Using Oculomotor Behavior as a Probe for Aberrant Predictive Coding

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Abstract

The brain continually generates predictions about incoming stimuli, allowing it to anticipate and respond to its environment appropriately. A mismatch between predictions and the actual stimulus generates a prediction error, which is used to update the brain's beliefs and facilitate a more precise prediction. Deficits in this pathway, at the sensorimotor level, have been implicated in schizophrenia, as underlying positive symptoms such as hallucinations. We hypothesized that aberrant predictive signaling at the sensorimotor level causes cognitive beliefs to exert a stronger influence on behavior, which can explain how false beliefs shape perception in schizophrenia. 24 healthy participants (14 males, 10 females) completed an oculomotor prediction task under two conditions, one in which the target was temporarily occluded. Using hierarchical drift diffusion models, we found that, in the absence of visual information, lower eye velocity was associated with a greater bias towards making premature predictions. Consistent with our hypothesis, impaired oculomotor behavior, which corresponded to aberrant sensorimotor predictive signaling, was correlated with a stronger influence of prior beliefs on behavior. Our findings can be used to reconcile the long-standing debate on whether positive symptoms of schizophrenia arise from aberrant perception or aberrant beliefs, by showing that the two are, in fact, related. Our findings also emphasize the role of visual input in determining how perception affects beliefs, by showing that an absence of visual information drives prior beliefs to exert a stronger influence on behavior to compensate for deficient predictive signaling at the sensorimotor level.

Using Oculomotor Behavior as a Probe for Aberrant Predictive Coding in Schizophrenia

Rather than a passive receiver of incoming information, the brain can be better thought of as a proactive system that analyzes information in relation to what it already knows and expects. The brain's ability to anticipate the input it'll receive is what allows it to respond and adapt to its surroundings so effectively. A well-established example of the brain processing novel information in light of existing knowledge is when it forms associations between new and familiar objects or concepts (Bar, 2007; Corlett et al., 2004). In addition to external input, the brain foresees internally generated stimuli in a similar manner. Corollary discharge, a mechanism by which the brain anticipates the sensory consequences of its own actions, allows it to distinguish between self-generated and externally generated stimuli (Angel, 1976; Ford, Palzes, Roach, & Mathalon, 2013). Both corollary discharge and association formation can be viewed under the lens of the theory of predictive coding (Sterzer et al., 2018; Corlett et al., 2004).

According to the predictive coding theory, the brain continually generates a set of internal predictions, based on prior knowledge, in order to appropriately respond to incoming events. Predictions are based on internal representations of the world that have been shaped by past experiences and are sent down from higher to lower levels of the information processing hierarchy, where they are compared to incoming sensory information (Sterzer, Voss, Schlagenhauf, & Heinz, 2019; Schmack, Rothkirch, Priller, & Sterzer, 2017). If the brain's predictions do not match the sensory input, a prediction error is generated, which is then fed back from lower to higher levels of the hierarchy to update the brain's belief models and facilitate a more precise prediction in the future (Friston, 2005; Fletcher & Frith, 2009). Given how the generation of predictions is integral to the proper interpretation of external and internal events, a deficit in the brain's predictive apparatus can result in significant dysfunction. Analysing the

brain's predictive behavior in the context of a mental disorder may help determine the precise mechanisms underlying the predictive signalling pathway.

Several studies have found impaired corollary discharge in individuals with schizophrenia, namely in the visual (Spering, Dias, Sanchez, Schütz, & Javitz, 2013; Lindner, Thier, Kircher, Haarmeier, Leube, 2005; Thakkar, Schall, Heckers, & Park, 2015) and auditory systems (Heinks-Maldando et al., 2007; Ford & Mathalon, 2005; Ford, et al., 2013). A relationship between the level of impairment and the severity of positive symptoms experienced has also been established (Lindner et al, 2005; Heinks-Maldando et al., 2007), suggesting that corollary discharge dysfunction at the sensorimotor level may reflect a similar breakdown in higher level cognitive processes (Subramanian, Alers, & Sommer, 2019) that give rise to the thought disorders observed in schizophrenia.

Under the predictive coding perspective, corollary discharges represent the predictive signals used by the brain to anticipate the sensory consequences of self-produced movements (Sterzer et al., 2018). Aberrant predictive signalling, as observed in corollary discharge dysfunction, causes individuals with schizophrenia to interpret these consequences as salient and stemming from outside sources rather than the self (Fletcher & Frith, 2009; Sterzer et al., 2018). To account for this unexpected event, the brain adopts a set of false beliefs, i.e. delusions (Kapur, 2003; Adams, Stephan, Brown, Frith, Friston, 2013). A deficit in predictive signalling may explain why patients with schizophrenia fail to utilize top-down perceptual cues in vision (Dima et al., 2009; Schneider et al., 2002). Perceptual instability has also been correlated with delusional ideation, supporting the notion that aberrant top-down predictive signalling is linked to positive symptoms of schizophrenia (Stuke, Weilnhammer, Sterzer, & Schmack, 2019).

Nonetheless, the persistence of delusions suggests a stronger influence of internal belief-driven predictions rather than the contrary (Fletcher & Frith, 2009). Delusions persist in the face of contradictory information (Corlett, Krystal, Taylor, Fletcher, 2009); they are resistant to alteration by prediction errors, which are generated when beliefs don't match sensory input (Pedreira, Pérez-Cuesta, Maldando, 2004). Stronger predictive signalling in higher cortical areas may explain why patients with schizophrenia responded prematurely on a ball-collision prediction task when compared to healthy controls, as observed by Limongi, Bohaterewicz, Nowicka, Plewka, & Friston (2018).

The study implemented hierarchical drift diffusion models to analyze the differences in task performance between patients with schizophrenia and healthy controls. Drift diffusion models are commonly used to infer the trajectory of one- and two-choice tasks (Ratcliff & McKoon, 2008). A schematic representation of a two-choice drift diffusion model (Figure 1) shows how the process of making a decision begins at the starting point and terminates at the decision threshold, when enough information has been gathered to make a choice, which in this case was "late". A shift in the starting point towards one choice decreases the threshold of information needed to make that choice, making it more likely it will be picked. Hence, the starting point is also referred to as *bias*. The rate at which information is accumulated to reach a decision is known as the drift rate. As a higher drift rate corresponds to an enhanced ability to collect sensory input, drift rate is also referred to as *sensory precision*. Drift-diffusion models also account for processes that precede the decision-making process, such as motor responses. Using HDDM to compare how decision threshold, starting point, drift rate and non-decision processes vary across different levels of a task can provide insight into the cognitive factors governing the decision-making process.

