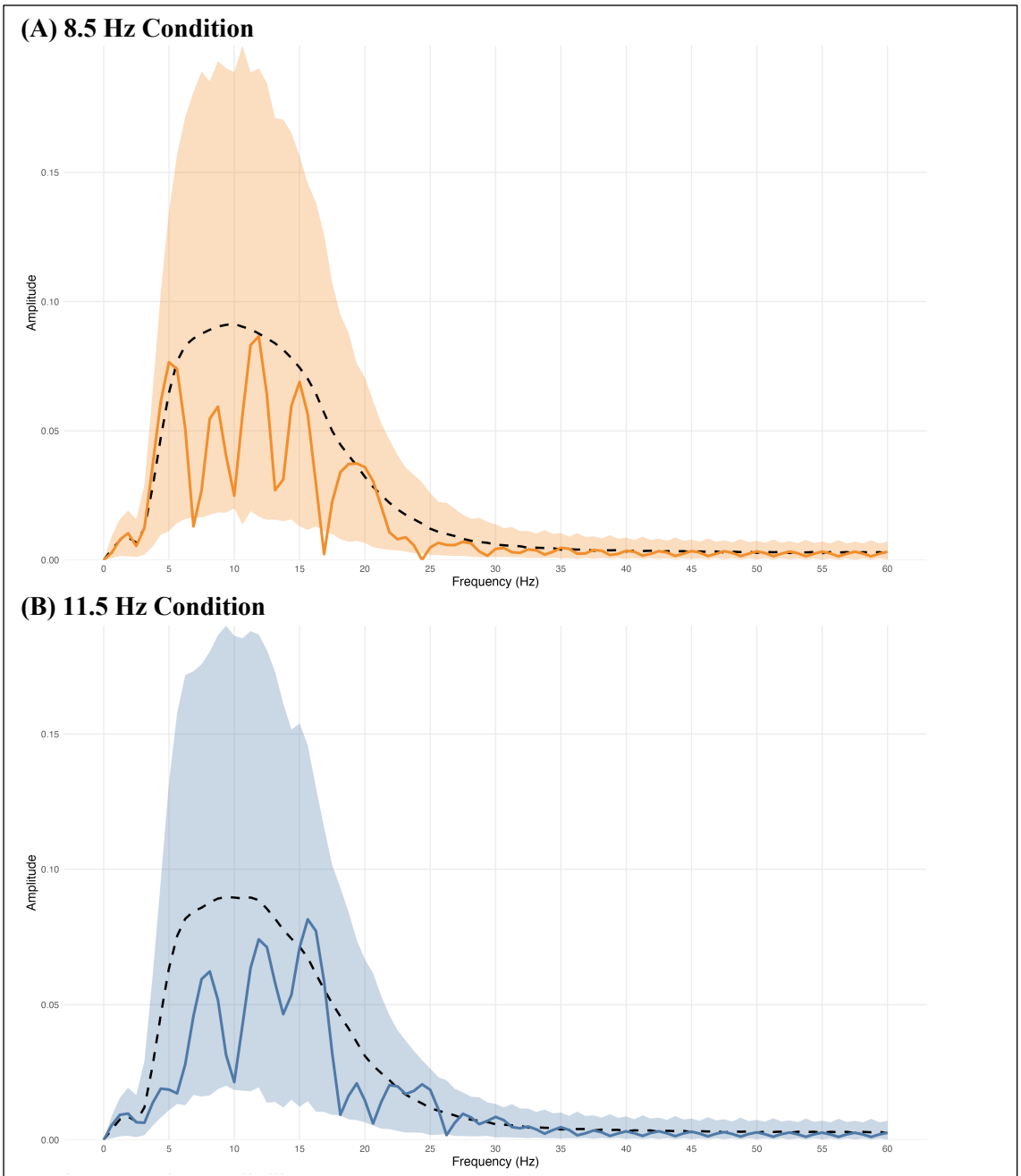


Fig 2.8. Group-level FFT data (4-18 Hz band-pass filter and 4x zero padding applied) for 8.5 Hz (orange) and 11.5 Hz (blue) entrainment conditions. The amplitude range of either FFT spectrum does not exceed the 95% critical value of our null distribution of amplitudes created by the permuted data set (ribbon).

Discussion

We found a significant difference in illusion magnitude for the different entrainment frequencies (with a smaller magnitude with a 11.5 Hz entrainment, versus

8.5 Hz), supporting our hypothesis that entrainment frequency influenced perception in the FE. Contrary to our second hypothesis however, we did not find an effect of either entrainment condition on the modulation of response rate across SOAs. Neither our goodness of fit nor amplitude test yielded a significant difference from that of noise. Assuming our methods of measurement were effective, this suggests that the FE seems to be based on mechanisms that are susceptible to alpha entrainment but not in a way that can be observed through our goodness of fit or amplitude tests. It is possible that this may be the result of an alerting effect difference between the slow versus fast entrainment conditions, but we were unable to test this theory with our current design. Alternatively, the FE may just be a more complex phenomenon than detection or segregation/integration tasks where the illusion is partly the result of visual sampling delays driven by the alpha rhythm but this effect is diluted by additional mechanisms that have their effects in higher levels of perception.

While a relationship between alpha entrainment and the FE may just not exist, there were several discrepancies that could be contributing to our null results in our modulation tests. First, we cannot directly infer any relationship about the effect of phase on the modulation (or lack thereof) present in the FE because we do not know the temporal relationship between the presentation of the entrainment stimulus and the peak phase of the participant's entrained alpha rhythm. Presumably, there is some afferent delay of unknown duration between these two variables ($t_{afferent}$), and alignment of oscillations would not be occurring exactly in time with the presentation of the rhythmic stimulus, but instead with the moment of arrival of the entrainment stimulus at initial sensory processing areas after $t_{afferent}$ (Fries, 2005; 2015). Although we try to limit the

effects of individual differences in neural rhythms by using an entrainment paradigm, $t_{afferent}$ could still be subject to individual variance and average out when combining data across participants. That being said, other studies *have* found a significant modulation in entrainment/dense-sampling designs even when averaging data across participants, so $t_{afferent}$ may not have enough variance between participants to completely eliminate the effect (Fiebelkorn et al. 2011; Ronconi et al., 2018; Chota & VanRullen, 2019). With this in mind, individual-level analysis should be done in our analysis, and this will be implemented in our follow up study in Chapter IV.

Whether individual differences in the afferent delay is a significant factor at play is of some debate in the literature as there may be some sort of anticipatory deployment of the alpha rhythm (or alternative neural mechanism) to align itself with the predicted onset of the entrainment stimulus (Eagleman & Sejnowski, 2007), although some studies have suggested that (at least in terms of auditory stimuli) neural oscillations undergo a complete phase reset when attending to an auditory tone in non-human primates (Lakatos et al., 2013; Lakatos et al., 2019) and in humans (de Graaf et al., 2013; Calderone et al., 2014), and can even completely phase-lock oscillations to frequencies present in speech patterns (Zoefel, et al., 2016). If phase-locking by neural rhythms to the entrainment stimulus is occurring, then individual differences in afferent delays could become a non-factor; however, in the current study, we have no measures to make any conclusions about this.

It is also entirely possible that while the literature has supported auditory areas completely phase-locking to the rhythmicity of an auditory stimulus, this relationship gets more ambiguous when cross-sensory entrainment is used. Fiebelkorn and colleagues

(2013) conducted a study using cross-sensory entrainment, demonstrating the ability of an auditory stimulus to modulate the detection rate of a visual target; however, this finding used purely behavioral data and could be susceptible to the same limitations as the current study. Even so, they were able to find a significant effect across participants, so this issue of afferent delays may not be great enough to prevent entrainment studies from demonstrating significant results across participants.

The findings of this experiment have led us to ask the question: how can we determine the time at which a sensory object arrives within one's perception? Theoretically, it would be at the peak of the alpha oscillation of the neuronal assemblies responsible for processing such information, but that leads to another question: are these local field potentials involved in generating the alpha frequency and building the gateway to our perception located at a sensory level, higher-order perceptual level, or both?

The literature has been very clear in support of the alpha rhythm as an underlying mechanism of our visual system; however, it has struggled disentangling at what points of the perceptual, cognitive and response processes it has an effect. For example, entrainment to a faster alpha rhythm than the participant's baseline has been reported to result in more rapid perception of stimuli than normal (Mathewson et al., 2009; 2010), but is this a result of increased sensitivity in early level visual areas, or is the change in alpha frequency speeding up the rate at which information is sent to our perceptual awareness?

As a result of these considerations, Experiment 2 attempts to characterize these unknown afferent delays by implementing an experimental paradigm that can subtract out the afferent delays that may be occurring in the Fröhlich task, as well as set the

foundation for a future EEG experiment that directly measures the phase of the alpha rhythm.

- Chapter End -

CHAPTER III

LOCALIZING THE FRÖHLICH EFFECT IN THE PERCEPTUAL HIERARCHY

Our visual system operates under the burden of neural delays – a simple "cost of business" that creates a mismatch in the timing between observed sensory events and their internal representations. This mismatch can affect perception in detection and temporal order judgment tasks, but does it also affect the perceived starting location of a moving object? Observers reliably mislocalize the starting position of a moving object in the direction of motion in the Fröhlich effect (FE), causing the target to appear further along its trajectory than in reality (Fröhlich, 1925). But where in the perceptual hierarchy does this displacement occur? The field still needs to clarify whether the FE, and potentially other movement illusions, reflect fundamental limits of sensory encoding or arise later in higher-level perceptual mechanisms.

Evidence of modulation at an early sensory level

One possibility is that the FE stems from a bias at the earliest stage of sensory processing. Discrete perception theory – which proposes that the visual system samples information in rhythmic chunks (VanRullen & Koch, 2003) – has been widely supported and naturally extends to motion perception (Hubbard et al., 2014; McLelland et al., 2016; Chota & VanRullen, 2019). If incoming sensory information is temporally averaged within sampling windows – the "soft" view of discrete perception – then less frequent sampling, and larger windows of averaging, could enlarge the displacement between a target's physical onset and its perceived one (Schneider, 2018). Krekelberg and Lappe

(1999) further argued that this averaging pulls perceived position toward the weighted mean of motion within the window, where more averaged motion results in a greater drift in perceived onset Alternatively, the "hard" view of discrete perception suggests that a stimulus appearing during an unfavorable processing phase could either be processed more slowly or deferred entirely until the next favorable moment (Schneider, 2018). In this view, neural oscillations have been suggested to gate the flow of perceptual input, allowing flow during periods of favorable processing and halting it during unfavorable times. To investigate discrete perception further, neural entrainment either through rhythmic sensory stimuli or transcranial magnetic stimulation has been used as a method for artificially manipulating these windows of processing and modulating the temporal resolution of our perception (Mathewson, et al., 2010; Calderone, et al., 2014).

Evidence for this phase-dependent sensitivity stems from findings that the phase of local field potentials in task-relevant neuronal assemblies was found to modulate the spikes rates of local neurons (Haegens, et al., 2011), and the phase of the alpha rhythm has been used specifically to predict the detection rates of near-threshold stimuli (Busch, et al., 2009; Dugue, et al., 2011; Mathewson, et al., 2011). In the case of a moving target, these fluctuations at the sensory level caused by phase-gating or discrete temporal sampling could produce the characteristic biases of the FE. Chota and VanRullen (2019) demonstrated that entrainment of neural oscillations at the alpha rhythm can periodically modulate the "lag" of the flash-lag effect, providing evidence that fluctuations in temporal perception are involved in at least one mislocalization effect in a periodic way. A similar phase-gating or discrete temporal sampling in early sensory processing might also produce the characteristic biases of the FE.

Overall, theories involving early sensory-level mechanisms suggest that timing and rhythmicity in perceptual processing influence where we perceive objects in space – not a predictive mechanism.

Evidence of modulation at a perceptual/decision level

An alternative account places the source of the FE at later stages of processing, at either the perceptual or decisional level, rather than at initial sensory encoding. For example, feedback mechanisms in the visual system have been shown to influence the timing of perception. Ro (2019) found that peak timing of TMS disruption in a metacontrast masking task aligned with peaks in the P2 component of the EEG as well as with participants' individual alpha frequency. If the speed of visual processing is tied to both the alpha frequency and the timing of late visual-evoked responses (P2), then similar feedback processes could also affect the perceived onset location of moving targets.

Motion extrapolation is a popular theory for the mechanism behind the FE, and one that would source from higher-order perceptual mechanisms. It suggests the final percept of the starting location of a moving stimulus is calculated as its physical location plus the adjustment by some visual mechanism to correct for spatial lag in order to facilitate tasks such as grasping or catching (Nijhawan, 1994; Baldo & Klein, 1995). A study by Maus and colleagues (2013) found that the perceived location of a target can be biased by the presence of nearby motion, even when the target itself remains stationary. This suggests that motion signals may activate mechanisms within area MT+ that extrapolate position. These findings have been extended further to localization illusions as well and have been used as a possible explanation for phenomenon such as the flash-lag effect (Hogendoorn, 2020). Motion extrapolation has been heavily corroborated by

the literature but does tend to imply that perception alone is responsible for this bias in localization: a fabricated propulsion as a perceptual remedy to the problem of afferent delays, rather than inherent to the mechanisms of the sensory system.

The FE could indeed also be partly affected by decisional-level biases as well. The onset repulsion effect (ORE) produces a bias in reported starting position opposite the direction of motion, even when perception is unchanged (Kerzel & Gegenfurtner, 2004; Hubbard & Motes, 2005). This suggests that in some contexts, observers may partially and unknowingly "compensate" for motion-induced shifts when making a motor response.

Is mislocalization an intrinsic consequence of early sensory encoding? Or is it the result of adjustments for our own neural delays at a higher level of perception? Each of these theories point to different mechanisms for mislocalization: prediction, temporal averaging, neural sampling, etc., and it's not entirely clear if these are mutually exclusive or distinct mechanisms. One way that we can attempt to disentangle these ideas is to probe at which level this effect may be happening.

Hypotheses

Several theories for the mechanisms of the FE suggest that biases could emerge at multiple stages of processing: from early sensory encoding to perceptual representation to decision-making and motor output. If the FE originates at the earliest sensory level, then its magnitude should be modulated by individual differences in sensory processing speed. In this case, participants who can detect the onset of a stimulus more quickly should also exhibit smaller mislocalization magnitudes, producing a positive correlation between a simple reaction time task measure (RT_{simple}) and illusion magnitude. Alternatively, if the

bias emerges later in perception, the relationship should instead be found between illusion magnitude and a two-alternative forced choice localization task ($RT_{decision}$).

