

# Inhibition of Return in the Oculomotor Decision Process: Dissociating Visual Target Discrimination From Saccade Readiness Delays

Jelmer P. de Vries  
Utrecht University

Frans A. J. Verstraten  
Utrecht University and The University of Sydney

Ignace T. C. Hooge  
Utrecht University

Jasper H. Fabius  
Utrecht University and University of Glasgow

Stefan Van der Stigchel  
Utrecht University


Saccades toward previously cued or fixated locations typically have longer latencies than those toward novel locations, a phenomenon known as inhibition of return (IOR). Despite extensive debate on its potential function, it remains unclear what the role of IOR in the oculomotor decision process is. Here, we ask whether the effect on eye movement planning is best characterized as a delay in visual target discrimination or as a reduction in readiness to execute the movement (saccade readiness). To evaluate this question, we use target-distractor tasks with clear speed-accuracy trade-offs. Simultaneously cueing both the target and distractor (or neither) we find longer latencies at the cued locations. Despite this delay in latencies, accuracy improves in line with the speed-accuracy trade-off curve (Experiment 1). This suggests that while visual target discrimination can progress unimpeded, saccade readiness is reduced. Based on this reduction in readiness we predict that the more saccades rely on visual target discrimination, the less their destination will be affected by inducing IOR. Indeed, after cueing either the target or an onset distractor (Experiment 2), short-latency, stimulus-driven, saccades are strongly biased away from the cued location, while the destinations of longer latency goal-driven saccades are affected only minimally. The fact that primarily stimulus-driven saccades are affected by inducing IOR is interesting as it can explain why the spatial bias associated with IOR is not consistently found.

## Public Significance Statement

This study provides a novel insight into how the planning of upcoming eye movements is impacted by prior attentional shifts. It is a well-established fact that saccades (rapid eye movements) toward previously cued or fixated locations are delayed, a phenomenon known as inhibition of return. However, we find that despite the delay in the execution of saccades, visual discrimination of peripheral targets is unaffected by cueing. Further evaluation shows that it is the destination of eye movements that are considered stimulus-driven (those drawn toward salient locations) that are primarily affected. Together, this suggests that the role of inhibition of return in ocular movement planning is mostly limited to biasing observers away from previous salient events, and is not, what was generally thought, a general foraging facilitator in search.

**Keywords:** inhibition of return, saccadic selection, oculomotor decision process, eye movements, search

This article was published Online First November 12, 2020.

 Jelmer P. de Vries, Helmholtz Institute, Division of Experimental Psychology, Utrecht University; Frans A. J. Verstraten, Helmholtz Institute, Division of Experimental Psychology, Utrecht University, and School of Psychology, Faculty of Science, The University of Sydney; Ignace T. C. Hooge, Helmholtz Institute, Division of Experimental Psychology, Utrecht University; Jasper H. Fabius, Helmholtz Institute, Division of Experimental Psychology, Utrecht University, and Institute of Neuroscience and Psychology, College of Medical, Veterinary and Life Sciences, University of Glasgow; Stefan Van der Stigchel, Helm-

holtz Institute, Division of Experimental Psychology, Utrecht University.

This research was partly funded by The Netherlands Organization for Scientific Research to Frans A. J. Verstraten (NWO-Grant 440–01-001). Data and the analysis code can be found on the Open Science Framework: [https://osf.io/5ktgu/?view\\_only=c7a0a2ef7d2d40f5aef2d64556958463](https://osf.io/5ktgu/?view_only=c7a0a2ef7d2d40f5aef2d64556958463).