Limongi et al. (2018) fit three different one-choice drift diffusion models to the data, each corresponding to a distinct hypothesis about which drift diffusion components best accounted for task performance. The differences between the two groups' performances were best explained for by the model that showed that patients with schizophrenia had a starting point closer to the decision threshold than that of healthy controls. Hence, schizophrenia patients needed to gather less information to make a prediction and had responded prematurely as a result. Researchers interpreted the patients' greater bias towards a choice as an indicator of stronger influence of prior beliefs, i.e. increased predictive signaling. By encoding bias as a measure of the strength of prior beliefs, HDDM can be powerful tool for assessing the influence of prior beliefs on any two-choice task.

Due to the substantial support for both weaker and stronger predictive signalling in psychosis, it has become crucial to establish a model that reconciles both conflicting theories. Evidence from corollary discharge studies strongly points to reduced predictive signalling as a cause of positive symptoms (Sterzer et al., 2018). On the other hand, an increase in predictive signalling better explains why delusions are maintained (Fletcher & Frith, 2009). Both processes are strongly rooted in evidence; under a unifying framework, researchers have proposed that the brain compensates for perceptual disturbances caused by aberrant predictive signals in lower sensory areas by strengthening the influence of predictive signals from higher cognitive areas on perception (Adams et al., 2013; Schmack et al., 2013). As a result, perception begins to largely be determined by internal predictions over external sensory information (Sterzer et al., 2018; Adams et al., 2013). This phenomenon not only explains the tenacity of delusions, but also conceptualizes hallucinations as a product of unduly precise prior beliefs (Powers, Kelley, &

Corlett, 2016; Schmack et al., 2017), providing a more comprehensive account of psychotic symptoms.

This view, by acknowledging that predictive signals are weakened and strengthened at different levels of the informational processing hierarchy (Schmack et al., 2013), has the potential to reconcile both the corollary discharge and predictive coding perspectives of psychosis. If predictive signalling in higher cortical areas is strengthened in order to compensate for reduced predictive signalling in lower cortical areas, then both phenomena should be observed in people exhibiting positive symptoms of schizophrenia. Hence, we hypothesized that a breakdown in corollary discharge at the sensorimotor level should be correlated with a stronger influence of prior cognitive beliefs on perception.

We tested this hypothesis by adapting the ball-collision task used by Limongi et al. (2018) to compare the responses of healthy individuals under two different visual conditions: one in which participants were able to track the moving object's entire trajectory before it collides, i.e. the non-occluded condition, and one in which the moving object transiently disappeared before collision, i.e. the occluded condition. In the latter condition, we aimed to simulate the perceptual instability experienced by patients with schizophrenia that leads them to rely on higher level predictions over sensory input (Adams et al., 2013; Adams, Perrinet, & Friston, 2012). In addition to reaction time, we also tracked participants' oculomotor responses as a measure of corollary discharge. The role of corollary discharge in the planning and execution of eye movements during smooth pursuit of a moving object has been well established (Richmond & Wurtz, 1980; Thakkar et al., 2015), making oculomotor behavior a suitable probe for corollary discharge function for our study.

We predicted that due to increased higher-level predictive signalling in the absence of precise visual input, prior beliefs should have a stronger influence on participants' responses on occluded trials than on non-occluded trials. Using HDDM to model the trajectory of the prediction process (Limongi et al., 2018), we aimed to establish a relationship between the influence of prior beliefs and oculomotor behavior, as a correlate of corollary discharge, in order to validate our hypothesis and provide support for the compensatory predictive signalling model (Schmack et al., 2013). Our findings will not only serve to unify two conflicting theories about aberrant perception, but also bridge the gap between computational and physiological perspectives of schizophrenia, allowing a broader understanding of the disorder, and of the brain's predictive apparatus as a whole.

Method

Participants

This study employed a within-subjects design, wherein each participant was exposed to both experimental conditions. 24 healthy volunteers were recruited (14 male, 10 female, M_{age} = 19.6, SD_{age} = 3.40). Four of the participants were recruited via word-of-mouth, while rest of the 20 participants were recruited through an undergraduate student research participation pool (SONA Systems). All participants provided written informed consent, and experimental procedures were approved by the Research Ethics Board of the University of Western Ontario (London, Ontario, Canada). Subjects were compensated 10 CAD for their participation in the study. All participants were right-handed and had normal or corrected-to-normal vision. Participants with corrected vision were instructed to wear contact lens instead of glasses to prevent obstruction of the infrared signal recorded by eye tracking apparatus. Four of the 24 total participant datasets were excluded from the final data analysis due to the failure of the apparatus

to detect the participant's eye movements. Trials on which participants blinked before the targets collided were also excluded from the data analysis as the system failed to track the average eye velocity in those cases.

Apparatus

We monitored monocular eye position (right eye) using the Eyelink 1000 eye-tracking system (SR Research), at a sampling rate of 500 Hz, across all trials of the task. Participants were seated 33 cm away from the computer screen, head stabilized by a chinrest. The eye tracking system was calibrated for each participant through a set of fixation trials. Participants were instructed to fixate on a yellow target on the screen for a duration of 2000-4000 ms. Targets appeared, one at a time, at the centre, and on both ends of the horizontal and vertical axes of the screen, to allow us to adjust for subject-specific oculomotor gain in all directions. Participants also responded manually during the task by pressing the right arrow key on a keyboard. Both the calibration and experimental procedures were performed in a darkened room to obtain a precise recording of the eye.

Experimental Procedure

The main objective of the task was to predict the time of collision of two targets, one moving, one stationary, as accurately as possible. Each participant completed two variations of the task, one in which the target was occluded for a short period of time, and one in which it wasn't; both conditions were randomly interspersed across 220 trials. To begin each trial, participants were required to fixate on a green circle that appeared on the left side of the screen for 200 ms (failure to fixate would result in a mistrial). Afterwards, two white squares (each spanning 1 degree of visual angle) appeared (Fig. 2), one on the left side (T1) of the screen, the same position as the initial green circle, and one at the center of the screen (T2). T1 was

stationary for 100, 150, 200, 250, 300, or 350 ms (randomly varied across trials) before it began moving to the right towards T2, at a constant speed of 10 deg/sec, until it collided with T2 at 1000 ms after onset of movement. A pilot run of the task did not reveal any effects of learning of collision time across trials, as participants did not show any significant improvement in performance over time.