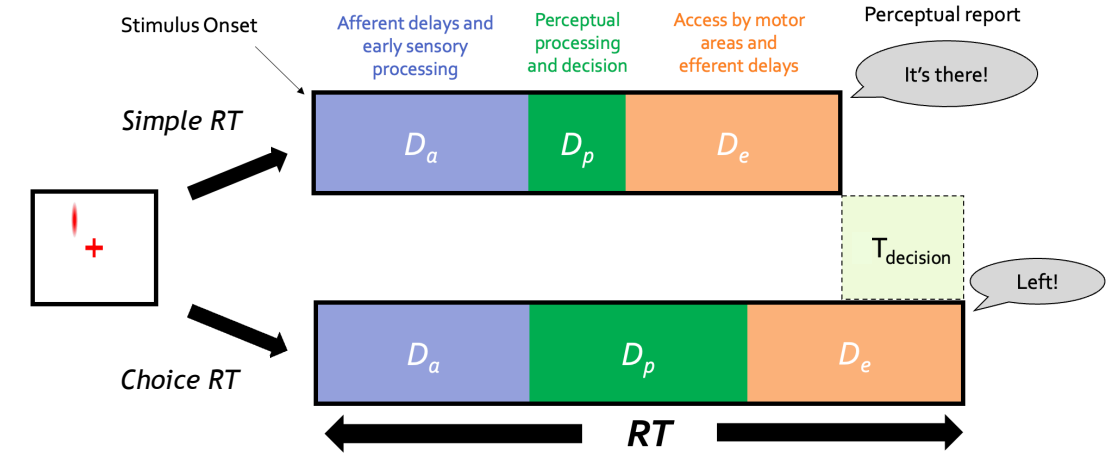


Fig. 3.1. Subtraction of RT_{simple} and RT_{choice} to calculate $t_{decision}$. With identical stimulus arrays across both tasks, we can subtract RT_{choice} from detection RT_{simple} to isolate the time to make a localization decision, accounting for afferent delays and efferent delays since these should be similar across both tasks. The increase in choice RT after introducing the forced-choice instruction results from an expansion of D_p (duration of perceptual/decisional processes).

Assessing the relationship between FE magnitude and these reaction time measures should provide a means by which we can determine the level of processing at which the FE is instantiated. Theoretically, the speed of processing at either level could be involved in how quickly a stimulus is processed and registered and could help distinguish between competing explanations of the FE. We aim to isolate specific delays in the perceptual process and investigate whether the extent of mislocalization in the FE is attributable to variations in delays at the perceptual and decision-making levels, rather than at early sensory levels. Given that there is evidence in support of involvement at multiple stages of processing, we expect to see a correlation between RT_{simple} and FE magnitude, supporting an effect at early sensory levels as well as a relationship between $t_{decision}$ and FE.

Methods and Procedures

Participants

Data from 40 participants (1 participant was removed from detection task analyses due to missing data) were collected using the Human Subjects pool at University of Oregon, providing course credits in exchange for participation in the study. All reported normal or corrected-to-normal vision and no history of neurological disorders. Procedures were approved by the University of Oregon Institutional Review Board (IRB), and written informed consent was obtained.

Stimuli and Apparatus

All stimuli were displayed on a 24-inch Zowie gaming monitor (with a digital image 11 in wide, 1024x768 resolution, and a 120 Hz refresh rate) 69 cm away. Participants rested on a chinrest during the experiment to ensure stability and a consistent distance from the screen. A central fixation point (0.34° visual angle) was present before, during, and after each trial. Target stimuli consisted of Gaussian-blurred ellipses (0.68° wide, 1.70° tall), located 1.59° of visual angle above the fixation point. For moving stimuli, targets moved at ±50.79°/s in two movement conditions: leftward and rightward. Stimulus presentation and response timing were managed by PsychoPy v2023.2.3

Procedures

Each participant completed three experimental blocks in a semi-fixed order (Staircasing Block > Simple RT Block (SRT) ~ Choice RT Block (CRT)), with built-in breaks every 30 minutes. The Staircasing Block was used to determine the magnitude of the FE for the moving stimulus. The SRT and CRT Blocks measured the participant's reaction time to a suddenly appearing target at multiple spatial locations across the screen

– a detection task and a forced-choice localization task. The target stimuli in the SRT and CRT Blocks had three conditions of movement: leftward motion, rightward motion, and nonmoving (control). Stimuli could appear at various x-coordinates along the computer screen, varying from -140px to 140px in 20px increments. This corresponds to a visual angle of -3.17° to +3.17° in 0.45° steps. Each spatial location was sampled 15 times.

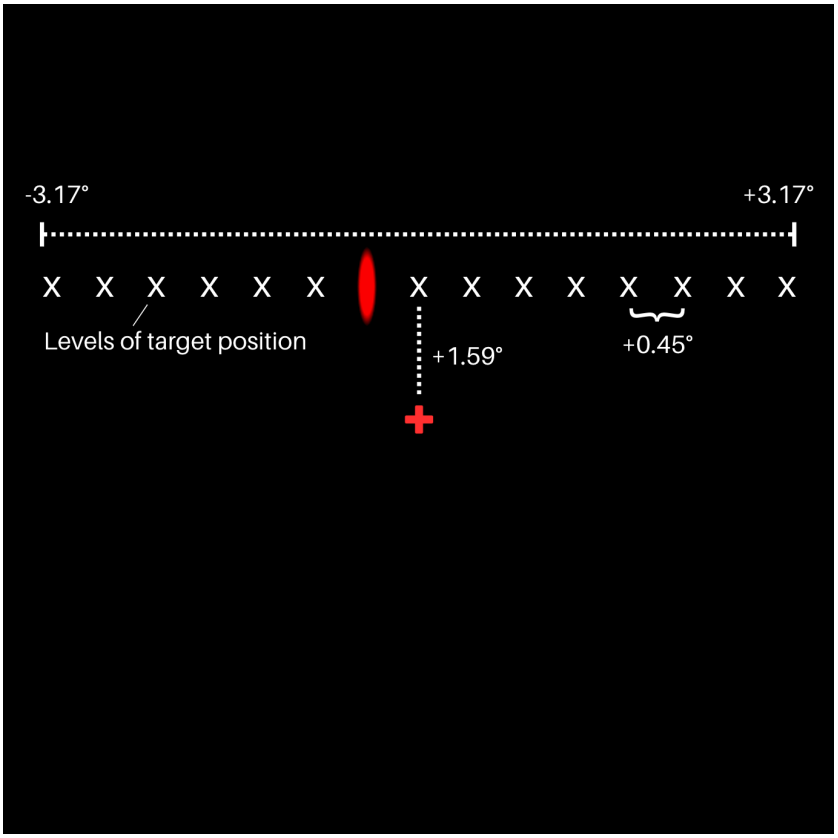


Fig. 3.2. Stimulus array of SRT and CRT Blocks. Target appeared 1.59° above the fixation point at one of 15 different locations (range from -3.17° to 3.17° in 0.45° increments).

To measure the magnitude of the FE in the Staircasing Block, participants directed their gaze to a central fixation point centered on the monitor. Upon trial initiation, the target stimulus appeared onscreen and moved across the screen with a rightward motion at a rate of 50.79°/s. Participants then used the keyboard to indicate if

they believed the target began its motion to the left or right of the fixation point. In each trial, the horizontal starting location of the stimulus stepped according to two interleaved 1-Up/1-Down staircases, with starting locations of –4.53° or 4.53° from screen center. The fixation point remained visible through the duration of the trial. After 250 trials in each staircase, the block was completed.

The SRT Block contained a detection task where participants were instructed to press the space bar immediately upon stimulus presentation. Upon trial initiation with the space bar, the target stimulus appeared and remained still (in the nonmoving condition) or moved across the screen in a rightward or leftward motion at a rate of ±50.79°/s. The target stimulus was presented at various SOAs (50 ms, 74 ms, and 92 ms) to minimize the possibility of the participant learning the exact timing of stimulus onset and using this to perfectly predict when to respond. Instead of staircasing the horizontal displacement of the starting position of movement, these were randomized between locations at ±3.17°, ±2.72°, ±2.26°, ±1.81°, ±1.36°, ±.91°, ±.45°, and 0.

These trials also included 3 levels of movement conditions (leftward moving, rightward moving, and nonmoving/static) and 15 trials that contained no target (catch trials). The participant was asked to respond as quickly and accurately as possible to the onset of the target, regardless of its starting position and motion characteristics. Upon detecting the onset of the target, the participant was instructed to press the space bar on the keyboard. This block was comprised of 14 trials in each condition ((15 presentation sites x 3 SOA intervals x 3 movement conditions + 15 control trials) x 14 repetitions; 1905 trials in total).

The CRT block presented an identical stimulus array and design to the SRT block, with one change to the instructions for the participant's response. Every aspect was identical, but in this block the participant was now asked to respond to whether the target began its motion to the left or right of the fixation point (regardless of its motion characteristics), using the 'F' and 'J' keys on the keyboard to input their response.

Results

Staircase Block

Participants showed mislocalizations in the target's starting position where targets were perceived as aligned with the fixation point, displaced along the direction of motion. The distribution of PSEs across participants showed a clear bias toward forward displacement, indicating that participants perceived the target as farther along its trajectory than in reality.

This behavioral signature replicates prior findings that the perceived initial position of a moving object is mislocalized in the direction of motion. Importantly, the staircase results provided individualized estimates of perceptual bias, which were later used to examine correlations with parameters derived from reaction time modeling in the CRT task. These individualized PSEs served as behavioral anchors for assessing whether sensory and decisional processing times aligned with each participant's own perceptual mislocalization.

Each participant's PSE was measured by filtering staircase step sizes to the smallest size, then averaging the staircase intensity at each trial. Before conducting any analyses, participants were excluded using an iterative filter for outliers. Participants with PSE beyond 2.5 SDs of the group mean were removed, then recomputed with the filtered

data, and repeated until no further points were excluded. To detect any presence of a mislocalization in our data, we conducted a one-sample t-test to determine if our participants' PSEs were significantly different from zero. We found significant differences in both the leftward (n = 38, M = 0.58°, SD = 0.78°, $t(37) = 4.60$, $p < .001$) and rightward movement conditions (n = 38, M = -0.72°, SD = 0.87°, $t(37) = -5.20$, $p < .001$), indicating strong shifts in perceived equality along the trajectory of motion.

Simple RTs and Choice RTs

To investigate whether FE magnitude (measured in a preliminary staircase task) was correlated with the duration of sensory or decisional processing, we compared correlations between illusion magnitude and reaction time measured in two tasks: a simple reaction time task (SRT) and a two-alternative forced choice localization task (CRT) with identical stimulus arrays. If the FE originates from delays at early sensory stages, we would expect participants with faster detection times to exhibit smaller illusion magnitudes. Conversely, if the effect reflects delays or biases arising at perceptual or decisional stages, the relationship should instead emerge within $t_{decision}$ (the subtraction of RT_{simple} from RT_{choice}). Analyses first assessed the correlation between each RT measure and illusion magnitude, followed by a model-based examination of RT patterns across screen position to explore the intricacies of the reaction time data.

Before testing any correlations with illusion magnitude, we first wanted to compare reaction times across tasks to ensure that the expected pattern . A paired samples t-test revealed that RT_{choice} (M = 0.46s, s = 0.08) was indeed larger than RT_{simple} (M = 0.33s, s = 0.19) as expected, $t(38) = 3.92$, $p < .001$. (Fig. 3.3).

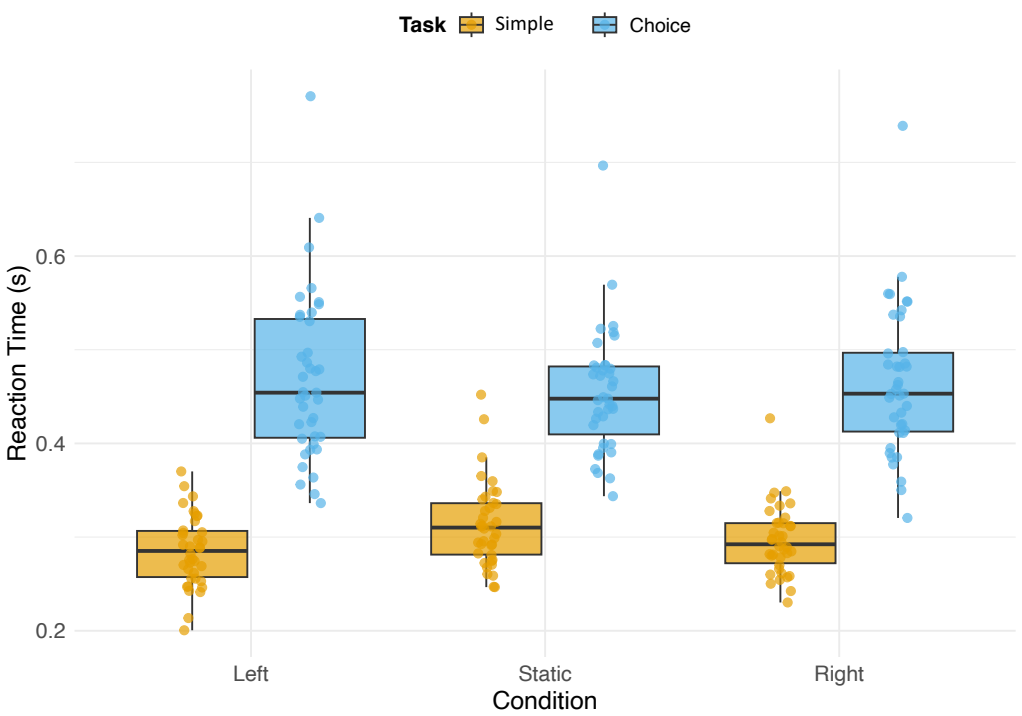


Fig. 3.3. Box plot of Simple Task RTs task versus Choice Task RTs. Significant differences were observed between tasks but not between movement conditions within tasks. Decision task reaction times were significantly higher than simple task reaction times in all movement conditions.

Correlation Between Reaction Time and Illusion Magnitude

To examine whether the magnitude of the FE was associated with processing speed at either the sensory or perceptual/decisional levels, we computed Pearson correlations between each participant's illusion magnitude (measured from our staircase procedure) and their RT_{simple}, RT_{choice}, and $t_{decision}$.

No significant correlations were found between illusion magnitude and any of the averaged RT values, (Fig. 3.4, 3.5, 3.6). The correlation between illusion magnitude and RT_{simple} ($r = 0.145$, $p = 0.273$) indicated no significant relationship between early sensory processing speed and FE. The correlation between illusion magnitude and RT_{choice} also failed to reach significance ($r = 0.094$, $p = 0.478$), suggesting no association between

decisional processing time and FE. To isolate the decision processing time, we calculated $t_{decision}$ (by subtracting RT_{simple} from RT_{choice}) but this also did not display a significant correlation ($r = 0.014$, $p = 0.917$). These results do not support the hypothesis that the FE is driven by early sensory delays or decisional processes, however, reaction times are more complex than simply averaging across participants, so a more complex analysis is needed to accurately dive into these relationships.