Correspondence concerning this article should be addressed to Jelmer P. de Vries, Helmholtz Institute, Division of Experimental Psychology, Utrecht University, Heidelberglaan 1, 3584CS Utrecht, the Netherlands. E-mail: [vriesdejelmer@gmail.com](mailto:vriesdejelmer@gmail.com)

When a location in the periphery is cued, for a brief period of time, saccades toward this location are facilitated (i.e., latencies are shortened; Posner, 1980). In a later study, it was shown that when this cueing period exceeds approximately 300 ms, saccades toward the cued location are associated with *longer*, rather than shorter latencies (Posner & Cohen, 1984).<sup>1</sup> Dubbing this phenomenon inhibition of return (IOR), it was suggested that the mechanism underlying this delay may play an important role in biasing observers toward novel locations (Klein, 1988; Posner, Rafal, Choate, & Vaughan, 1985): Repeatedly fixating the same locations when trying to find an object can deteriorate the performance of search. In line with the notion that IOR facilitates search, increased fixation durations also precede saccades toward previously fixated locations while searching complex scenes (e.g., Dodd, Van der Stigchel, & Hollingworth, 2009; Klein & MacInnes, 1999). However, if IOR is indeed a manifestation of an internal bias against revisiting previously fixated locations, the destination of saccades should be affected as well. Yet, while the delay in saccade initiation has been found consistently, evidence that IOR biases saccade destinations in search is not clear cut.

Some studies focusing on eye movements in choice tasks have found a bias away from cued or fixated locations (e.g., Boot, McCarley, Kramer, & Peterson, 2004; Fabius, Schut, & Van der Stigchel, 2016; Godijn & Theeuwes, 2004; Harman, Posner, Rothbart, & Thomas-Thrapp, 1994; Posner et al., 1985). Notably, Posner and colleagues found a bias away from the previously cued location when they asked observers to move their eyes in a comfortable direction, as quickly as possible, after two dots were presented in rapid succession. Studying memory in search McCarley and colleagues found that eye movements were biased toward novel items over decoys presented at previously visited locations (McCarley, Wang, Kramer, Irwin, & Peterson, 2003). Nevertheless, evaluating the frequency of return saccades during search of natural scenes has demonstrated that observers frequently refixate locations (Hooge, Over, van Wezel, & Frens, 2005; Smith & Henderson, 2011). As no baseline can be determined (the proportion of return saccades without active IOR is unknown), it has been argued that the number of return saccades may even be greater without IOR (Bays & Husain, 2012). Because the debate on the functional role appears to be at an impasse, the current article shifts the focus to improve understanding of how eye movement planning is affected when IOR is induced: we ask *what* aspect of the oculomotor decision process is affected by inducing IOR and apply our findings to predict *when* inducing IOR actually biases saccades.

To make any observation on how inducing IOR affects the oculomotor decision process, we first need to consider the events leading up to the execution of the saccade. Unfortunately, the exact sequence of events remains elusive and many specific aspects are still a matter of debate. While many models focusing on saccades toward a single target predict the latency distribution well, behavior has proven more difficult to predict when multiple elements are presented simultaneously. The fact that short-latency saccades are often biased toward salient distractors has sparked lively debates about potential conflicts between bottom-up and top-down processes (e.g., Bacon & Egeth, 1994; de Vries, Hooge, Wiering, & Verstraten, 2011; Donk & Van Zoest, 2008; Leber & Egeth, 2006; Theeuwes & Burger, 1998). Nevertheless, we believe that—broadly speaking—one can distinguish between the ability to

visually discriminate potential targets (i.e., visual target discrimination) in the periphery, and the readiness to execute saccades promptly toward a peripheral location (i.e., saccade readiness).