Participants were instructed to estimate the time of collision and time their response, i.e. key press, so that the two events (the response and the collision) occurred simultaneously. In the occluded variant of the task, T1 transiently disappeared at 300 ms after onset of movement, and reappeared at 1000 ms, right before collision (Figure 2B). In both types of trials, upon collision, T1 stopped and T2 started moving towards the right at the same speed as T1 (10 deg/sec) for another 1000 ms, after which the trial ended and the screen went blank, before the next trial began. The inter-trial interval was varied across trials (100, 150, 200, 250, 300, or 350 ms)

Data Analysis

Two measures of task performance were obtained during the procedure: (1) oculomotor behavior and (2) manual response. The manual response, referred to as reaction time (RT), was measured as the time at which the key was pressed after T1 began moving, and was analyzed relative to the time of collision, which was 1000 ms post-onset of T1 movement. RTs less than 1000 ms after T1 began moving were termed ‘early’, while RTs greater than 1000 ms after T1 began moving were termed ‘late’. This classification was included in the analysis as an additional factor ‘Bias’, to assess whether there was an influence of prior-held beliefs on participants’ decision to respond early or late. The difference between RT and the collision time for each trial was calculated to obtain the absolute prediction error (PE). For measures of oculomotor behavior, average eye velocity at 250 ms post-onset of T1 movement (EV_{250}) was

chosen as the parameter of interest. As the task involves the tracking of a moving object, we chose to analyze eye velocity as it is a significant component of smooth pursuit eye movements (SPEM). Pursuit gain, defined as the ratio of eye velocity to the velocity of the target being tracked, is a well-established measure of oculomotor function (Kathmann, Hochrein, Uwer, & Bondy, 2003), making eye velocity a suitable parameter to measure. We chose to analyze velocity at 250 ms due to the fact that the eye usually achieves a stable velocity by then and is hence a reliable measure of oculomotor function.

To test the significance of our results before performing further analysis, we evaluated the within-subject effects of trial type on absolute PE and EV_{250} using a paired t-test. To account for the uneven number of trials for each subject, we also chose to run a mixed-effects regression model to assess the effects of trial type on absolute PE and EV_{250}, as it considers the information at the level of each trial, rather than the average of all trials (Rothen, Seth, & Ward). Using a mixed-effects model also allowed us to test the effects of bias, i.e. whether participants' decision to respond early or late affected response time and oculomotor behavior. We modeled main factors Trial type (Non-occluded vs. Occluded), Bias (Early vs. Late) and their interaction Trial type x Bias as fixed effects. Subjects and Trial Number were included as random effects.

Then, we fit a total of six drift-diffusion models (Wiecki, Sofer, & Frank, 2013) to the data, each of which corresponded to a distinct hypothesis about which component(s) best explained the differences in task performance between both trial types. Table 1 defines each of the models employed, in terms of which parameters were varied and fixed. Table 2 provides a list and description of each HDDM parameter. Overall, each of the models either varied drift rate (v), starting point (z), or both, based on our prediction that differences in absolute PE across both conditions would be best explained by either or both of these parameters, as per results of a

similar study in the past (Limongi et al., 2018). As decision threshold (a) and non-decision processes (t) were not theorized as having any effects on task performance, these parameters were kept fixed across models. Three of the six models included EV_{250} as a covariate, to determine the effects of oculomotor behavior on task performance, while the other three models sought to account for the differences in task performance independent of oculomotor behavior. We used the deviance information criterion (DIC) to select the best-fit model among all six models, as well as in each set of three (oculomotor and non-oculomotor models). Upon determining the best-fit oculomotor model, we plotted the relationship between EV_{250} and each of the other HDDM parameters that were found to significantly affect task performance in order to examine the exact mechanism by which oculomotor behavior accounted for differences in task performance across conditions.

Results

Under both conditions, participants responded early on a higher proportion of trials than late; nonetheless, the proportion of 'early' trials was higher in the non-occluded condition (80.66%) than the occluded condition (67.41%), (Table 3). Due to the difference in proportion of trials that were early/late across trial type, we decided to assess the effects of Bias, defined as the decision to respond early or late, on response time and oculomotor behavior, as well as effects of the interaction between Bias and Trial Type.

Absolute PE

Subjects had a significantly lower absolute PE on non-occluded trials (M=0.062 sec, SD=0.022 sec) than on occluded trials (M=0.090 sec, SD=0.036 sec), $t(19) = 3.667$, $p = 0.002$, 95% CI = [0.012, 0.044], (Table 4; Figure 3). The mixed-effects model analysis also revealed a significant main effect of trial type on absolute PE, wherein subjects had a lower absolute PE on

non-occluded trials (Trial type[Non-occluded]: estimate = -0.0164, *SE* = 0.0054 *t*(3763) = -14.65, $p < 0.001$). Hence, participants made larger temporal estimation errors during the occluded trials, suggesting visual input enhances the formation of precise predictions.

The model also revealed a significant main effect of bias (Bias[Late]: estimate = -0.0093, *SE* = 0.0012, *t*(3793) = -7.68, $p < 0.001$), wherein participants had a lower absolute PE when they responded late, compared to when they responded early. Hence, participants made larger temporal estimation errors when underestimating the collision time than when overestimating it.. There was no significant effect of interaction between trial type and bias (estimate = -0.0018, *SE* = 0.0011, *t*(3782) = -1.62, $p = 0.1064$). Hence, the type of trial did not influence the absolute PE of participants in early vs. late trials, nor did the decision to respond early/late differentially affect the absolute PE in non-occluded vs. occluded trials.

Average Eye Velocity

A paired t-test assessing participants' EV_{250} (*M*=9.271 deg/sec, *SD*=1.972 deg/sec) across trial type did not show a significant difference in EV_{250} between non-occluded and occluded trials (*M*=8.994 deg/sec, *SD*=2.347 deg/sec), *t*(19) = 1.049, $p = 0.307$, 95% CI = [-0.276, 0.830]; Table 4). Further analysis using a mixed-effects regression model, however, did reveal that participants had significantly higher EV_{250} in the non-occluded condition than the occluded condition (Trial type[Non-occluded]: estimate = 0.3064, *SE* = 0.0556, *t*(3813) = 5.52, $p < 0.001$). Hence, participants' oculomotor behavior was significantly altered across visual conditions, as participants reported lower eye velocity in the absence of visual input.

Our analysis also revealed a significant main effect of bias; participants reported higher EV_{250} when they responded late, compared to when they responded early (Bias[Late]: estimate = 0.2294, *SE* = 0.0602, *t*(3836) = 3.81, $p < 0.001$). Hence, bias towards one decision due to prior

beliefs can account for differences in oculomotor behavior. Finally, there was also a significant effect of interaction between trial type and bias on EV_{250} (Trial type[Non-occluded]* Bias[Late]: estimate = 0.2374, *SE* = 0.0559, $t(3825) = 4.25$, $p < 0.001$). Participants had higher EV_{250} during non-occluded trials when they responded late than when they responded early and had higher EV_{250} during late trials under the non-occluded condition than during late trials under the occluded condition.