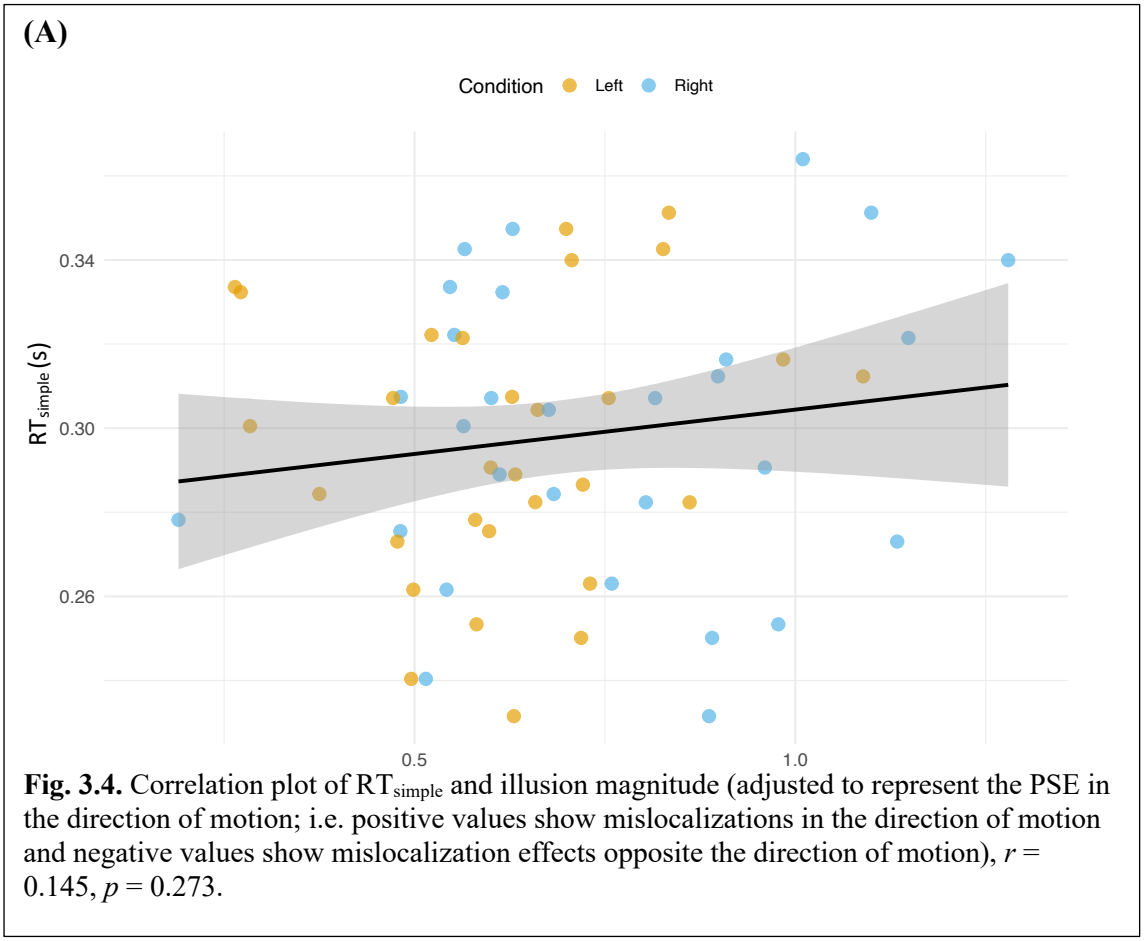


Fig. 3.4. Correlation plot of RT_{simple} and illusion magnitude (adjusted to represent the PSE in the direction of motion; i.e. positive values show mislocalizations in the direction of motion and negative values show mislocalization effects opposite the direction of motion), $r = 0.145$, $p = 0.273$.

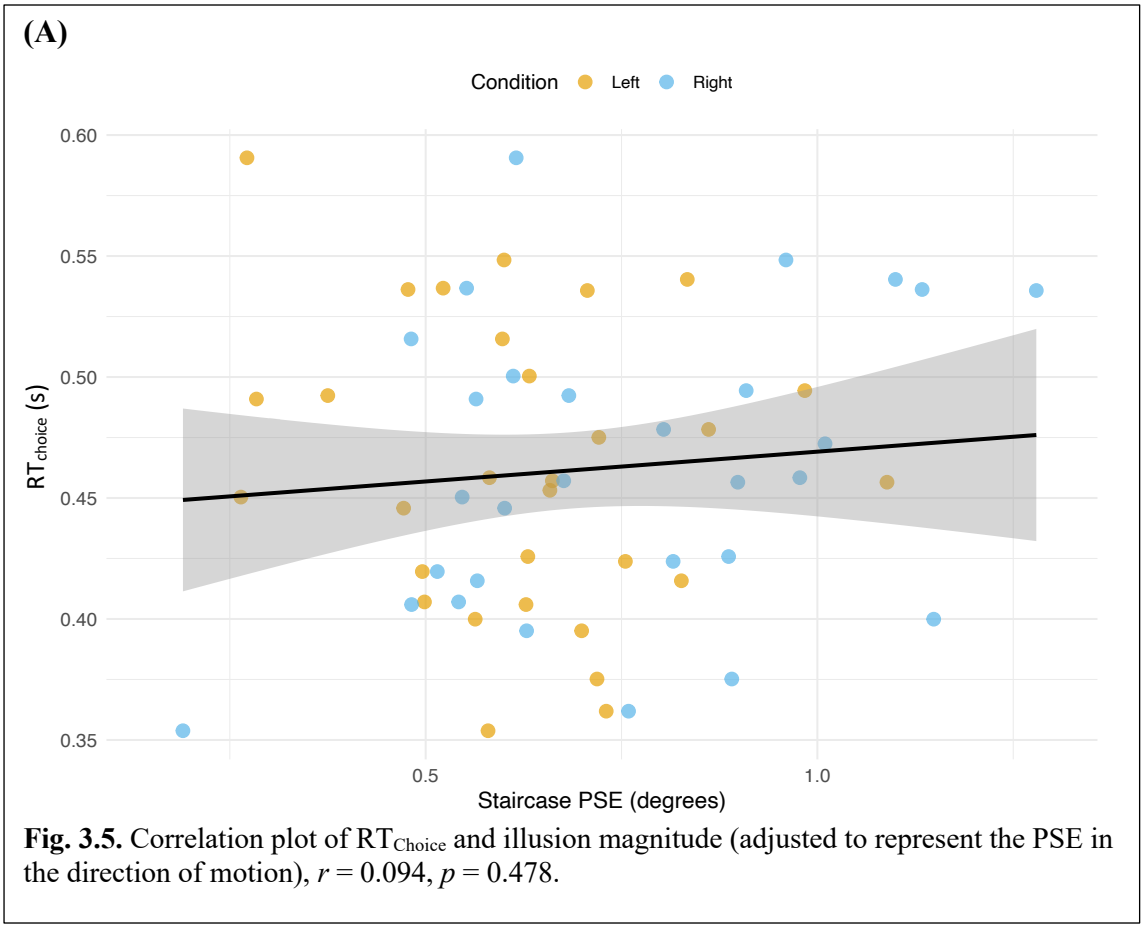


Fig. 3.5. Correlation plot of RT_{Choice} and illusion magnitude (adjusted to represent the PSE in the direction of motion), $r = 0.094$, $p = 0.478$.

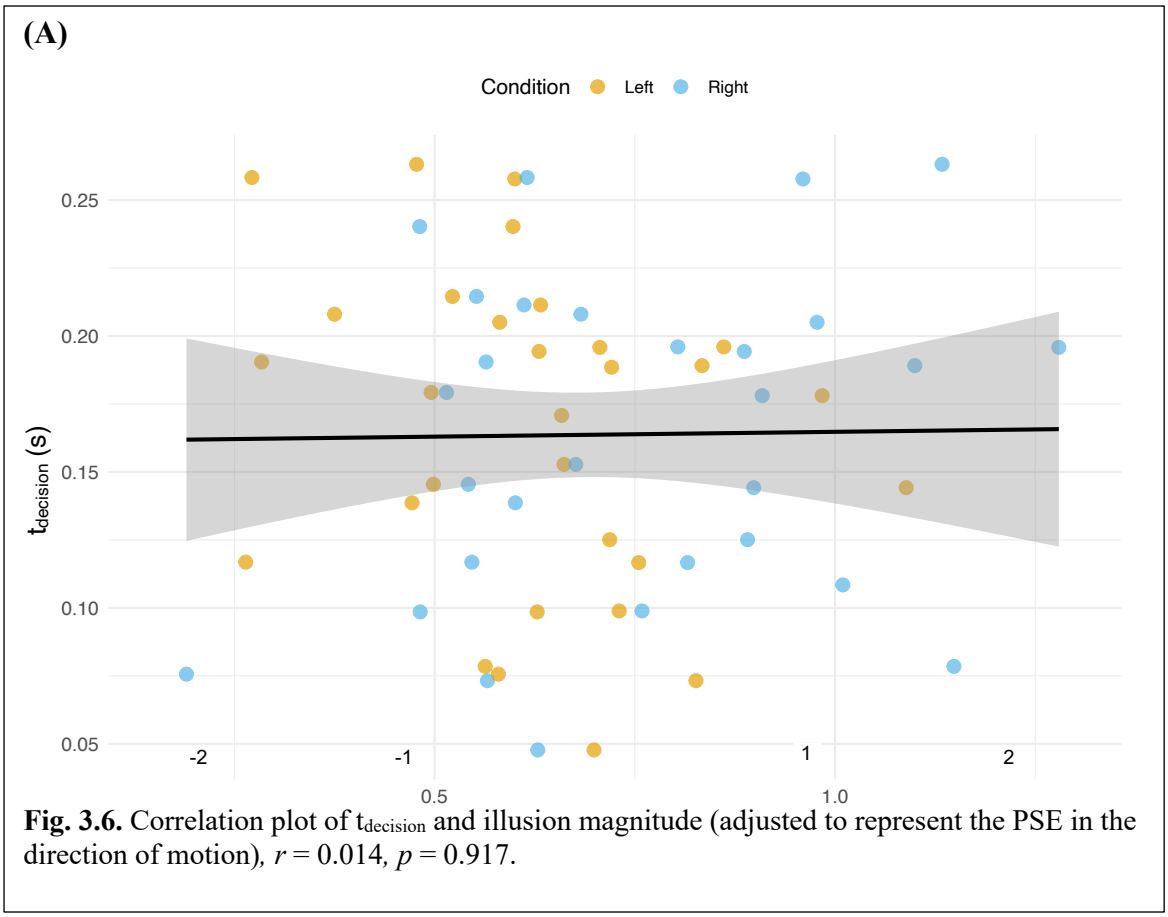


Fig. 3.6. Correlation plot of $t_{decision}$ and illusion magnitude (adjusted to represent the PSE in the direction of motion), $r = 0.014$, $p = 0.917$.

3-way ANOVA (Location x Task x Movement)

Although our initial analyses failed to find a significant relationship between average reaction times and the magnitude of the FE, a closer examination also showed that the reaction times were affected by a complex interaction between task, movement condition and starting location (Fig. 2.7). This demonstrated a need for a more complex analysis in order to fully explore any possible relationships between reaction times and FE magnitude.

We conducted a repeated measures 3-way ANOVA test on the reaction times and found a significant main effect of Task, $F(1, 35) = 264.24$, $p < .001$, and Location, $F(14, 490) = 10.11$, $p < .001$. A Mauchly's test indicated violations of sphericity for effects

involving movement direction, and no main effect of movement direction was found when adjusting for this violation using a Greenhouse-Geisser adjustment, $F(2, 70) = 24.73$, adj. $p = .084$.

There were significant two-way interactions between all three variables: Task x Direction: $F(2, 70) = 24.73$, $p < .001$, Task x PSE: $F(14, 490) = 10.75$, $p < .001$, and Direction x PSE: $F(28, 980) = 27.11$, $p < .001$, all contributed to an effect on RT. The three-way interaction between our variables was also significant, $F(28, 980) = 32.06$, $p < .001$. Thus, there are robust main effects of Task and Location and highly significant interactions between all three variables.

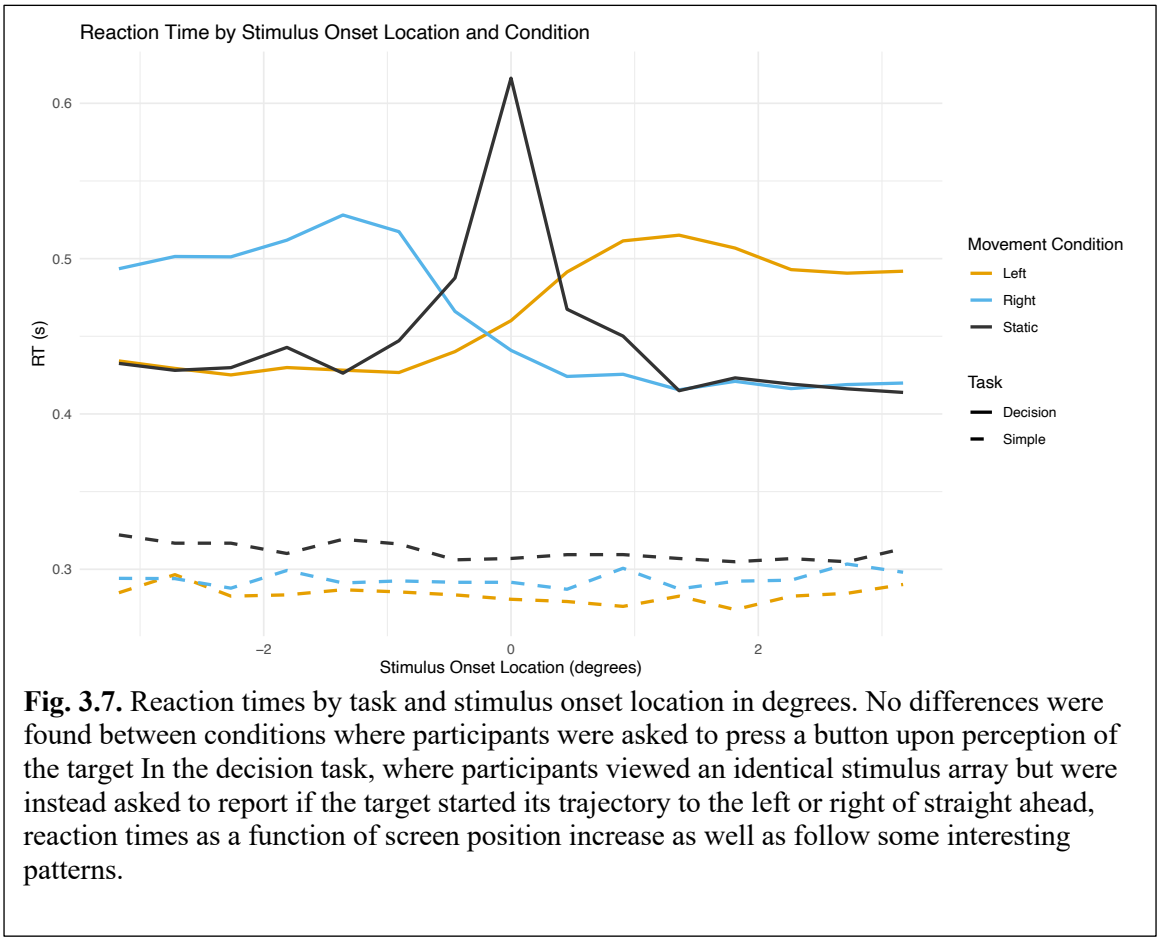


Fig. 3.7. Reaction times by task and stimulus onset location in degrees. No differences were found between conditions where participants were asked to press a button upon perception of the target In the decision task, where participants viewed an identical stimulus array but were instead asked to report if the target started its trajectory to the left or right of straight ahead, reaction times as a function of screen position increase as well as follow some interesting patterns.