We are not the first to investigate what processing stages are affected in IOR. The question of what is inhibited when eliciting IOR has been addressed many times before (e.g., Fuentes, Vivas, & Humphreys, 1999; Reuter-Lorenz, Jha, & Rosenquist, 1996). While initially the phenomenon was postulated as a purely attentional effect (Posner et al., 1985). Over time, the question became whether IOR affects so called *input*-based or *output*-based processes (e.g., Klein & Hilchey, 2011; Taylor & Klein, 1998, 2000). Input-based processes are those considered to be within the attentional/perceptual domain. Output-based processes, on the other hand, are those linked to processing stages involving response and decision making. This distinction is close to the one we utilize here. However, as we are interested in the effects of inducing IOR on the oculomotor decision process, the current distinction is chosen from a functional perspective, specific to the oculomotor decision process. This was done because processes that are joined under input-based and output-based are not always clearly separate in terms of eye movement preparation. For instance, input-based processes often include attentional processes. At the same time it has often been argued that attention is directly coupled to motor execution (most notably the premotor theory of attention; Rizzolatti, Riggio, Dascola, & Umiltá, 1987), what is essentially an output-based process.

Previous studies focusing on IOR found that several performance measures are affected when inducing IOR. Yet, the pattern of results is not always consistent. With regards to visual perception, it has been shown that contrast sensitivity is decreased at locations where IOR is induced (Sapir, Jackson, Butler, Paul, & Abrams, 2013). At the same time, performance in temporal order judgment tasks and the illusory line-motion appear to be unaffected (Klein, Schmidt, & Müller, 1998; Maylor & Hockey, 1985; Schmidt, 1996; note that response speeds *can* be affected though, see e.g., Gibson & Egeth, 1994), suggesting that visual perception is not affected by inducing IOR. Similarly, there is also uncertainty on how the preparation of saccade execution is affected by inducing IOR. For instance, saccade endpoints in the global effect (also known as saccade averaging) have been shown to be influenced by the presentation of cues (De Vries, Van der Stigchel, Hooge, & Verstraten, 2016; Watanabe, 2001). The fact that changes in saccade characteristics do not seem to go hand in hand with the latency effect, however, complicates the matter even further. Evaluating saccade curvature, Godijn and Theeuwes (2004) found that curvature was most affected when the time between the cue and target is short, while the increase in latencies was largest when this time period was longer. Thus, even though a peripheral cue can affect the trajectory of a saccade, this effect can still be distinct from the delay in latency and, as such, likely relies on a different underlying mechanism.

A general complicating factor in determining the mechanism underlying IOR, is that IOR has become an umbrella term used to

<sup>1</sup> Note that later studies have shown that the initial facilitatory effect directly after cue presentation can be elusive and often response delays are found after period much shorter than 300 ms (for an overview, see Table 1 in Collie, Maruff, Yucel, Danckert, & Currie, 2000).

label any response delay as the result of a potential attentional shift (see [Berlucchi, 2006](#) for a discussion). Most likely IOR elicited by different means also relies on different underlying processes (e.g., cueing a peripheral location vs. having the observer making a saccade). Physiological research has shown that cueing a peripheral location leads to short-term depression of afferent visual signals synapsing at the superior colliculus ([Dorris, Klein, Everling, & Munoz, 2002](#); [Fecteau & Munoz, 2005](#)). In line with this finding, it was suggested that the delay in latencies shortly after a peripheral cue, may be the result of the depression of these incoming signals ([Satel, Wang, Trappenberg, & Klein, 2011](#)). However, given that this short-term depression only lasts for about 500 ms, it has been argued that the depression does not last long enough to explain latency delays when the period between the cue and saccade is longer ([Hilchey, Klein, & Satel, 2014](#)). Moreover, short-term depression as a result of a peripheral cue is logically unable to explain IOR induced by fixating a location. The fact that different processes likely underlie the various delays in saccade initiation that are all dubbed IOR can potentially explain why many findings on IOR stand in apparent conflict.