Hierarchical Drift Diffusion Models

Based on a comparison of the DIC numbers (Table 5), M_3 was determined to be the best fit (DIC_{M3} = -7482) across all six models, while M_6 was determined to be the best fit (DIC_{M6} = -7443) within the oculomotor family of models. The differences in absolute PE across trial type were best accounted for by differences in both "v", i.e. drift rate (sensory precision), and "z", i.e. starting point (bias towards prior beliefs), regardless of the inclusion of oculomotor behavior as a covariate. Despite our finding that a non-oculomotor HDDM model better accounted for the results than an oculomotor HDDM model, the fact that oculomotor behavior was significantly different across both task conditions (as revealed by our mixed-effects model analysis) warranted a deeper analysis into the mechanism by which EV_{250} mediated the effects of sensory precision and bias on task performance. Hence, we plotted the relationship between EV_{250} and sensory precision (Figure 4) and bias (Figure 5), respectively, for both non-occluded and occluded conditions, based on the parameter estimates of M_6 (Table 6).

We found that in both the occluded and non-occluded condition, EV_{250} was positively correlated with starting point "z", i.e. a higher eye velocity was associated with greater bias towards responding late (Figure 4). In the case of our drift diffusion model, a larger "z" value corresponded to a greater bias towards responding late, while a smaller "z" value corresponded

to a greater bias towards responding early. EV_{250} and "z" were more strongly positively correlated in the non-occluded condition (slope = 0.0058) than the occluded (slope = 0.0023); hence an increase in eye velocity led to a greater bias towards responding late in the non-occluded condition than in the occluded condition.

With respect to sensory precision (Figure 5), we found that EV_{250} was positively correlated with the level of sensory precision (slope = -0.1030) in the non-occluded condition. In this case, a negative slope value was interpreted as positive correlation due to the fact that drift rate had a negative sign. In HDDM, the sign of the drift rate merely denotes the decision that was made by majority of participants; as majority of the participants in our study had responded early, drift rate had a negative sign. Had the majority responded late, the drift rate would have been positive. Hence, a higher eye velocity, in our study, was associated with more negative drift rate, i.e. higher level of sensory precision, in the non-occluded condition. On the other hand, we found that EV_{250} was negatively correlated with sensory precision in the occluded condition (slope = 0.0662); a higher eye velocity was associated with a less negative drift rate, i.e. lower level of sensory precision. Hence, lower eye velocity was associated with higher sensory precision, i.e. quality of sensory input, in the absence of visual input, while higher eye velocity facilitated an increase in sensory precision when adequate visual information was available.

Figure 6 depicts a graphical representation of how the drift diffusion parameters, bias "z" and sensory precision "v", relate to one another at different velocities. In the non-occluded condition, as eye velocity *increased*, bias towards responding *late* and level of sensory precision increased. Conversely, in the occluded condition, as eye velocity *decreased*, bias towards responding *early* and level of sensory precision increased. Hence, the type of trial (non-

occluded/occluded) determined how oculomotor behavior mediated the effects of bias and sensory precision on task performance.

Discussion

Our study analyzed the relationship between oculomotor behavior and the brain's ability to precisely predict the collision of two squares under two different visual conditions: one in which the participants were be able to track the square's entire trajectory before it collided, and the other in which the square was transiently occluded in an attempt to induce a state of perceptual instability that, as we predicted, led the participants to rely more on their prior beliefs over sensory input. We found that participants made significantly larger absolute prediction errors on occluded trials than non-occluded trials, suggesting that visual input is necessary for facilitating precise predictions. This is in line with the predictive coding theory that forms the basis of our study. The brain requires precise sensory information in order to correctly update its predictions and respond to its surroundings properly (Friston, 2005; Fletcher & Frith, 2009). A lack of adequate visual input, as experienced in the occluded condition, hinders the brain from updating its internal representations of the world, hence precluding it from being able to effectively adapt and respond to a changing environment, which in this case was a moving square. As a result, it makes larger prediction errors, as we've observed in our study.

Direct evidence for aberrant predictive processing in the brain can be found at the sensorimotor level, by observing behavioral correlates of corollary discharge, such as oculomotor behavior (Richmond & Wurtz, 1980; Thakkar et al., 2015). If the brain's predictive mechanisms are truly impaired in the absence of visual input, then oculomotor behavior should differ significantly across the non-occluded and occluded conditions. Indeed, we found that the average eye velocity at 250 ms post-trial onset, our chosen oculomotor parameter, was

significantly lower during occluded trials than non-occluded trials. Eye velocity is directly related to pursuit gain, a measure of how well an individual smoothly tracks a moving object. Pursuit gain is defined as the ratio of eye velocity to target velocity (Kathmann, et al., 2003). Given that the target velocity does not change throughout the trial, a lower eye velocity signifies a lower pursuit gain, suggesting a failure of corollary discharge to plan and execute eye movements to track a moving object successfully (Thakkar, Diwadkar, & Rolfs, 2017). Hence, deficits in pursuit gain due to lower eye velocity may indicate a breakdown in predictive signaling at the sensorimotor level.

We hypothesized that decreased predictive signaling at the sensorimotor level, in the absence of visual input, is compensated by increased predictive signaling from higher-level cognitive areas, causing prior beliefs to exert a stronger influence on behavior. As predicted, we found that, in the absence of visual input, lower eye velocity was correlated with a stronger influence of prior beliefs on participants' decision to respond early. Given that participants predominantly responded early in both conditions, lower eye velocity enhanced the participant's ability to reach a decision through greater reliance on prior beliefs to guide their actions. This may explain why participants have significantly lower eye velocity on occluded trials than on non-occluded trials. Lower eye velocity also helps compensate for the lack of adequate visual information by enhancing the quality of sensory information collected. Abnormalities in smooth pursuit eye movements have been reported in patients with schizophrenia. Patients with both chronic and recent onset schizophrenia (Thaker, Ross, Buchanan, Adami, & Medoff, 1999), as well as relatives of patients (Hong, Avila, Adami, Elliot, & Thaker, 2003; Kathmann, et al., 2003) have exhibited lower pursuit gain than controls. The patients' inability to use extra-retinal cues, such as corollary discharge, to predict the trajectory of and successfully track a moving

object is marked by lower eye velocity. Our results suggest that a lack of sufficient visual input drives patients with schizophrenia to adopt lower eye velocities to enhance the efficiency of sensory input, to make up for insufficient visual information from the environment.

On the other hand, prior beliefs have less of an influence on task performance in the presence of adequate visual input. Participants have significantly higher eye velocity on non-occluded trials than occluded trials; higher eye velocity, in non-occluded trials, is associated with a greater bias towards responding late. As majority of participants responded early on non-occluded trials, bias due to prior held beliefs contributed less to behavioral outcomes. Thus, prior beliefs exert a greater influence on behavior in the absence of adequate visual input than in the presence of it, due to differences in eye velocity across both conditions. Consistent with our hypothesis, decreased predictive signalling at the sensorimotor level, which we had operationalized as altered oculomotor behavior, is strongly associated with an increased influence of higher-level internal beliefs.