Most prevalent in the data is an observed effect of uncertainty as the starting position of the target gets closer to the reference landmark: the center of the screen (Fig. 3.7). Looking at the CRT data, the static stimulus showed the greatest amount of uncertainty where targets shown closer to the center of the screen had higher rates of uncertainty and a higher overall reaction time. The leftward and rightward motion conditions were also subject to this increase in uncertainty, however, the peaks of those curves are shifted away from the center of the screen and in the direction of motion, perhaps caused by the mislocalization of the target's starting position due to the FE. These peaks are not as robust as the one in the static condition, potentially due to variability in the magnitude of the FE on a trial-by-trial basis.

Interference Effect

Curiously, the CRT curves for leftward and rightward objects have interesting structures, not purely a Gaussian curve since the leading edge of the curve and the trailing edge are not equal. We seem to be capturing an additional variable in our data, that we believed to be akin to the Simon effect where RTs are slower when stimulus location and response location are incongruent compared to when they are congruent (Simon & Rudell, 1967).

Due to this consideration, we needed to subtract the trend caused by this interference in order to isolate the true peak reaction time present in the data. Curves in the left and right motion conditions for the choice task displayed a shape resembling the sum of a Gaussian (highest perceptual uncertainty) and a sigmoidal function (interference effect), and so we create fits within participants in order to model this effect (Fig. 3.8).

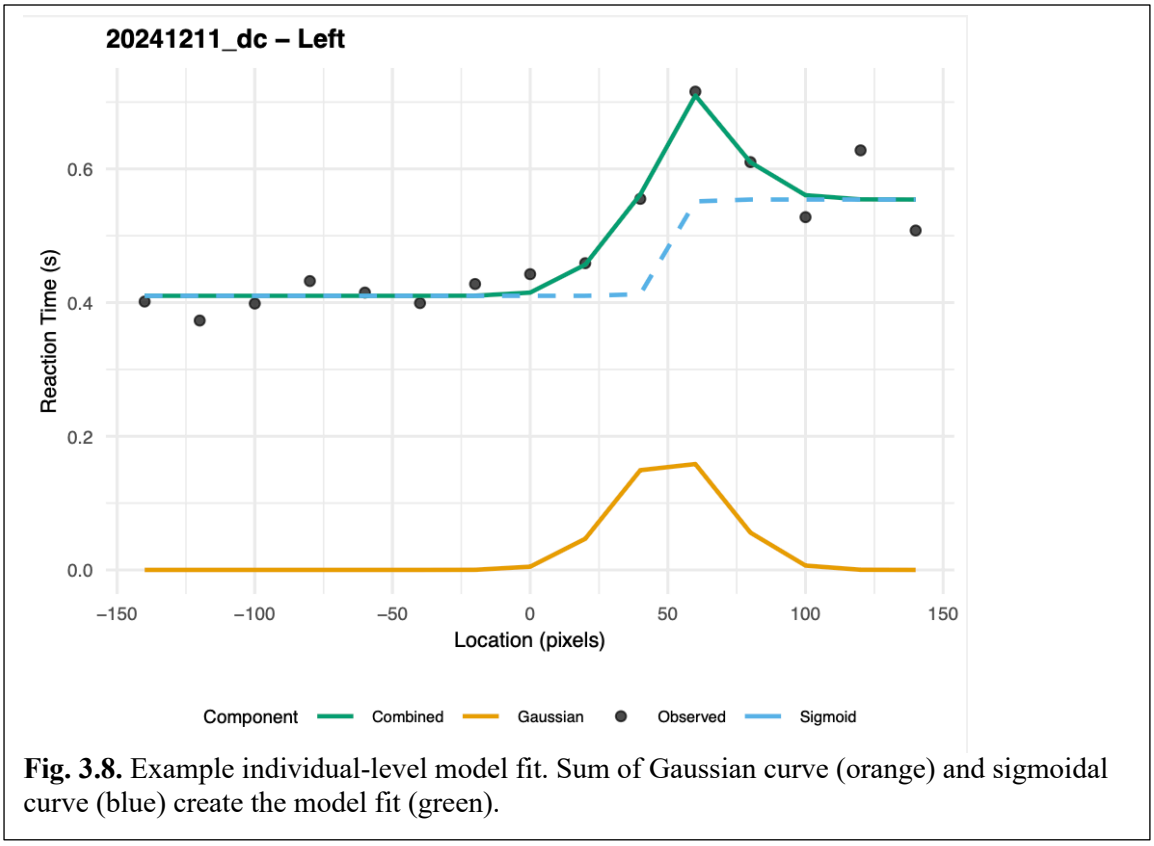


Fig. 3.8. Example individual-level model fit. Sum of Gaussian curve (orange) and sigmoidal curve (blue) create the model fit (green).

Model Fitting

RT data from the CRT task were modeled as the sum of two components: a Gaussian term, capturing the increase in RT near the point of subjective equality (PSE) where perceptual uncertainty is highest, and a sigmoidal term, capturing the interference effect when motion direction conflicted with starting position. The model took the form:

$$RT \sim base + \frac{A_g}{\sigma\sqrt{2\pi}} \cdot e^{-\frac{(P - b^1)^2}{(2s^2)}} + \frac{A_s}{\left(1 + e^{-k(P - x^0)}\right)}$$

where:

- x = target's horizontal starting location in pixels
- A_g = amplitude of the Gaussian component (strength of uncertainty; constrained to [-∞ , 40]) in ms

- μ = Gaussian center (location of peak uncertainty; constrained to [-140, 140]) in pixels
- σ = Gaussian width (spread of uncertainty; constrained to [-∞, 50]) in pixels
- A_s = amplitude of the sigmoid component (strength of interference effect; constrained to [-0.2, 0.2]) in ms
- k = slope of the sigmoid (constrained to [-∞, 0.4]) in pixels/ms
- x_0 = inflection point of the sigmoid function (location of perceived straight ahead; constrained to [-140, 140]) in pixels
- b = baseline RT (constrained to [-∞, 0.75]) in ms

Fitting was done at the group-level and individual-level. First, RT data were averaged across participants to produce a group-level dataset for each motion direction (leftward, rightward, and static) at each level of screen position. Afterwards, we fit a group-level model using Excel Solver to minimize the sum of squared error between observed and fit RTs. These fits provided a stable set of parameters for the individual fits.

Next, the same function was fit to each participant's data, again for each motion direction, using the group-level parameters as initial values. From each individual fit, we extracted the Gaussian center (μ) and the sigmoid inflection point (x_0) for analysis since these variables should be indicative of the location of the participant's perceived straight ahead.

Decision Task Model Fits – Gaussian center (b1)

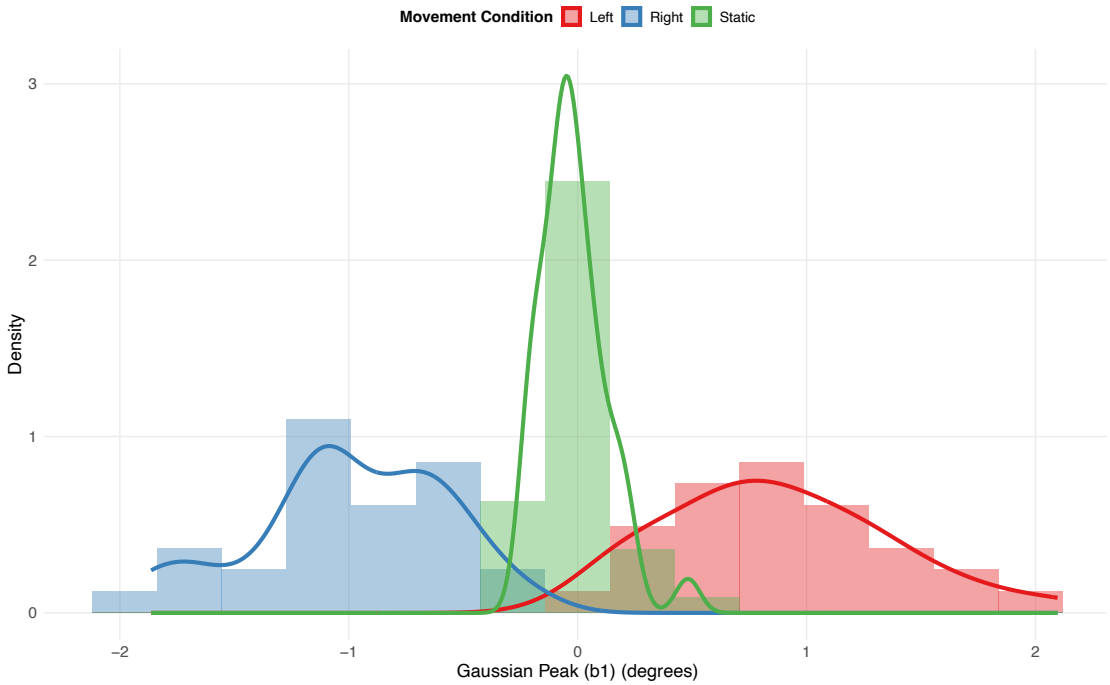


Fig. 3.9. Density plot of the distribution of b_1 (Gaussian center) estimates by stimulus onset location**.** Leftward estimates show a shift of estimates in the positive direction, representing the perceptual shift caused by leftward motion. Targets moving leftward appear further along their trajectory in participant's perception causing a target with a positive screen position to appear at a more negative one. This same effect can be seen flipped for rightward motion.

We interpreted the position of the peak of our Gaussian component (b_1) as the location of greatest perceptual uncertainty, i.e., where decisions were slowest due to increased uncertainty in localization. Isolating the Gaussian center component in the model fits show different clusters of Gaussian center estimates based on the direction of motion, which is expected considering the FE (Fig. 3.9). In our model estimates, there were a few participants (11%) where the curve fitting results in negative amplitudes for the Gaussian component. Since a negative Gaussian amplitude is difficult to interpret, we excluded these participants from subsequent analyses. We demonstrate that the removal of these participants did not have a notable effect on our correlation analysis (Fig. 3.10).

If the shift in peak uncertainty *is* caused by the FE, then the individual differences in peak Gaussian component should be correlated with the PSE in the Staircasing Block. We tested whether the isolated Gaussian center component aligned with the perceptual mislocalization associated with the FE as measures by the PSE in our Staircasing Block. Notably, we observed a significant positive correlation between illusion magnitude and the Gaussian center parameters in both the left and right conditions, $r = 0.31$, $p = 0.248$ (Fig. 3.10). This suggests that the regions of highest latency coincide with zones of highest perceptual ambiguity derived independently from the staircase method. The Gaussian component that we isolated from the data provides a RT measure of the same distortion exhibited in the perceptual reports.

We also wanted to explore if the RT value in our model fit at the b1 value correlated with the RT value of our fit at the subject's PSE. Following our hypothesis, if speed of processing is affecting both RTs and FE magnitude, then we should see a correlation between the two, with shorter RTs lead to smaller illusion magnitudes. To test the relationship between RT_{choice} and FE magnitude, we computed Pearson correlations between each participant's illusion magnitude and the RT value of our model fit. No significant relationship was found ($r = 0.11$, $p = 0.380$; Fig. 3.11), suggesting that the illusion is not simply brought about by processing delays that can be assessed through

reaction times.

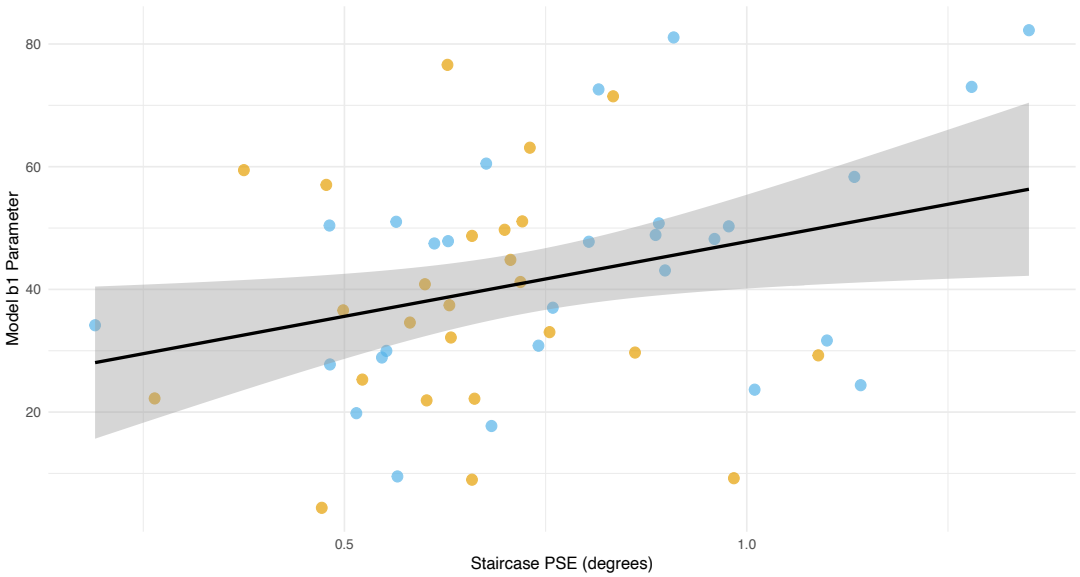


Fig. 3.10. Correlation plot of Staircase PSE by Gaussian center parameter estimates by participant, $r = 0.31$, $p = .025$.

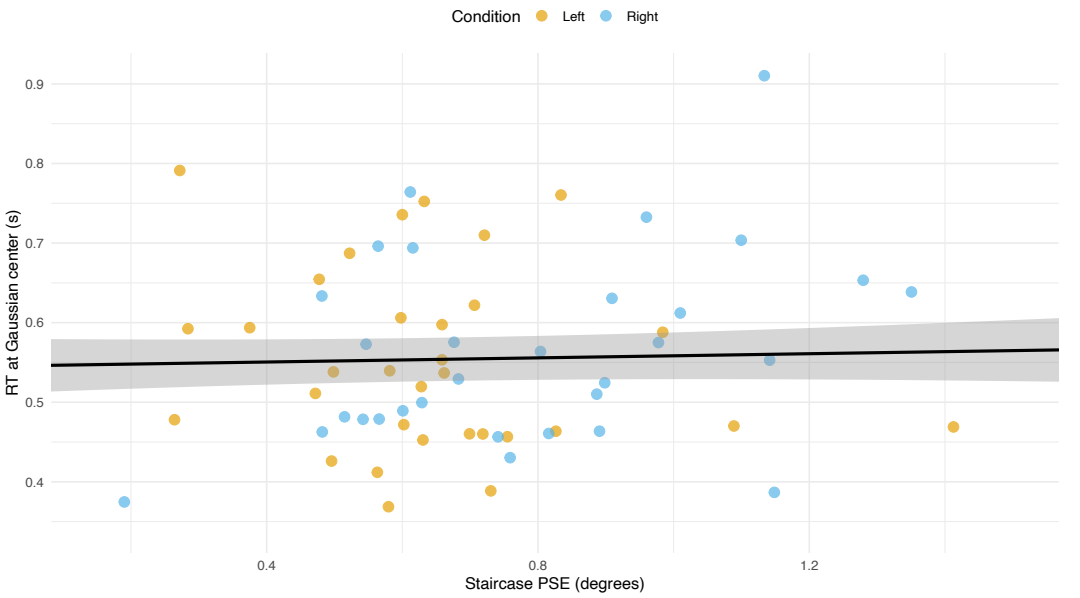


Fig. 3.11. Correlation plot of illusion magnitude by RT values at the Gaussian center parameter estimates by participant, $r = 0.11$, $p = 0.380$.