Considerable progress in resolving some of the above-mentioned conflicts has been made since it became clear that two forms of IOR could be delineated (e.g., [Taylor & Klein, 1998, 2000](#)). The extent to which eye movements are involved appears to be an important factor in determining the type of IOR. Early on, [Kingstone and Pratt \(1999\)](#) found that IOR was stronger when an eye movement had to be executed, than when no eye movement was required. More recently, [Hilchey and colleagues \(2014\)](#) demonstrated that previous reports of output-based effects ([Ivanoff & Klein, 2001](#)) became solely input-based when eye movements were explicitly discouraged. Using an antisaccade task, they demonstrated that by having observers make a saccade away from a cue, IOR at the cued location appeared to be input-based. As such it seems that when eye movements are prepared toward a cue, output-based IOR is induced. On the other hand, when eye movements are not prepared, IOR seems to be input-based. For a review detailing work on the distinction between the two forms see ([Klein & Redden, 2018](#)). In the current study we focus on the effects of *inducing IOR* using a peripheral cue *while eye movements are allowed*. Therefore, it may well be that the results will point to output-based processes being most affected; in our distinction this would show as a decrease in saccade readiness.

The typical single cueing paradigm does not allow us to distinguish delays in visual discrimination from a reduction in saccade readiness. A problematic issue with this setup is that delays in both modalities (visual and motor) lead to very similar predictions for behavior. Imagine that after the presentation of a peripheral cue, saccades are biased away from the cued location. On the one hand, this bias can be explained by delays in visual target discrimination. That is, because evidence for the presence of a potential target at the cued location builds up slower than at uncued locations, the probability that signals at uncued locations trigger a saccade first increases even though they may resemble the target less than the object at the cued location. On the other hand, a reduction in saccade readiness can also explain a bias away from the cued location. While visual target discrimination may provide a strong signal toward the cued location, when triggering the motor action requires more input at this location than at uncued locations, there is a higher probability that an uncued location attracts the saccade.

Thus, both delays in visual target discrimination as well as a reduction in saccade readiness can explain a bias away from a cued location. To distinguish which of these is delayed in IOR we require a departure from the classical IOR paradigm where only one element is cued.

For this reason, we focus on how inducing IOR affects the oculomotor decision process by introducing a paradigm with two distinctly different predictions depending on whether IOR can best be explained as a delay in target selection, or a reduction in saccade readiness. Previous IOR studies have used target-distractor discrimination paradigms to investigate the general question of what stages of processing are affected in IOR ([Pratt & Abrams, 1999](#); [Redden, Hilchey, & Klein, 2016](#)). Here, we combine a basic target-distractor choice paradigm with a double cueing paradigm (see [De Vries et al., 2016](#)) with the intent of inducing IOR at both the target and a distractor location, simultaneously. Evaluating the ability to correctly select the target as a function of latency when all relevant locations are cued, versus when only irrelevant locations are cued will allow us to classify IOR. Pre-viewing the findings of Experiment 1, IOR appears to be best characterized as reduced saccade readiness, while visual target discrimination remains unaffected. Based on the finding that the readiness to execute a saccade is reduced, we hypothesize that only very short-latency (highly stimulus-driven) saccades are biased away from cued locations, as these saccades are least influenced by top-down visual target discrimination. In Experiment 2, we introduce a capture paradigm to evaluate whether indeed the destination of stimulus-driven saccades is most affected by inducing IOR.