Support for this compensatory mechanism has been found in studies on the influence of prior beliefs on the perception of ambiguous stimuli (Schmack et al., 2013) in healthy individuals. Researchers quantified the strength of lower-level sensory predictions based on the ability to sustain a stable percept of an ambiguous stimulus over repeated presentations. Hence, perceptual instability indicated decreased predictive signaling at the sensorimotor level and was also found to positively correlate with the influence of a belief-induced bias on perception. In participants with unstable sensory representations, perceptual inference relied on cognitive beliefs to a greater extent. Similarly, in the context of our study, the lack of visual input induced a state of perceptual instability that led to a greater influence of internal biases on the decision to respond early.

Perceptual instability and the consequent increase in influence in prior beliefs have been correlated with delusional proneness in both healthy and schizophrenic populations (Schmack et al., 2013; Teufel et al., 2019), suggesting that the imbalance in predictive signaling at different levels of the information processing hierarchy underlies positive symptoms of schizophrenia. This notion is further backed by neural evidence; higher connectivity between the orbitofrontal cortex, an area encoding beliefs, and the visual cortex, in patients with schizophrenia, indicates increased predictive signalling in higher-level cognitive areas (Schmack et al., 2017). Understanding schizophrenia symptomology as the result of both decreased and increased predictive signalling at different levels of the brain allows the reconciliation of both corollary discharge (Spering et al., 2013; Heinks-Maldando et al., 2007) and belief-driven models of schizophrenia (Corlett et al., 2019), as both account for symptoms at different levels of the predictive signaling hierarchy, the perceptual and cognitive, respectively.

This view, nonetheless, has been challenged. Stuke et al. (2019) found that decreased predictive signaling during a perceptual task was associated with greater delusional ideation but failed to establish a relationship between delusional ideation and the influence of prior beliefs on a cognitive decision-making task. However, the authors acknowledged that the cognitive tasks used in the study were ill-suited to gauge the influence of prior beliefs on performance, and hence were not reflective of the true relationship between delusional proneness and predictive signaling in higher-level areas. To account for this discrepancy, we implemented hierarchical drift diffusion models in our analysis. The HDDM parameter “z”, i.e. the starting point, was a direct measure of belief-induced bias, which allowed us to quantify the impact of prior beliefs on behavior and confidently conclude that prior beliefs had a greater influence on participants’ decision to respond early in a state of perceptual instability.

For our study, we chose to observe oculomotor behavior and its effects on task performance in the absence/presence of visual input. One of the limitations of our study was that although average eye velocity was significantly different across trial type and correlated with sensory precision and bias, the results were better explained by a model that did not take oculomotor behavior into account as a covariate. In future studies, we suggest modeling task performance data with respect to a wider range of oculomotor parameters, such as the location of eye gaze in relation to the target, to identify an oculomotor model that may possibly account for results better than a non-oculomotor model. Gaze location also provides insight into corollary discharge function (Thakkar et al., 2017), and is hence an ideal model parameter to consider. Another limitation was that that oculomotor data is only a behavioral correlate of underlying corollary discharge mechanisms. We suggest supplementing this data with more direct, neural measures of corollary discharge activity that have been validated in past studies, such as EEG/MEG (Heinks-Maldonado et al., 2007), to enhance quantification of decreased predictive signalling at the sensorimotor level.

Overall, our study highlights the importance of considering both perceptual and belief-driven models of schizophrenia in the study of its pathology. Although significant, the perceptual deficits observed in schizophrenia alone cannot account for the symptoms of what is primarily a disorder of consciousness. The mechanism by which impaired perception translates into more complex syndromes, such as thought disorders and persistent delusions, has not been previously defined. Our study supports an integrative framework that conceptualizes aberrant beliefs as a *consequence* of aberrant perception. Through the novel application of drift diffusion models, we observed that the presence/absence of adequate visual information determines how perceptual

processes affect the influence of internal beliefs on behavior, suggesting that in schizophrenia, perceptual abnormalities may give rise to aberrant beliefs through a similar mechanism.

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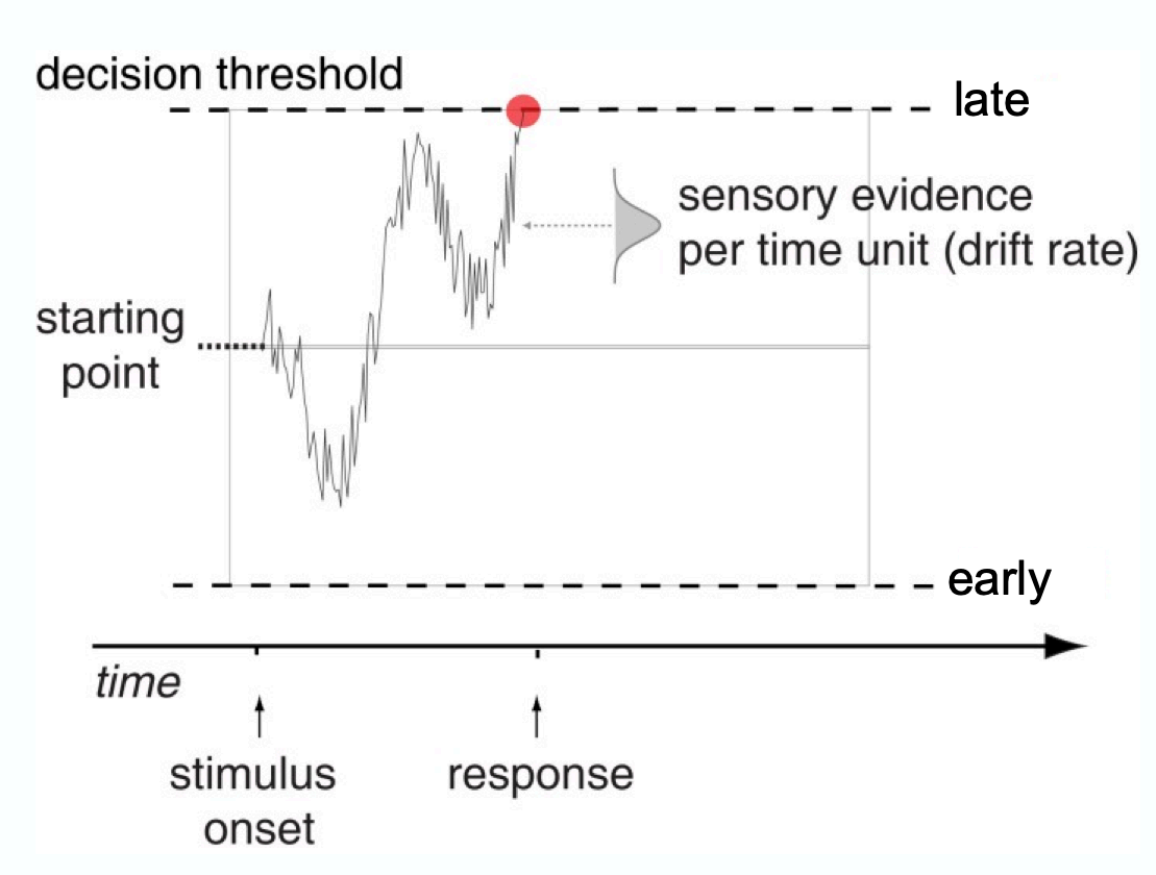
Figure 1