Discussion

The present study investigated whether localization biases in the FE reflect early sensory-level delays, higher-order perceptual shifts, or decisional/motor biases. We examined how simple task RTs and forced-choice localization RTs measures related to each participant's illusion magnitude (PSE). Ultimately, our results did not clearly implicate any particular level of processing as the source of the FE.

Our results replicate the core finding of the FE, where participants reliably mislocalize the starting location of a moving target in the direction of motion. RT_{choice} consistently exceeded RT_{simple}, and since our stimulus array in both tasks was identical, we could subtract the two time courses to isolate $t_{decision}$ (Fig. 3.1). However, even with this isolation, neither RT_{simple}, RT_{choice}, or $t_{decision}$ showed a significant correlation with illusion magnitude, demonstrating that at least in the averaged RT measures, neither processing speed nor decision latency alone can explain the variability in FE across individuals.

As a post-hoc analysis after finding the presence of an interference effect in our data, we did more complex modeling to capture the effects present in the data. We isolated RT_{choice} patterns across stimulus onset locations into Gaussian and sigmoidal components to account for the observed effects of response uncertainty and interference. The center of our Gaussian fit (b_1), interpreted as the location of greatest perceptual uncertainty, aligned closely with the location of each participant's illusion magnitude. This relationship was statistically significant and symmetric across left and right motion directions, indicating that the zone of peak RTs correspond to the same spatial offset where participants subjectively perceive alignment between the moving target and

fixation. The main takeaway from this significant result is that we found an effect of the FE present in the RT data. This also suggests that in the FE, the representation of starting location is already biased by the time that a decision is being made. Increased RT_{choice} at the PSE likely reflects increased perceptual uncertainty from the already biased perceived starting location.

Motion extrapolation suggests that there are visual mechanisms in place that account for the delays of the visual system and predict where a moving object "should" be, shifting the internal representation of target location in the direction of motion (Nijhawan, 1994; Maus, et al., 2013; Hogendoorn et al., 2020). Temporal averaging and neural oscillatory sampling suggest that motion is processed in discrete windows with each one pulling the perceived starting location toward the weighted average of motion within that window (Krekelberg & Lappe, 1999; Schneider, 2018). Our results could not distinguish between these theories as both would happen before decisions are made and could explain why participants' illusion magnitudes align with peak RT position in our model fit.

Ultimately, we did not find a relationship between any specific level of processing and the FE. One possibility is that the FE does not stem from one particular point in the perceptual process but is rather an integration of multiple processing stages. In this explanation, the FE may not rely on a single oscillatory mechanism, similar to the findings of Morrow and Samaha (2021). This could also help to explain the lack of significant findings in our Experiment 1 (Chapter 2), where the modulation in one layer of processing is insufficient enough to change the overall perceptual outcome in the FE.

The null results between the FE magnitude and our RT components further support this theory where the FE operates across distributed sources (such as attentional shift, sensory gating, and motion extrapolation) and is then resistant to correlations that isolate only one of these elements. In this case, the lack of correlation between any one isolated component reveals that the FE is a more complicated phenomenon than we initially theorized.

- Chapter End -

CHAPTER IV

DO TEMPORAL SAMPLING MECHANISMS GENERALIZE ACROSS VISUAL ILLUSIONS?

Perception does not unfold instantaneously, but instead through signals that ebb and flow with the brain's own rhythmicity. Research into the mechanisms underlying many visual illusions suggests the role of a gating mechanism that shapes the flow of incoming sensory information, alternating between moments of high and low activation to shape when inputs are combined or separated in time (VanRullen & Koch, 2003). In vision, this rhythmic structure has been linked to alpha-band activity of the EEG and shown to leave measurable signatures in behavior.

One way to probe these dynamics is by using sensory entrainment – rhythmic, external, sensory stimulation that can align relevant brain rhythms to the frequency of the stimulus. Prior work has demonstrated how entrainment at the alpha rhythm can influence visual detection up to 300-500 ms post-entrainment (De Graaf, et al., 2013; Spaak et al., 2014). Ronconi and Melcher (2017) used this approach to investigate the Two-Flash Fusion (TFF) effect – a phenomenon where two subsequent flashes are equally likely to be perceived as one flash or two flashes if the inter-stimulus interval (ISI) between the flashes is close to the temporal resolution of an observer's visual system. They delivered a short audiovisual entrainment sequence followed by dense sampling of the subject's perceptual report across dozens of time points within a 300 ms time frame. They reported a clear oscillation in behavioral reports based on the pre-

stimulus entrainment frequency used. VanRullen (2016) discusses how modulation of the perceptual threshold may result in differences in the perceived timing of stimuli (Fig. 1.3), and this same mechanism may also underlie instances of separation or fusion in the TFF.

In the current study, we attempt to replicate and expand upon these findings into the motion localization domain, investigating if these modulations extend to localization illusions such as the Fröhlich effect (FE) – where the perceived starting location of a moving target is biased in the direction of its trajectory. The displacement between perceived and physical starting location in this phenomenon has been tied to timing-dependent mechanisms such as rhythmic sampling and temporal averaging accounts (Krekelberg & Lappe, 1999; Schneider, 2018). If phase-modulated sampling gates when motion signals reach awareness, then entrainment should periodically shift the perceived starting point, just as it shifts fusion in the TFF. The same oscillatory mechanism that underlies segregation/integration may also bias perceived onset of motion.

Our design follows the general template used by Ronconi and Melcher (2017), in order to compare these two illusions (TFF vs. FE) using identical entrainment stimuli across both tasks to determine if they are driven by similar mechanisms. We replicate their dense sampling procedure to probe for oscillatory components near the entrained rhythm present in the behavioral time series of perceptual reports in both illusion blocks. We also implement some changes to improve upon the experimental design from Experiment 1 (Chapter 2). A visual entrainment stimulus was added in addition to the auditory stimulus to maximize the likelihood and strength of entrainment. In Experiment 1, we did not have a way to support that our neural entrainment was successful, so we use

the study by Ronconi and Melcher (2017) to this effect. If we can replicate their findings with entrainment on the two-flash fusion effect, that will demonstrate that our entrainment was successful. We predict that if the FE and TFF share early sampling mechanisms then their behavioral oscillations should both reflect the presented entrainment frequency. Alternatively, if these two are driven by separate mechanisms, we may observe the absence of a modulation within one task but not the other.

Methods and Procedures

Participants

Twenty-eight participants were tested using the Psychology Human Subjects pool at University of Oregon. All participants were compensated with course credit in exchange for participation, provided informed consent and reported normal or corrected-to-normal vision and no history of neurological disorders, epilepsy, or medications that may cause susceptibility to epilepsy. Procedures were approved by the University of Oregon Institutional Review Board (IRB). Two participants were dropped from the FE task analysis for completing fewer than 80% of trials within the allotted time.

Stimuli and Apparatus

Stimuli were presented on a 24-inch Samsung gaming monitor (with a digital image 11in wide, 1024x768 resolution, and a 240 Hz refresh rate), positioned 69 cm from the participants' eyes. A central fixation point (0.16° visual angle) remained on screen before, during, and after each trial. Stimulus presentation was confined to a range of ±200 pixels or ±4.53° visual angle horizontally from the fixation point on a gray background. To minimize expectancy, stimulus onset asynchrony (SOA), vertical target position, and

motion direction (in the FE task) were randomized within blocks. Stimulus presentation and response collection were managed by PsychoPy v2024.2.4.

The study employed a within-subjects design with two task conditions: FE task and the TFF task. Both tasks used a combined auditory/visual entrainment stimulus that consisted of a 440 Hz sinusoidal tone ("Tone A" in PsychoPy) that played through over-ear headphones for 25 ms every 117 ms (8.5 Hz) in sync with full-contrast, flashing rectangular bars 9.32° wide x 1.13° high, 2.83° above and below the fixation point. Sixteen entrainment pulses preceded the target sequence. The SOA was then varied (8.33 ms – 233 ms in 8.33 ms increments) between the last entrainment stimulus and target onset, resulting in 28 levels of SOA and an effective sampling rate of 120 Hz.

The FE target consisted of a vertically oriented, Gaussian-blurred ellipse (0.68° wide, 1.70° tall), presented either 1.59° of visual angle above or below the fixation point. On each trial, the target moved either leftward or rightward at ±50.79°/s for a duration of 500 ms.

Targets in the two-flash fusion (TFF) task consisted of solid filled circles with a radius of 0.17° visual angle and a Gaussian blur presented either 1.59° above or below the fixation point. After entrainment and SOA delay, two brief flashes appeared at the same location, separated by 41.7 ms (10 frames), matching a previous study with the two-flash fusion task done by Ronconi and Melcher (2017). The parameters of our entrainment stimulus and two-flash fusion design are meant to mimic that of the experiment done by Ronconi and Melcher in 2017.

Procedure

Participants were placed in a dark room to complete both experimental blocks in a randomized order (FE ~ TFF), with designated breaks after each block. The FE block consisted of a staircasing phase to estimate each participant's PSE, followed by the FE entrainment task. The TFF block consisted of only the entrainment TFF task (no staircasing phase was needed) using the same entrainment design and dense temporal sampling as the FE entrainment task. The entire session lasted about 100 – 115 minutes.

Fröhlich Staircasing Block

Before the FE entrainment task, we estimated the magnitude of the FE for each participant using four interleaved staircases: Left-Upper, Right-Upper, Left-Lower, and Right-Lower. The "Left" and "Right" staircases had horizontal starting locations of -4.53° and +4.53° from fixation, respectively. "Upper" and "Lower" targets were positioned +1.59° and -1.59° above/below the fixation point, respectively.

Upon trial initiation, the target stimulus appeared at each staircase's respective starting location and moved across the screen in a rightward motion at a rate of ±50.79°/s. Each staircase trial used an SOA value of 72 ms. All staircases decreased in step size with each reversal until a minimum step size of ±0.05° was reached (step sizes included ±1.45°, ±0.73°, ±0.36°, ±.18°, ±0.09°, and ±0.05°). Participants judged whether the starting point of the target was left ('F' key) or right ('J' key) of fixation using a keyboard to indicate their response. The fixation point remained visible throughout the duration of each trial. The block was completed after 100 trials in each staircase.

Once the staircasing block was complete, we calculated PSE of each staircase by filtering down to the smallest step size and then averaging the magnitude of the displacement between starting position and fixation point. The absolute value average of

the “Left” and “Right” Staircases (after filtering down to the smallest step size) was used to determine the “Upper” and “Lower” PSEs. These PSEs were used to determine the horizonal starting location of upper and lower targets for trials in the subsequent FE entrainment phase.

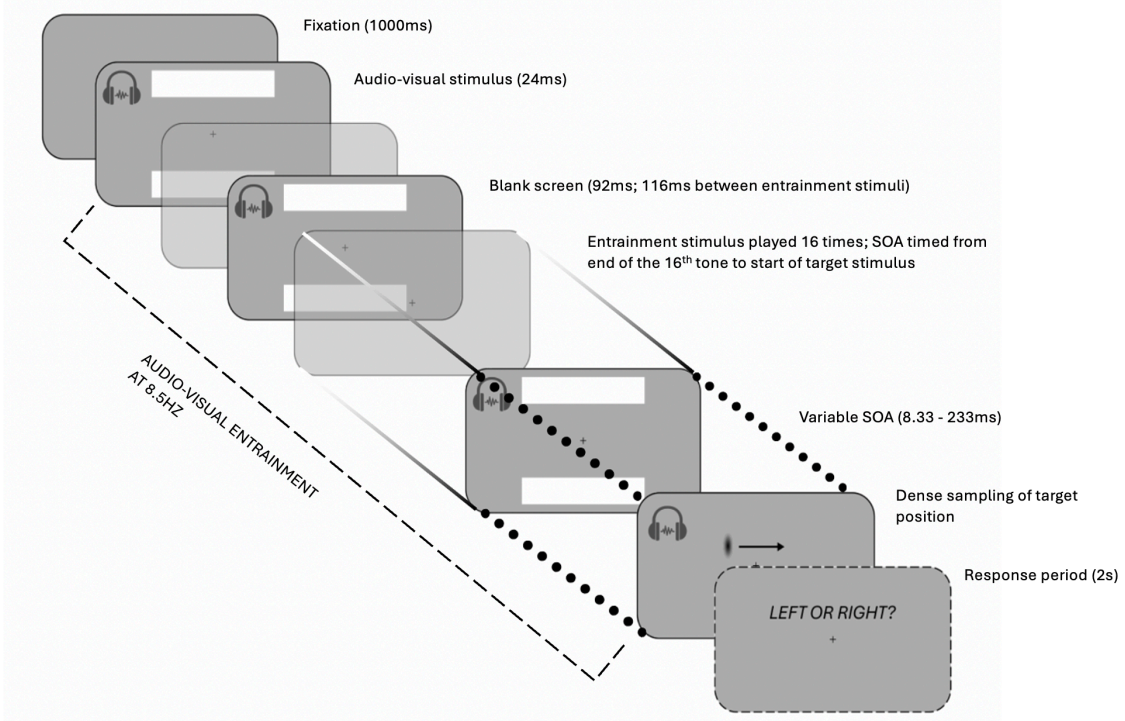


Fig. 4.1. Schematic of FE task procedure. After the audio-visual entrainment sequence at 8.5 Hz, participants report of perceived starting location in the Fröhlich effect was densely sampled to probe for effects of the entrainment rhythm on perceptual report.

Fröhlich Task

Participants were asked to report whether the starting position of the moving target was left (‘F’ key) or right (‘J’ key) of fixation.The FE task reused the same display as the staircasing procedure but fixed the horizontal starting location of the moving target at the participant’s PSE on every trial (control trials with a horizontal starting location of the PSE ±20% were also included, so as to provide some obvious variance to in starting

locations). Two levels of vertical target starting locations (1.59° above or below the fixation point) were included to ensure further uncertainty in the target's starting location. Control trials used the participant's PSE ±20%. Each trial began with a spacebar press, a brief delay of 1000 ms, then the audiovisual entrainment stimulus train (16 tones; 117 ms spacing between). After the presentation of the 16th entrainment stimulus, the target presentation began with an SOA between 8.33 ms and 233 ms (in 8.33 ms steps) to densely sample from the subject's resultant entrained perceptual oscillations (Fig. 4.1). This range of SOAs was used to effectively sample from nearly three cycles of the alpha rhythm (outside of this range, entrainment effects have been found to begin to deteriorate (de Graaf et al., 2013; Spaak et al., 2014)). The target appeared and moved with the same properties of the moving target used in the staircasing task. Participants reported with a keyboard press whether the target began its motion to the left or right of fixation. Participants completed 392 experimental trials (7 trials each x 28 levels of SOA x 1 level of Displacement x 2 levels of Y position) and 42 number of control trials (7 trials each x 3 levels of SOA x 2 levels of vertical location). Targets were shown at each participant's point of subjective equality.