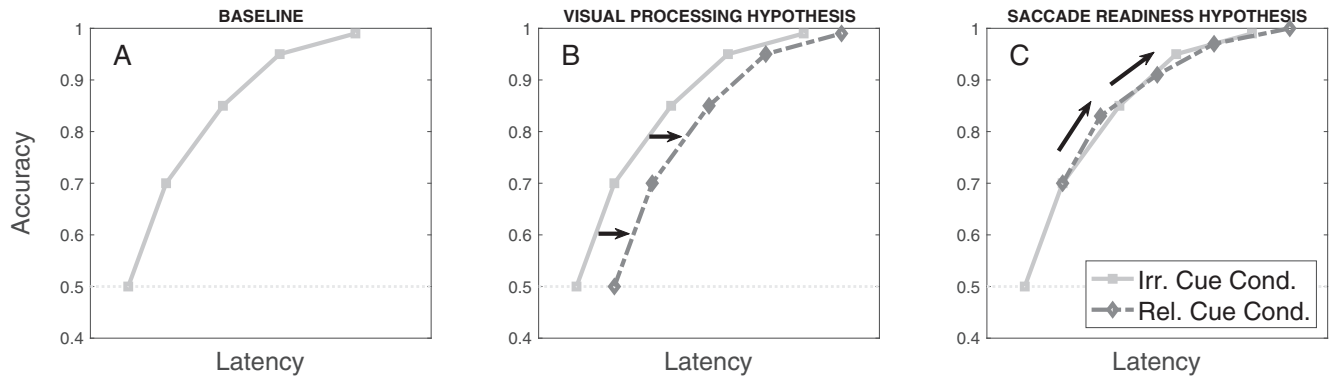
## Experiment 1A

The paradigm of Experiment 1A relies on a saccade task where a target has to be selected over a more conspicuous distractor. In such tasks, performance is typically dependent on the saccade latency: short latency saccades deviate toward the distractor, while longer latency saccades are more frequently directed toward the target (e.g., [van Zoest & Donk, 2006](#)). A hypothetical result of such a task is presented in [Figure 1A](#).

## Hypotheses

Previously, the speed–accuracy trade-off has been used to study IOR using manual responses (e.g., [Ivanoff & Klein, 2006](#)). Regarding saccades, there are a number of theories on why accuracy improves with saccade latency. However, the idea that longer latencies allow for prolonged visual processing of target and distractors is prevalent in all. When we combine a target-distractor paradigm with a double cueing paradigm where either *both* the target and distractor location are cued, simultaneously (*relevant cue condition*), or *only* irrelevant locations are cued (*irrelevant cue condition*), two distinct predictions emerge depending on whether delays in visual target discrimination or reduced saccade readiness underlies IOR.

To contrast the two predictions, we use the speed-accuracy curve in [Figure 1A](#) as the no-IOR baseline (i.e., we take this as the hypothetical result from the irrelevant cue condition). When *visual target discrimination* processes are delayed by the cues, evidence accumulation in favor of the target over the distractor should be slower when both are cued (*Visual Target Discrimination [VTD]*)



**Figure 1.** Predictions for selection as a function of saccade latency. In tasks where a target has to be selected over a conspicuous distractor, accuracy typically increases as a function of latency (A: hypothetical performance represented by light gray line). When inhibition of return (IOR) is properly induced at the target and distractor location, simultaneously, saccade latencies to both will be prolonged. If the prolongation is because of delays in visual target discrimination, saccades should be executed after longer latencies, but without any improvement in the speed–accuracy trade-off. We expect the curve to translate rightward (B: dark gray dash-dotted curve). Alternatively, saccade readiness is reduced, and visual target discrimination is allowed to progress unimpeded with the delay latencies. In this case, with the longer latencies, we expect accuracy to improve in line with the speed–accuracy trade-off as when IOR is not induced (C: dark gray dash-dotted curve).

*Hypothesis*). As the evidence to distinguish the target from the distractor builds up slower, saccades will be initiated later, but no improvement in accuracy should be found. Therefore, we predict the same speed–accuracy curve, only shifted with the prolongation of the latencies: the curve for this condition would be translated right of the original, in line with the latency increase (Figure 1B). On the other hand, inducing IOR may not affect visual target discrimination, but merely reduce the readiness to execute a saccade (*Saccade Readiness [SR] Hypothesis*). When this reduction in readiness occurs at the cued locations, more input from visual target discrimination processes is required to trigger a saccade. Consequently, prolonged input from visual discrimination processes allows for more time to distinguish the target from the distractor. Hence, the increase in saccade latencies should lead to a performance increase along the same speed–accuracy trade-off as in the irrelevant cue condition: performance follows the same curve, but the curve starts later and extends beyond the baseline curve (Figure 1C). These two predictions are, of course, extremes: In proposing the current distinction we rely on the notion that execution of a visually guided saccade requires, at the least, visual input to be processed for target discrimination on the one hand, and preparation of a saccade on the other hand. Studies focusing on the underlying mechanisms have demonstrated that the superior colliculus, a crucial hub in saccade generation, receives fast local sensory inputs undergoing minimal processing (often referred to as the exogenous pathway) and slower inputs from higher order visual processing (often referred to as the endogenous pathway). However, while it is tempting to follow a narrative where eye movement generation relies on two strictly segregated pathways operating in parallel, in reality a large number of brain areas is involved in (see for instance Figure 3.2 of Hall & Moschovakis, 2004). As such it is unlikely that the actual outcome matches one of our predictions perfectly. A Bayesian analysis using (*comparative*) Bayes Factors can tell us which of these predictions fits the outcome of the experiment best and, as such, allow us to classify