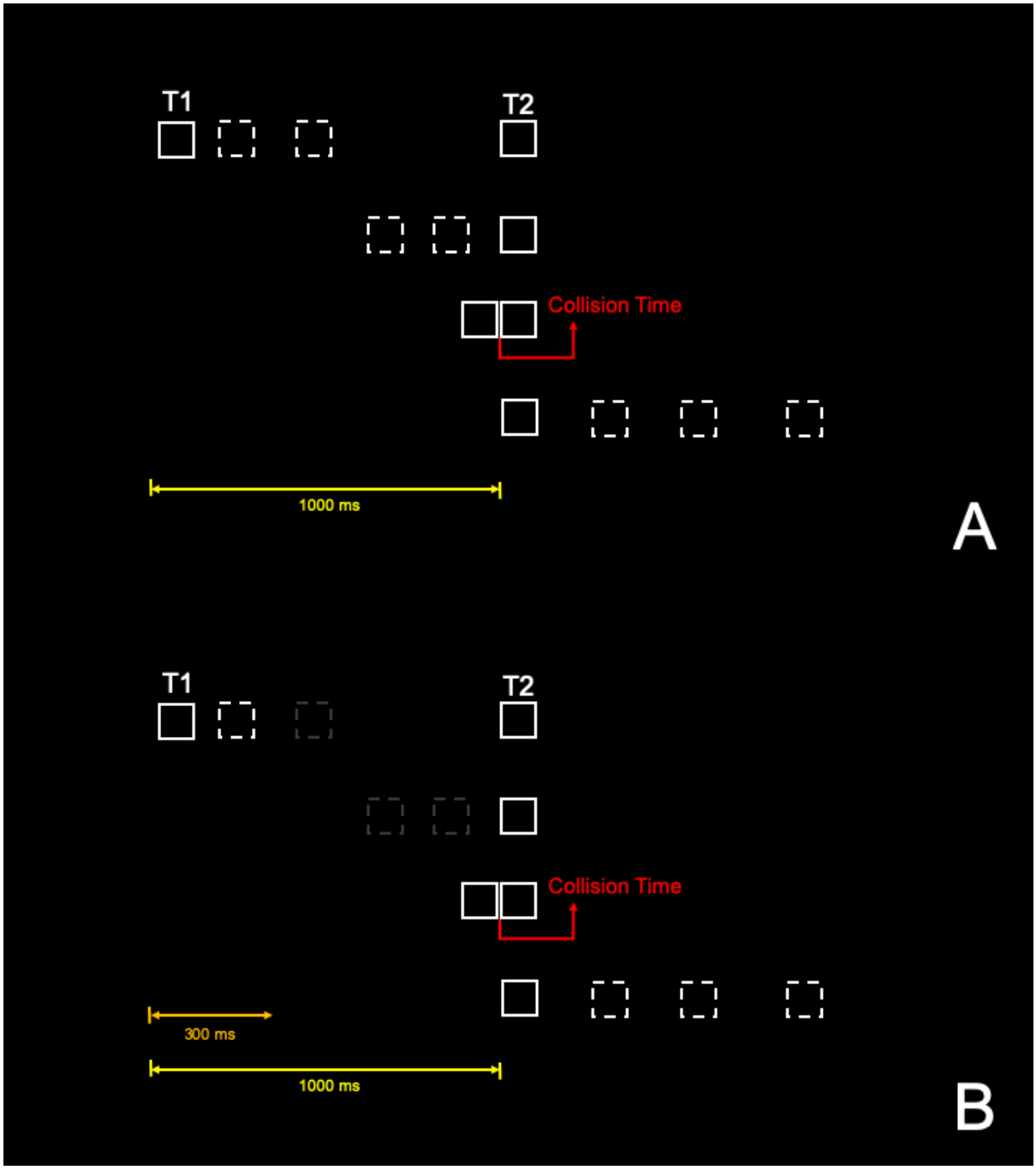
Schematic representation of the drift-diffusion model



Note. A sample trajectory of a trial where a late decision is made. The decision-making process commences from the starting point after a short delay, due to non-decision processes, and concludes at the decision threshold after gathering enough information. The rate at which information is accumulated is known as the drift rate. Adapted from "Bias in the brain: a diffusion model analysis of prior probability and potential payoff," by M.J. Mulder et al., 2012, *Journal of Neuroscience*, *32*(7), p. 2335-2343. Copyright 2012 by the Journal of Neuroscience.

Figure 2

Task Design



Note. T1 moved towards and collided with T2 at 1000 ms and stopped; T2 started moving towards the right. T1 was entirely visible during non-occluded trials (A) but disappeared at 300ms and reappeared at 1000 ms during occluded trials (B).

Table 1

Parameter Definitions for each model

Model	Free parameters	Fixed parameters
M_1	v	z, a, t
M_2	z	v, a, t
M_3	v,z	a, t
M_4	v, EV_{250}	a, t, z
M_5	z, EV_{250}	a, t, v
M_6	v,z, EV_{250}	a, t

Note. EV_{750} = average eye velocity at 250 ms post trial onset. Parameter definitions can be found in Table 2.

Table 2

Descriptions of relevant HDDM parameters, and their interpretation in the context of a prediction task.