Two-Flash Fusion Task

TFF task trials followed the same structure as the FE entrainment task but with a two-flash stimulus instead of a moving target. Trials were initiated with a space bar press followed by a delay of 1000 ms, then 16 presentations of the audiovisual entrainment stimulus at an 8.5 Hz rhythm (116 ms between flashes), the SOA delay, followed by two subsequently flashed circular target stimuli with an ISI of 42 ms (Fig. 4.2). Control trials in this block used ISIs of 0 ms to combine the two target stimuli into one flashed

stimulus. Participants were then asked to report whether they perceived one or two flashes. Participants responded using the 'F' key for one perceived flash and 'J' key for two. Participants completed 392 experimental trials (7 trials each x 28 levels of SOA x 1 level of ISI x 2 levels of Y position) and 112 control trials (7 trials each x 8 levels of SOA x 1 level of ISI x 2 levels of Y position).

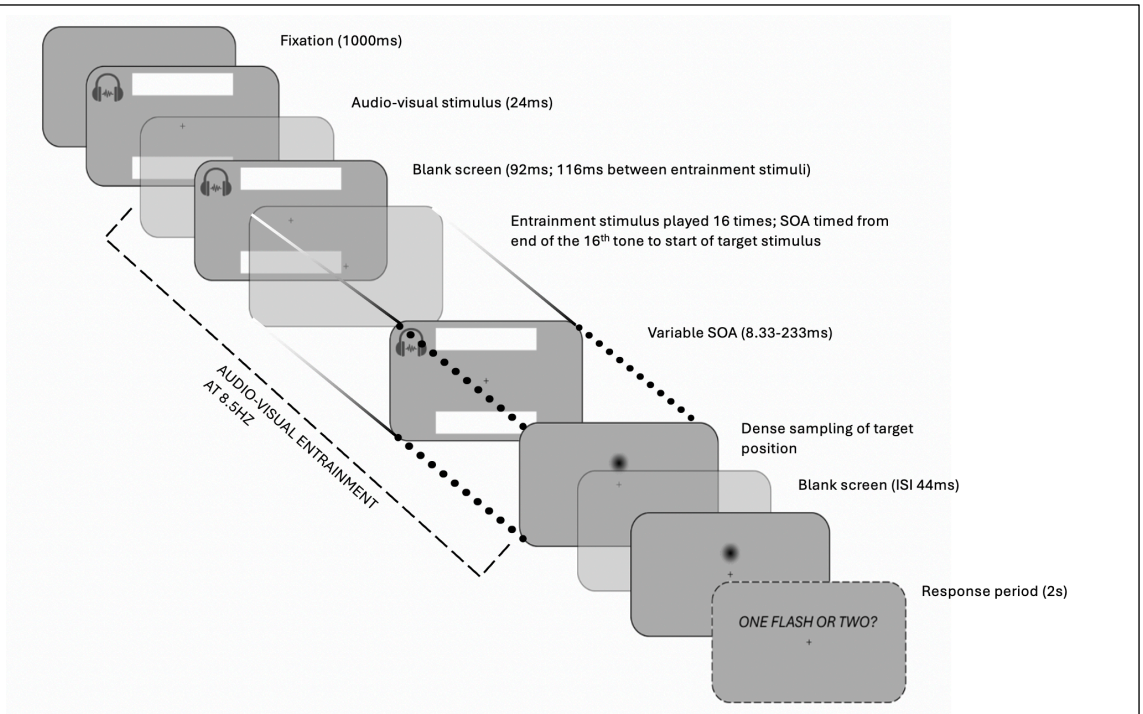


Fig. 4.2. Schematic of TFF task procedure. After the audio-visual entrainment sequence at 8.5 Hz, participants report of number of perceived flashes in the two-flash fusion effect was densely sampled to probe for effects of the entrainment rhythm on perceptual report.

Preprocessing of Time Series Data

Time series data for each task block was collected for 28 participants in the TFF task and 26 participants in the FE task (2 participants removed from FE condition due to insufficient number of trials completed, <80%). Data from both tasks was filtered to exclude any participants with PSEs beyond 3 SDs of the group mean or response rates above 90%, however, this did not apply to any participants. The left-response rate (LRR)

in the FE task and the two-flash rate (TFR) in the TFF task were densely sampled across 28 different SOAs (Fig. 4.3). All analyses were done in R (v4.5.2)

Results

Individual time series of both task blocks were detrended using natural cubic splines to remove the potential masking effects causing a bias of earlier SOAs to exhibit lower temporal resolution due to their proximity to the entrainment stimulus (Fig. 4.3A). Following detrending, a 4 – 18 Hz bandpass Butterworth filter (order 2 IIR) was applied to each individual time series to isolate the frequency range of interest before performing frequency analyses (Fig. 4.3B). Prior to aggregation, individual time series were also permuted 1000 times by shuffling the SOA labels across the x-axis to remove time-dependent patterns in the data. The permuted, shuffled individual time series comprised our null data set for testing the significance of our frequency of interest in both tasks. Once observed and permuted individual time series were preprocessed, they were aggregated across participants by SOA to create the group-level time series.

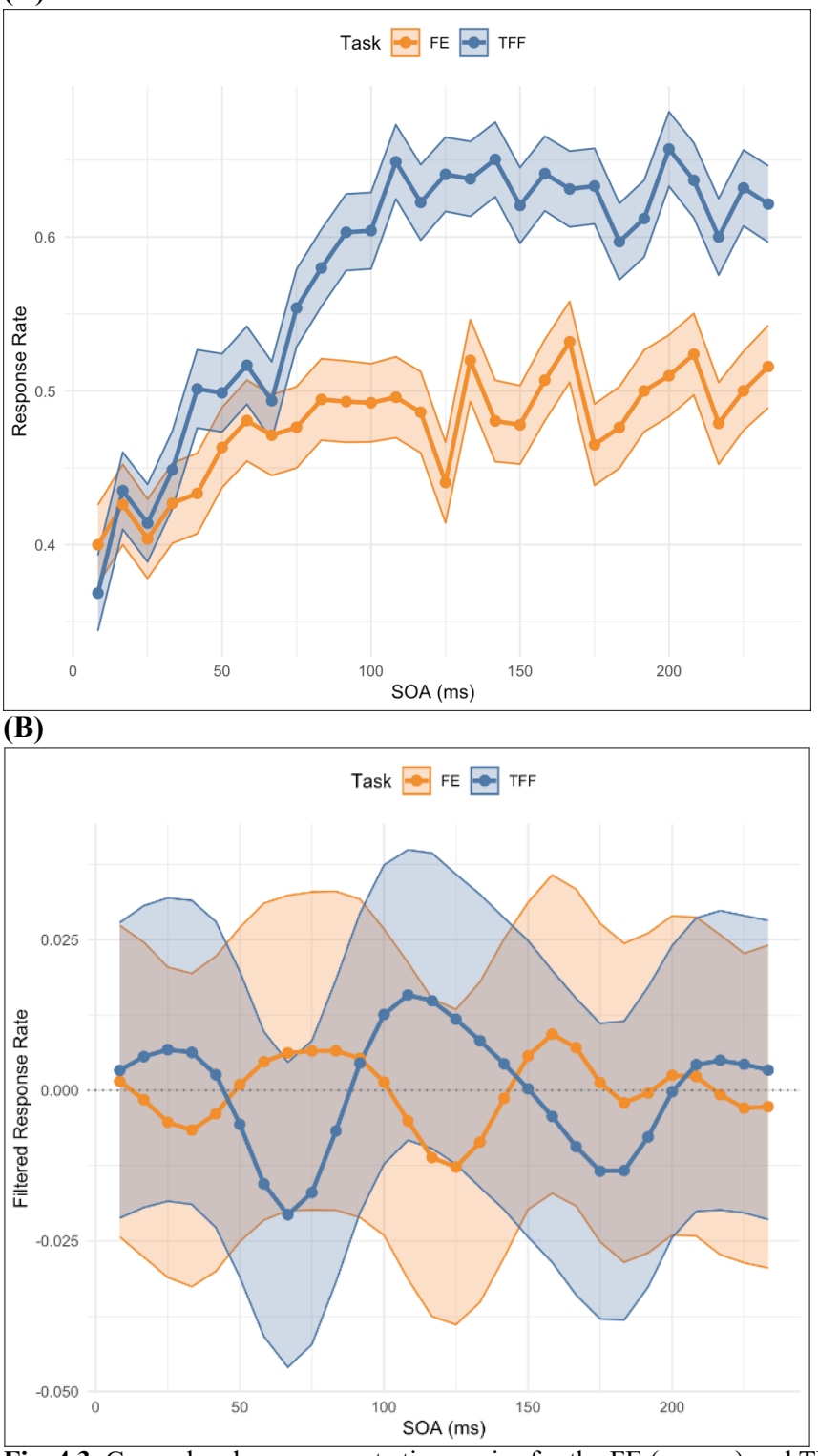


Fig. 4.3. Group-level response rate time series for the FE (orange) and TFF tasks (blue) across 28 SOA conditions (A) before preprocessing (B) and after spline detrending and filtering to 4 – 18 Hz.

Sinusoidal-fitting Permutation Analysis

To determine the presence of any modulations in behavioral data at the entrainment frequency, we measured the fit of an 8.5 Hz sinusoid to the behavioral time series averaged across participants (Fig. 4.4; Ronconi & Melcher, 2017; Fiebelkorn, et al., 2011). The goodness of fit of this sinusoid to our observed data was calculated as the Adj-R^2 value and compared against the critical value ($\alpha = 0.05$) obtained from a null distribution of the goodness of fit values from the 1000 permutations of the original data. The goodness of fit for the sinusoidal function was calculated as the following with all parameters allowed to vary freely:

$$y = \mu + a \cdot cos(2\pi f x) + b \cdot sin(2\pi f x)$$

where μ represents the mean response, *a* and *b* represent the cosine and sine coefficients, and *f* is the frequency parameter. All parameters were allowed to vary freely in the sinusoidal fit of our permutation data. For the fit of our observed data set, frequency was constrained to the entrainment frequency in order to robustly test the presence of our observed oscillatory pattern modulated by the entrainment frequency compared to those created by the null data set.

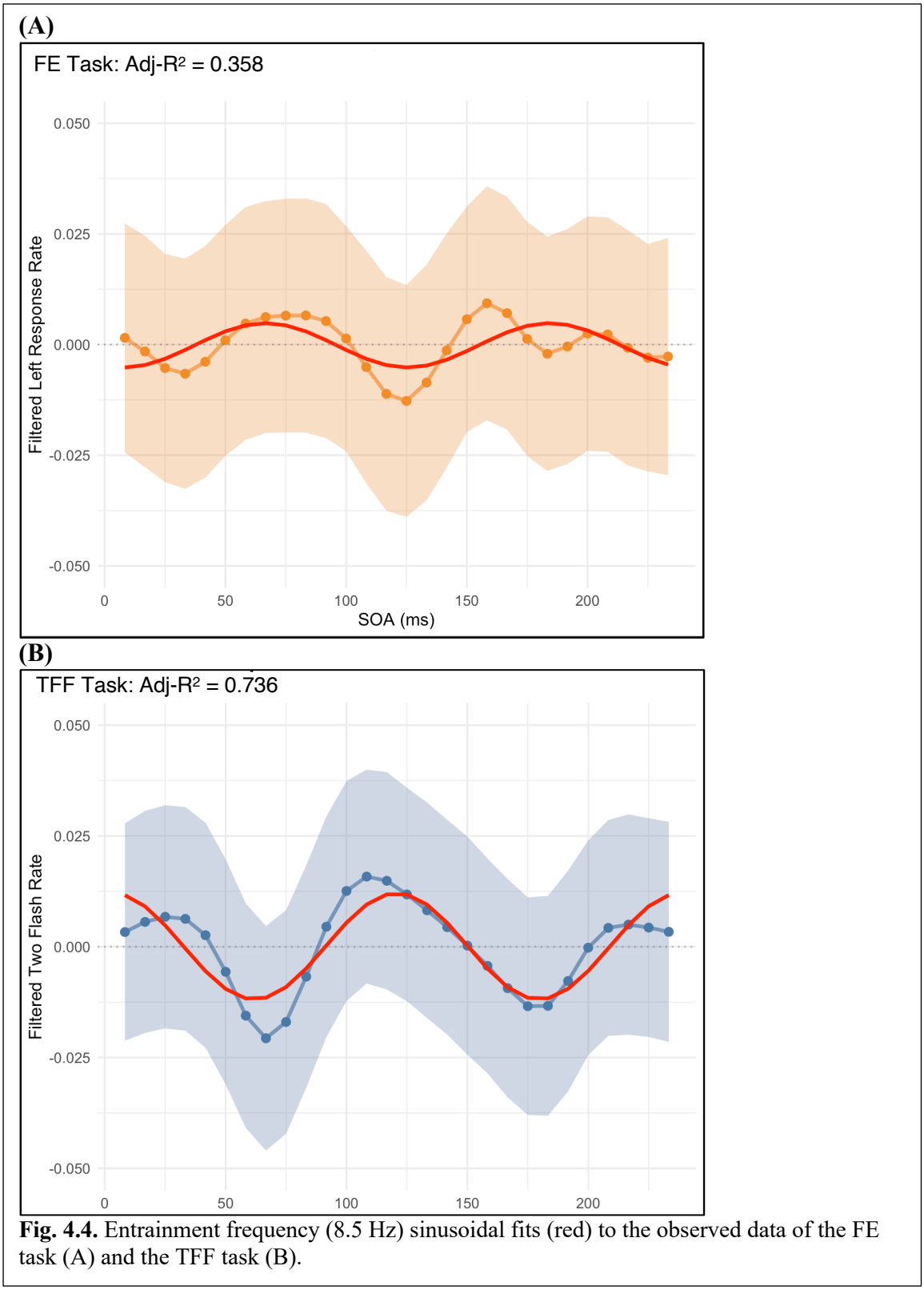


Fig. 4.4. Entrainment frequency (8.5 Hz) sinusoidal fits (red) to the observed data of the FE task (A) and the TFF task (B).

Our observed Adj-R^2 values for both tasks were compared to our null distribution of Adj-R^2 values obtained from the permuted, aggregate data set (Fig. 4.5). The TFF task showed a robust goodness of fit at 8.5 Hz that exceeded the null distribution of goodness of fit values (Adj-R^2 = 0.736, critical value = 0.366, $p < .001$), whereas the FE task goodness of fit did not exceed the 95th percentile of our null distribution (Adj-R^2 = 0.358, critical value = 0.373, $p = 0.063$), indicating some reliable oscillatory behavior in the structure of two-flash response data but not Fröhlich task. The TFF task data can be seen to exhibit a much larger effect of entrainment on the response data.