HDDM parameter	Description
a	Decision threshold; amount of information needed to make a decision
t	Non-decision processes; delay caused by processes preceding decision, such as stimulus encoding
z	Starting point; bias towards prior held beliefs
v	Drift rate; sensory precision

Table 3

Proportion of total responses that were early/late for each condition

	Non-occluded	Occluded
Early (%)	80.66	67.41
Late (%)	19.34	32.59

Table 4

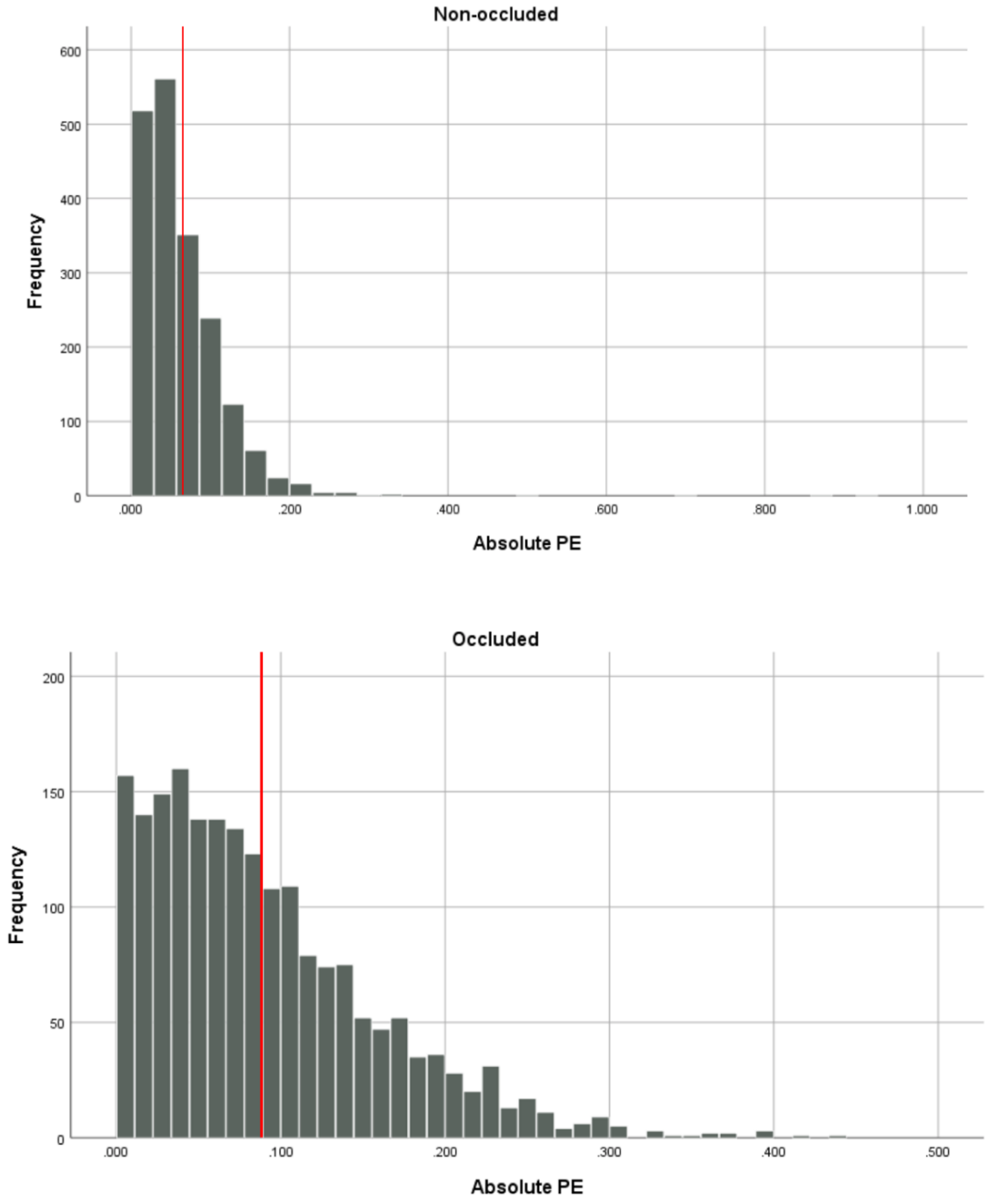
Descriptive Statistics

	Mean (Standard Deviation)	
	Non-occluded	Occluded
Absolute PE (sec)	0.077 (0.033)	
	0.062 (0.022)	0.090 (0.036)
EV_{250} (deg/sec)	9.133 (1.972)	
	9.271 (1.559)	8.994 (2.347)

Note. Mean absolute PE and EV_{250} for total trials, and for each trial type: non-occluded, occluded.

Figure 3

Distributions of absolute PE for each condition



Note. Red vertical line denotes mean. On average, participants had lower absolute PE on non-occluded trials than non-occluded trials.

Table 5

DIC number for each model.

Model	Free Parameters	DIC
M_1	*v*	-7459
M_2	*z*	-7304
M_3	*v, z*	-7482
M_4	*v*, EV_{250}	-7429
M_5	*z*, EV_{250}	-7311
M_6	*v, z*, EV_{250}	-7443

Note. The lower the DIC, the better the fit of the model to the data.

Table 6

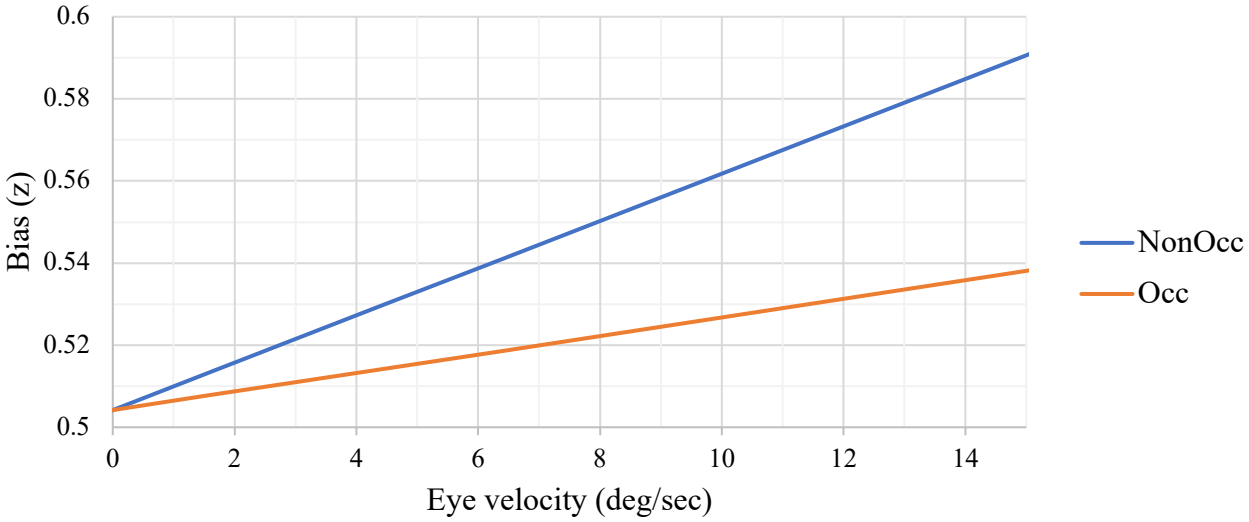
Estimates of relevant parameters of M_6

	v		*z*	
	NonOcc	Occ	NonOcc	Occ
Slope	-0.1030	0.0662	0.0058	0.0023
y-Intercept	-1.9256	-1.9256	0.5042	0.5042

Note. Slope values indicate how sensory precision and bias vary with respect to eye velocity. y-Intercept indicates the values of sensory precision and bias when eye velocity is zero.

Figure 4

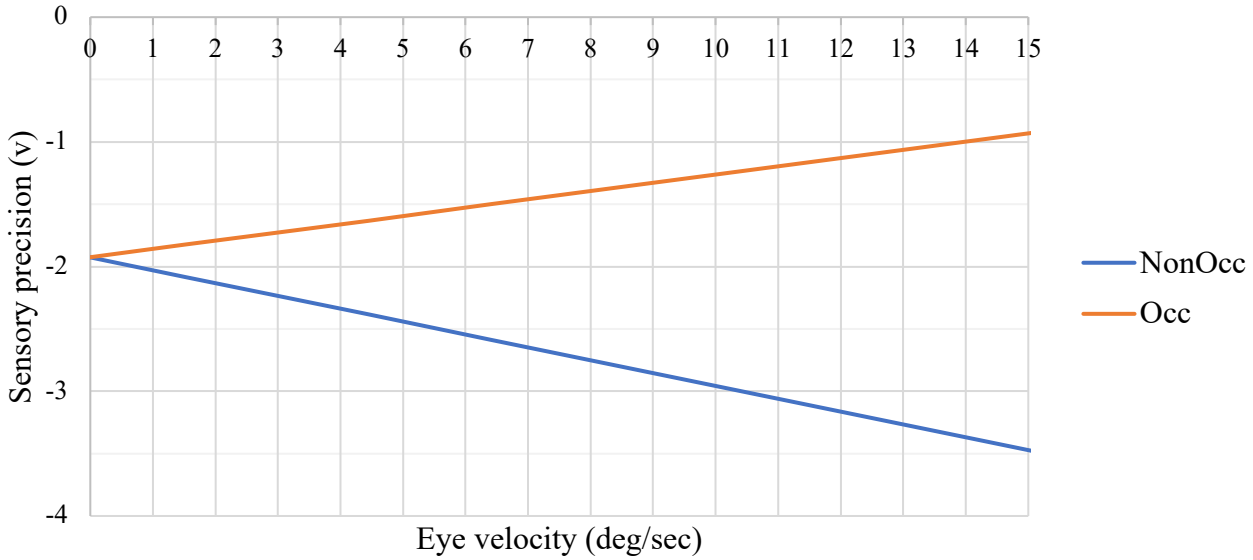
Relationship between EV_{250} *and bias towards prior beliefs in non-occluded and occluded conditions.*



Note. Eye velocity is positively correlated with level of bias in both occluded and non-occluded conditions, but more strongly positively correlated in the non-occluded condition

Figure 5

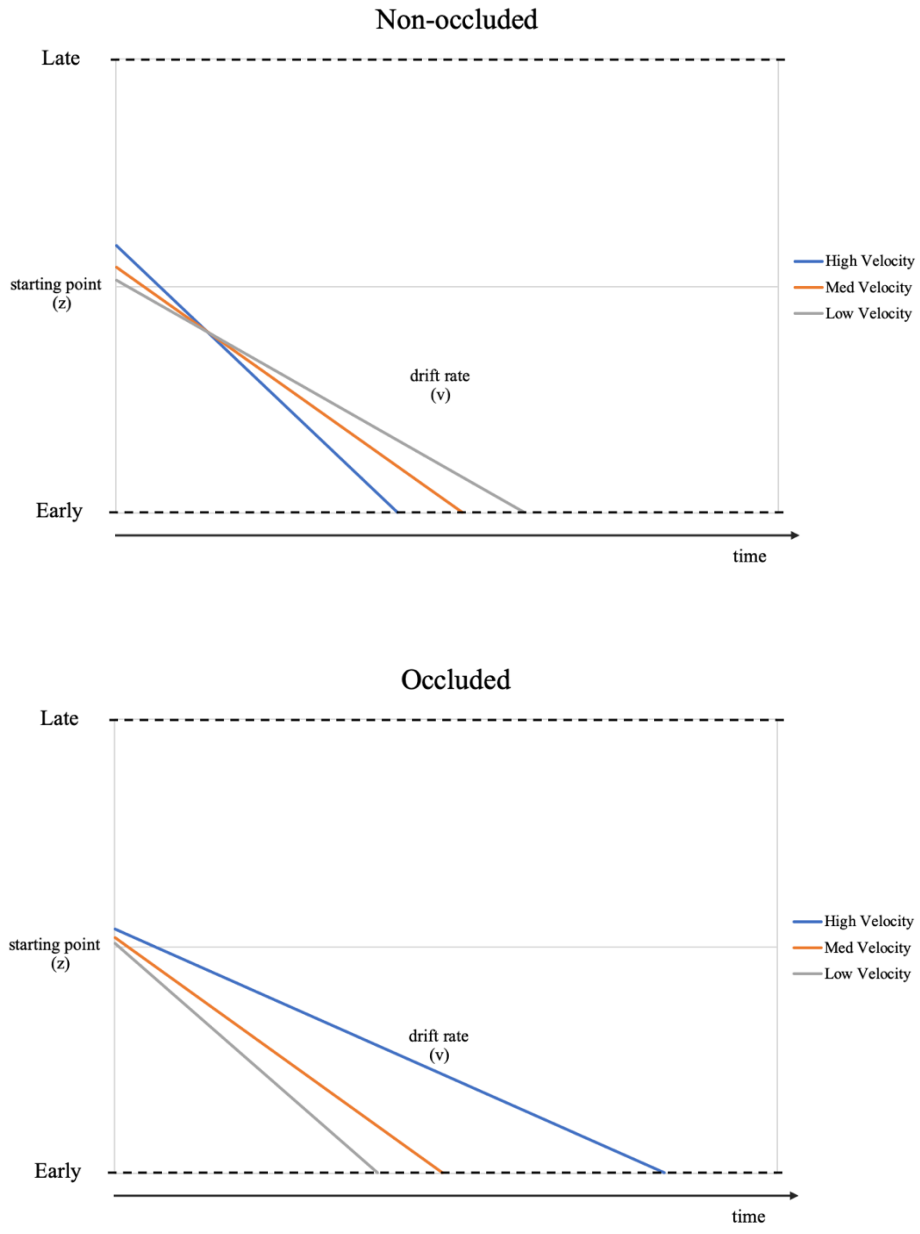
Relationship between EV_{250} and sensory precision in non-occluded and occluded conditions.



Note. Eye velocity is positively correlated with the magnitude of sensory precision in non-occluded condition, but negatively correlated in the occluded condition.

Figure 6

Graphical representation of how EV_{250} mediates starting point and drift rate across non-occluded and occluded conditions.



Note. In non-occluded trials, sensory precision (v) and bias towards *late* response (z) increase, as velocity *increases*. In occluded trials, sensory precision (v) and bias towards *early* response (z) increase, as velocity *decreases*.