Fast-Fourier Transform

We analyzed the response rate time series by SOA with a real-valued FFT (RFFT). Prior to transformation, each participant's time series was: detrended with a natural cubic spline to remove masking effects of the entrainment stimulus, band-pass filtered (second-order Butterworth) from 4 – 18 Hz to isolate the alpha-range components, and padded to increase the frequency resolution using a 4x zero-padding. These preprocessing steps were done for both our observed data as well as for 1000 permutations of our data to create a null data set where SOA labels were randomly shuffled to erase time-dependent patterns.

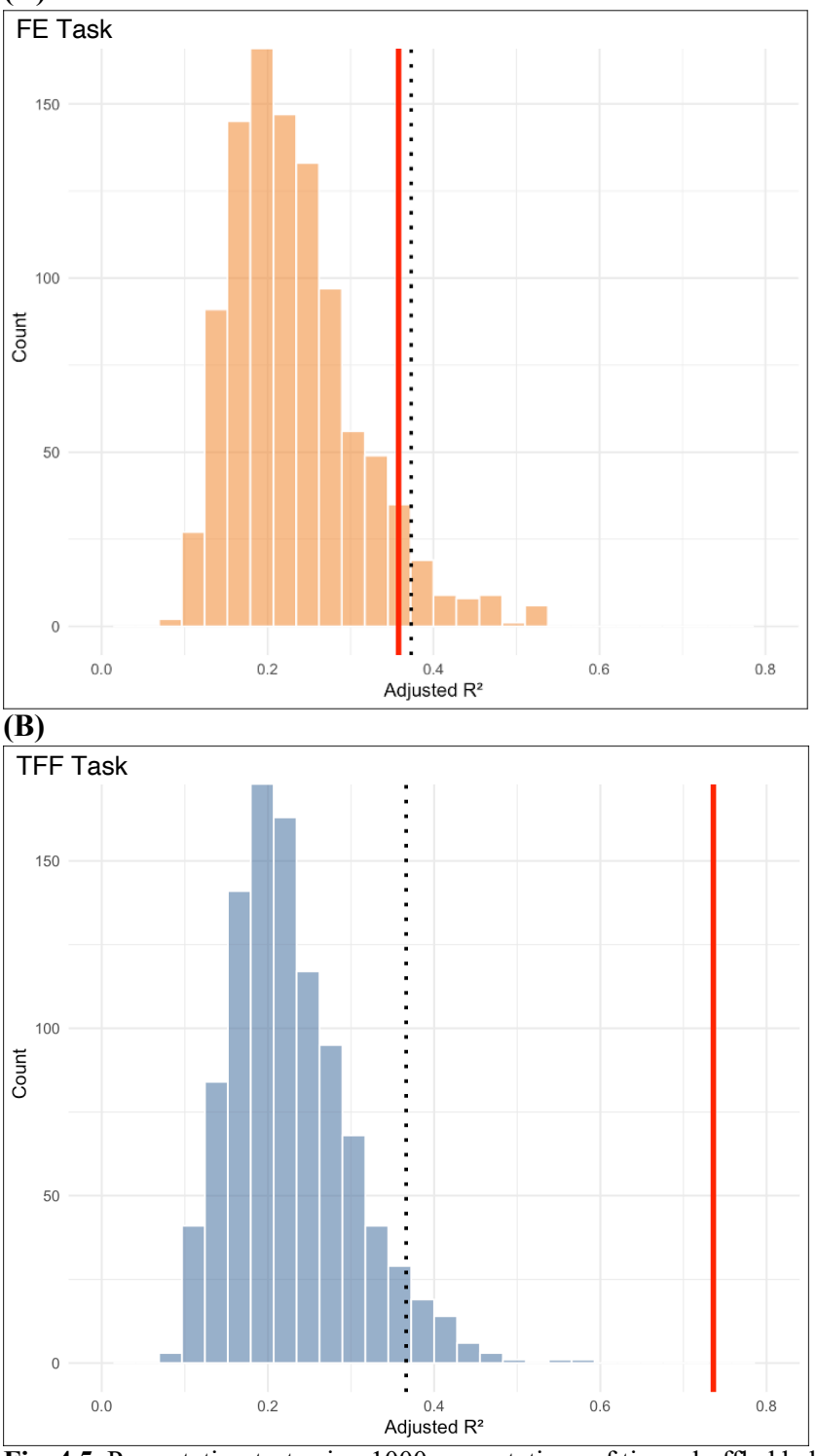


Fig. 4.5. Permutation test using 1000 permutations of time-shuffled behavioral data in each task condition. Goodness of fit (Adj-R^2) calculated for each permutation to create a null distribution with which to compare the goodness of fit of the observed data.

FFT Amplitude Permutation Analysis

In order to analyze the magnitude of the effect of the 8.5 Hz modulation in our behavioral data, RFFTs were conducted on the preprocessed aggregate time series for each task block (Fig. 4.6). Amplitude values were extracted from each task condition's FFT for each frequency in our range of interest (4 – 18 Hz) in both our observed and permuted data set. *P*-values were calculated as the percentile of the amplitude values in our observed data against the 95th percentile boundary of amplitude values of the permuted distribution (Fig. 4.6)

When analyzing the amplitudes of our FFTs at the entrainment frequency (8.5 Hz), we found that amplitudes for the FE task condition were not significantly higher than those observed in the distribution of null amplitudes at 8.5 Hz ($Amplitude_{FE} = 0.190$, critical value = 0.260, $p = 0.398$). However, for the TFF task, we observed a much higher amplitude at our entrained frequency ($Amplitude_{TFF} = 0.261$, critical value = 0.260, $p = 0.047$).

We extended this analysis to all frequencies of interest in our range and calculated the 95th percentile range of our permuted distribution of amplitudes (Fig. 4.6). For the FE task, none of our observed amplitude values fell outside of the 95% interval of our permuted data, so we cannot reliably say that there was a significant difference. For the TFF data, amplitude values fell outside of the 95% range of our null distribution at 8.5 Hz ($p = 0.047$) and 9.5 Hz ($p = 0.023$), demonstrating a significant frequency component present in the time series matching our entrainment frequency.

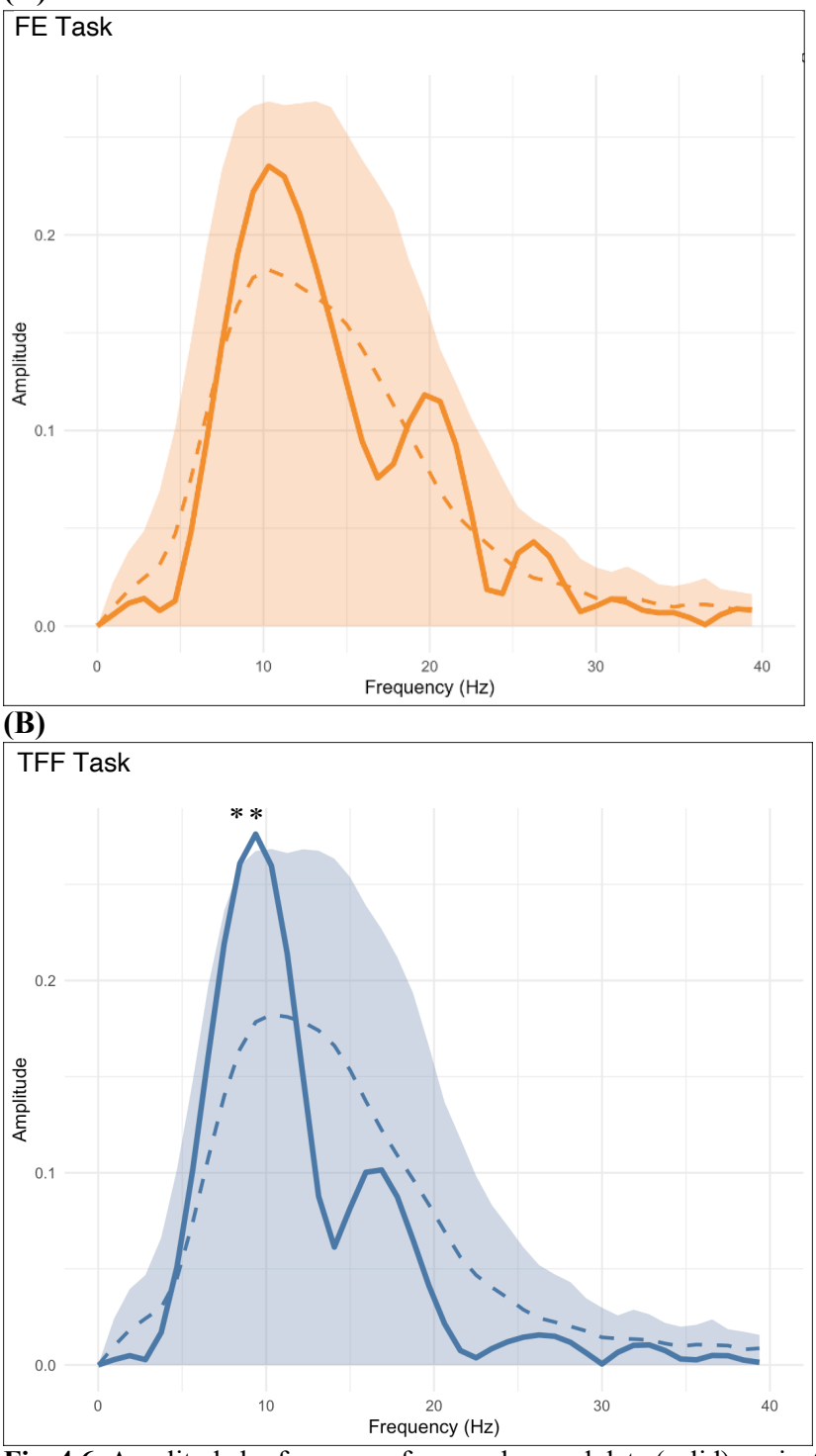


Fig. 4.6. Amplitude by frequency for our observed data (solid) against the amplitude by frequency of our null permutation data (dashed). The ribbon around the dashed line depicts the 95% range of amplitude values of our null distribution.

Phase Concentration of Perceptual Oscillations

The third test in analyzing the presence of the entrainment rhythm in the behavioral response patterns of both task conditions is measuring the phase concentration across participants. To measure this, we used a Rayleigh test for nonuniformity of circular data (Fisher, 1995) using the CircStat package in R. Neither entrainment group showed significant phase concentration in any direction (FE task: $z = 0.07$, $p = 0.887$; TFF task: $z = 0.22$, $p = 0.257$; Fig. 4.7). Additionally, we analyzed the phase-amplitude coupling between the FE and TFF tasks to determine if the amplitude of the effect had any sort of phase alignment and found no significant coupling in either task (FE: *MI* =

0.042, $p = 0.6191$; TFF: $MI = 0.0243$, $p = 0.517$).

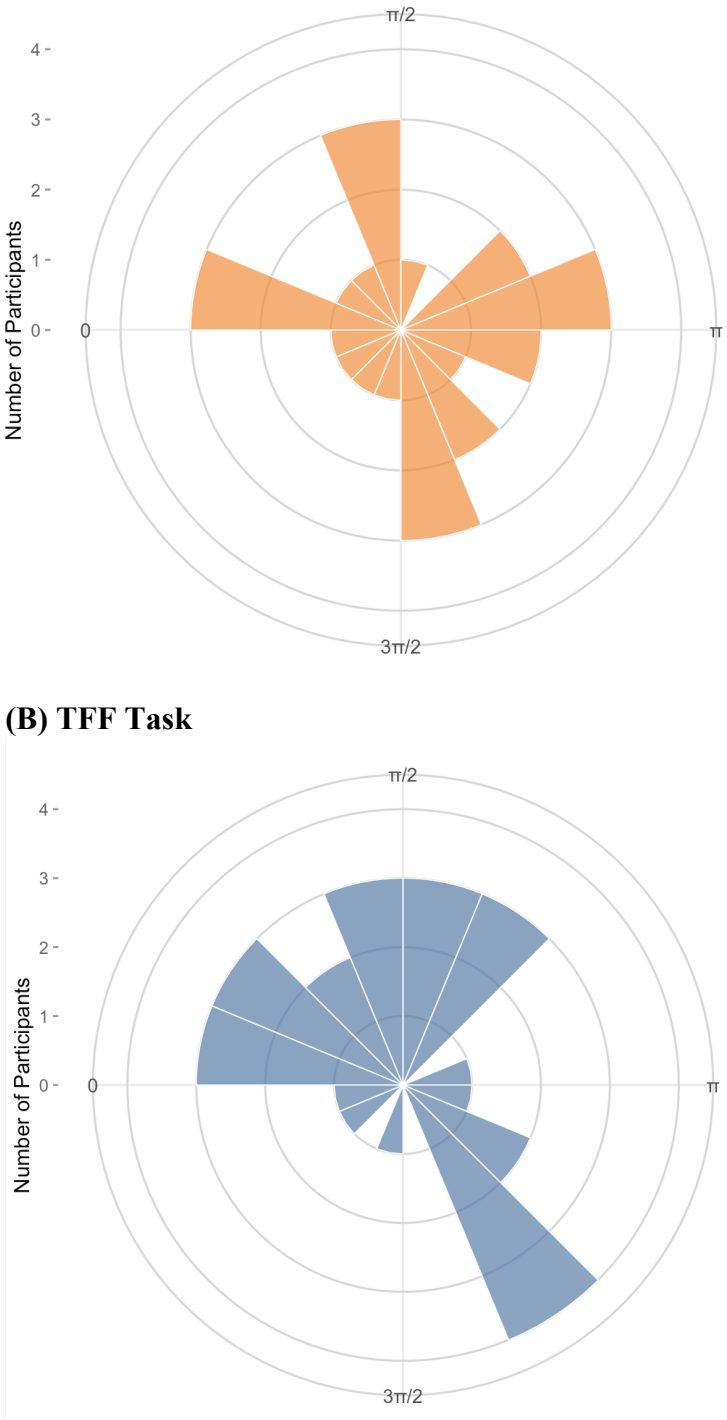
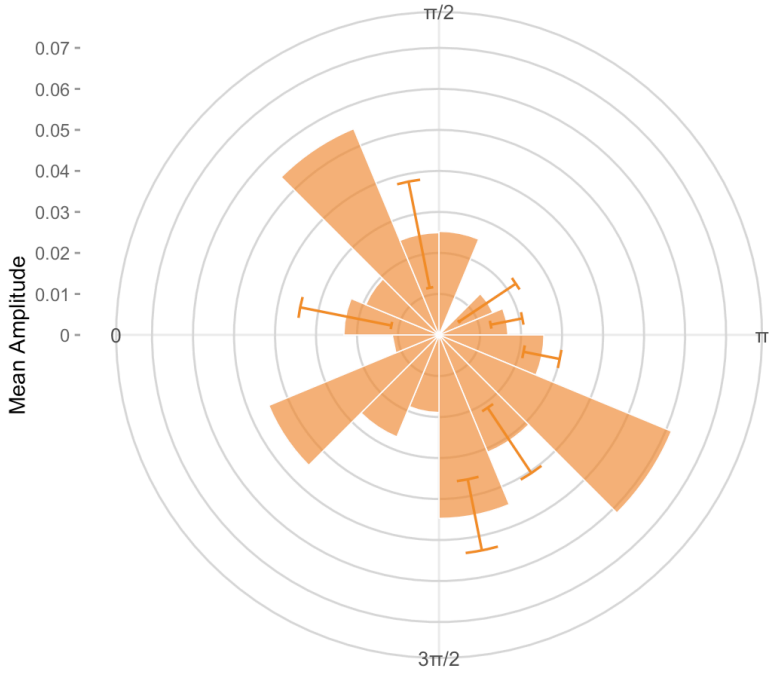


Fig. 4.7. Phase concentration by participant for each task condition.

(A) FE Task



(B) TFF Task

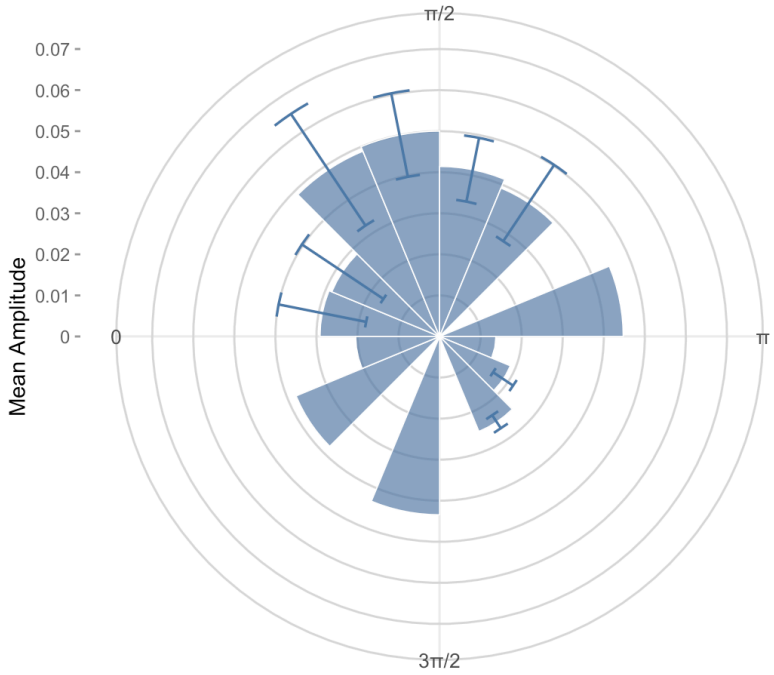


Fig. 4.8. Average amplitude across phase by participant for each task condition.

Discussion

This experiment sought to explore whether the two-flash fusion (TFF) phenomenon and the Fröhlich effect (FE) share similar temporal sampling mechanisms in a way where entrainment of perceptual oscillations would modulate behavioral response rates. Using an 8.5 Hz audiovisual entrainment stimulus train and dense behavioral sampling design similar to other studies in the oscillatory literature (Mathewson et al., 2010; Ronconi & Melcher, 2017; Wutz et al., 2018), we had three main findings. First, we observed robust oscillations in the behavioral time series of the TFF task. After detrending and filtering the response time series, a clear 8.5-9 Hz oscillatory component arose. A sinusoidal fit to the aggregate data at 8.5 Hz showed significantly better goodness of fit than permuted nulls, and the FFT analysis revealed an increase in power at both 8.5 Hz and 9 Hz, slightly exceeding the 95% confidence interval of the null distribution. This outcome replicates prior reports (Wutz et al., 2016; Ronconi et al., 2017; Ronconi et al., 2018; Wutz et al., 2018) that rhythmic entrainment can bias integration/segregation performance.

Conversely, applying the same preprocessing and analyses to the FE data yielded no significant oscillatory modulations in the behavioral data, with neither the sinusoidal goodness of fit nor the observed amplitude spectrum crossing the 95% confidence interval determined by the null distribution of the permuted data. If alpha-frequency band phase modulates FE, its effect on localization judgments was weak under the design of the current study. The absence of an effect does not rule out an effect of discrete perception on the FE as theorized by Schneider (2018), but it does suggest that FE may

be influenced by additional factors such as higher-order motion extrapolation or decision-based effects.

Lastly, Rayleigh circular tests of uniformity on participants' preprocessed time series did not show significant consistency of phase alignment in any particular direction for either task, despite other studies that used similar designs finding significant phase consistency. When adding the amplitude to this analysis, using a phase-amplitude coupling test, there still was not any presence of a significant effect within participants. Any oscillatory component that existed at the participant level did not line up to a common phase across observers at the group-level despite our entrainment stimulus. It is possible that since we are not directly measuring neural rhythms directly that there is some sort of disconnect between the presentation of the entrainment stimulus and the peak of a participant's affected perceptual oscillation, peculiar to each individual subject. Onset of the entrainment stimulus and the peak of an observer's entrained oscillations cannot be perfectly aligned since this process cannot be instantaneous; there must be some sort of delay between the two and that delay may differ from participant to participant introducing extra variability in a comparison across participants. We assume a fixed relationship between the entrainment stimulus train and the internal rhythm but any variance in that delay (possibly by different transmission times, different processing latencies) could smear phase alignment at the group level.

Altogether, these results replicate some of the findings of Ronconi and Melcher (2017) in their exploration of the effect of entrainment on the two-flash fusion phenomenon, however, they did not generalize to the Fröhlich effect. Pre-stimulus onset entrainment seems to leave a measurable rhythmic effect on response rates in the TFF

task but not in the localization response rates of the FE task. The same entrainment done in the FE task produced much no significant rhythmic signatures indicating that the FE does not stem from perceptual gating.

Potential Reasons for Differences in Findings

The alpha oscillatory literature has generally correlated alpha-band rhythms to temporal integration/segregation (Samaha & Postle, 2015; VanRullen, 2016; Wutz et al., 2018.), and our findings in the TFF data support that claim. Our FE results on the other hand, despite our hypothesis, do not support this theory, at least not when we carry the assumption that the Fröhlich effect is operating from a mechanism similar to that of segregation/integration.

One account for the FE suggests temporal sampling as the reason for the disconnect between a moving target's perceived versus veridical starting position (Schneider, 2018). In this theory, a target's perceived position updates based on where it falls within a "perceptual snapshot" or integration window. If evidence is accumulated within a window and averaged, perceived position will drift toward the window's mean (Krekelberg & Lappe, 1999; VanRullen, 2016). Entrainment literature has supported that our temporal sampling of our environment can be influenced by entrainment (De Graaf et al., 2013; Mathewson et al., 2010), and with that in mind, our results suggest that the FE is not strongly modulated by perceptual gating.

These two tasks although both seemingly reliant on temporal resolution may be operating on different perceptual mechanisms on the larger scale. The TFF effect is designed to probe early visual sampling, for example, do two near-temporal-threshold events fall within the same window and fuse or in adjacent windows and segregate? FE in

contrast reflects where a moving target began, an estimate that mixes early sampling with later computations (motion integration, position updating, motion extrapolation, decision criteria). If later stages contribute to more of the variance in the FE, effects of early alpha phase or discrete sampling can be diluted at the behavioral level. Our results support the conclusion that sensory level effects are not contributing to the FE. Further research should explore the contributions of higher-level mechanisms, such as motion extrapolation, toward the FE and if their variance dominates the final position estimate. If the mechanism for the FE operates at a higher-level than entrainment has an effect, then that could explain why we did not find an effect of the phase reset induced by entrainment at modulating the FE.

Using an entrainment design at 8.5 Hz, we replicated the oscillatory signatures in two-flash fusion but found no evidence that the same rhythmic gate shapes Fröhlich mislocalization. Mapping how and where rhythmic sampling interfaces with motion and decision processes will be key to explaining when temporal architecture generalizes across illusions and when it doesn't.

- Chapter End -

CHAPTER V

ALPHA OSCILLATIONS AND THE FROHLICH EFFECT

Discrete perception theory has been heavily corroborated by the perception literature, encompassed by the quote:

"…Two distinct events will be judged as simultaneous or sequential depending not only on the time interval between them, but also their temporal relationship to some intrinsic discrete neuronal process" (VanRullen & Koch, 2003).

Alpha-band oscillations are a strong contender for this "intrinsic discrete neuronal process" as a way for the brain to organize and structure visual perception in time. Previous literature has shown that entrainment of alpha-band neural oscillations can lead to modulations in detection as well as segregation/integration tasks which has motivated further experiments into testing whether that same rhythmic gating can influence localization tasks such as the Fröhlich effect (Busch et al., 2009; Mathewson et al., 2010; Samaha & Postle, 2015; Wutz et al., 2018). If the perception and perceived timing of visual stimuli is modulated through the alpha rhythm, does that effect extend to the perceived starting location of moving stimuli in the FE? The following series of experiments explores this question and takes this one step further by asking – if the alpha frequency does indeed modulate perception, then at what stage of the hierarchy does it act? At what stage does the FE occur? Early sensory stages, later perceptual stages, or both?

The first experiment dives into whether or not entrainment of alpha-band neural oscillations can have an effect on localization illusions in the same way that it has been found to affect detection and segregation/integration (Mathewson et al., 2010; Ronconi et al., 2017; Wutz et al., 2018). If a moving target is processed more slowly due to perception at an unfavorable phase of processing, then presumably it will have moved further along its trajectory before processing is complete and extend the bias in starting position seen in the FE.

We used a rhythmic auditory entrainment stimulus alongside dense sampling to (1) compare illusion magnitude across entrainment frequency, and (2) probe whether a behavioral time series created from FE localization judgments could reflect post-entrainment oscillations. We confirmed our first hypothesis that faster entrainment would lead to smaller illusion magnitude with a paired samples t-test, showing significantly lower illusion magnitude in the fast entrainment condition compared to slow entrainment. This indicates some role of entrainment in the mechanisms of the FE. However, despite this finding and contrary to several studies that have shown frequency-specific alpha entrainment, we did not find an effect of entrainment on the behavioral time series of the FE (Ronconi et al., 2018; Chota & VanRullen, 2019). Could the impact of entrainment differ between localization illusions and, for example, detection tasks? Perhaps if the FE depends on distinct mechanisms that operate at a different level of the perceptual hierarchy than sensory entrainment or involves *more* mechanisms than those that are affected by entrainment (such as attentional shift or motion extrapolation), effects of entrainment could be diluted by the time of the response.

In the second experiment, we sought to understand at what level of the perceptual hierarchy the FE seems to occur. If the FE sources from a high-level perceptual or decisional area as opposed to a low-level sensory one, then this could explain the findings from the first experiment for why we were unable to find a connection between alpha entrainment and the FE. This experiment explored correlations between reaction time in a simple detection task (SRT), a two-alternative forced choice FE task (CRT), and the magnitude of the FE of each participant (PSE) to determine if the magnitude of the FE contributed more variance at the decisional level rather than at the detection level. Overall, none of our variables were correlated with one another, leaving more questions than answers. In our post-hoc analysis, we did find a correlation between the position of peak RT for a localization decision and the magnitude of the FE, but this probably tells us little about the mechanisms of the FE and simply gives us a RT version for measuring the FE.

In the third experiment, we directly compared entrainment effects in the FE task to a task that has demonstrated entrainment effects in previous literature – the two-flash-fusion task (TFF; Ronconi & Melcher, 2017). We sought to replicate another study that found entrainment effects on a phenomenon distinct from the FE as a way to confirm that our entrainment was successful. If our entrainment can be seen to affect the TFF – thereby replicating the study by Ronconi and Melcher – but not the FE, then this could explain the results of the first experiment while providing some evidence that the mechanisms on which the FE relies differ from that of the TFF. Our analysis showed just that. TFF behavioral data showed clear oscillatory signatures with the goodness of fit of a sinusoidal fit at the entrained rhythm (adj-R^2) and the observed amplitude value at the

entrained frequency falling outside the 95th percentile range of our null distribution, while the FE behavioral data did not cross permutation thresholds. Ultimately, this experiment was successful in uncovering that FE behavioral data is resilient to entrainment effects, although the exact reason may be unknown. A similar study done by Morrow and Samaha (2021) found similar results where modulations in the FE and the flash-lag effect (another similar localization illusion) were not significantly correlated. The exact reasoning why the FE appears to be a special case for localization illusions is still unclear.

These series of experiments have concluded the following findings: (1) TFF and FE behavioral time series rely on different mechanisms, as evidenced by FE's lower susceptibility to entrainment, and (2) FE may be operating with a mechanism (or mix of mechanisms) higher than where entrainment phase resets are able to have an observable effect.

First off, it is apparent that the TFF and FE phenomena utilize some different mechanisms as evident by the TFF having strong entrainment susceptibility in contrast to the behavioral time series of the FE. Future work should explore why localization illusions such as the FE appear resistant to entrainment. Given the extensive literature demonstrating that alpha-band entrainment can modulate perceptual outcomes, the failure to observe a modulation in the localization tasks following entrainment suggests that not all perceptual phenomena are equally susceptible to entrainment.

One explanation is that the mechanisms responsible for localization illusions are operating at a higher perceptual level, incorporating more information throughout the decision than in tasks such as the TFF. The FE may be a more complex perceptual

phenomenon, incorporating both early-level sensory sampling (as in Schneider, 2018), attentional shifts (Adamian & Cavanagh, 2017), and higher-order processes such as motion extrapolation (Eagleman & Sejnowski, 2007). Unlike TOJ tasks or the TFF task, which depend primarily on temporal segregation at the sensory level, FE tasks may invoke motion-sensitive and/or attentional systems that operate over larger time scales or with more constraints than at the lower level. Additionally, if localization is computed via predictive mechanisms and a postdictive response, as proposed by Eagleman and Sejnowski (2007) or Nijhawan (2008), then the temporal dynamics of that mechanism may be less susceptible to the instantaneous phase at stimulus onset and instead by higher-level internal oscillations resistant to modulations by external rhythmic input.

Another possible explanation could be that the neural sources of the FE specifically are less responsive to entrainment than those implicated in other illusions. If the effect involves activity in motor areas, such as MT/V5, or frontoparietal areas involved in spatial updating or decision making, then these areas may not be as susceptible to rhythmic entrainment stimuli.

Finally, there is the possibility that variability in the endogenous alpha frequency or in entrainment susceptibility between our participants obscured potential effects. If the FE is coupled with each individual's rhythm, the external rhythms that attempt to impose a frequency too inconsistent with their endogenous one could disrupt potential findings, although other studies exploring entrainment and the alpha rhythm have seemed to be unaffected by this potential confound so this likely is not the case (Mathewson et. al., 2010; Ronconi et. al., 2018).

Altogether, these findings suggest that either (1) the FE *could* be temporally structured, but in a way that is too complex to be easily affected by entrainment, or (2) there truly is no relationship between the FE and the modulation in perception associated with the alpha rhythm. This finding offers an interesting perspective that not all perceptual phenomena may be susceptible to rhythmic intervention or based in mechanisms associated with discrete perception at all. Future research should explore under what conditions and through what pathways can external rhythmic entrainment have an impact on the internal processes and outputs of our perception. Understanding the limits of entrainment can help to explore the brain's perceptual processes just as much as understanding its successes and help us to uncover how and *where* these oscillatory mechanisms interface and influence our conscious visual experience.

- Chapter End -

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