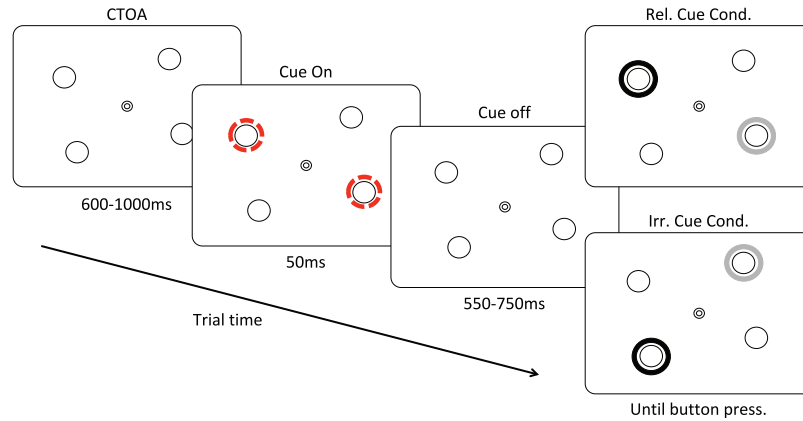
whether IOR is primarily driven by delays in visual target discrimination or a reduction in saccade readiness.

## Method

**Observers.** The number of observers is based on previous studies focusing on either saccadic selection or inhibition return (de Vries et al., 2011; De Vries, Van der Stigchel, Hooge, & Verstraten, 2018; De Vries et al., 2016). Ten observers (4 female; aged 18 through 25) naïve as to the purpose of the experiment, participated in the experiment. Observers were recruited through a public website and mailing lists and were paid a small monetary reward (7 euro/hour) for their participation. The study was conducted, and written informed consent of each observer was obtained, according to the principles expressed in the Declaration of Helsinki. The research reported in this article involves healthy human participants, and does not utilize any invasive techniques, substance administration, or psychological manipulations. Therefore, compliant with Dutch law, this study only required, and falls under the general approval from our internal faculty board (Faculty’s Advisory Committee under the Medical Research [Human Subjects] Act [WMO Advisory Committee] at Utrecht University).

**Stimulus.** Stimulus displays consisted of four white disks (diameter: 1.61 degrees of visual angle), each with a small black dot at the center (0.18 degrees). The disks are located on the corners of an imaginary square, randomly orientated around its center, on a midgray background at equal distance from fixation (9.2 degrees). A schematic of the trial chronology can be found in Figure 2. We will refer to these disks as *placeholders*, as their sole purpose is having well-established locations to induce IOR at. IOR was elicited at two of the four locations by cueing the placeholders using red rings (diameter: 2.75 degrees; thickness: 0.34 degrees) in a similar manner as in de Vries and colleagues’ study (De Vries et al., 2016). Following a cue–target onset asynchrony, a target (a dark-gray ring) and a more conspicuous distractor (a





*Figure 2.* Illustration of the trial chronology in Experiment 1A. Each trial starts with a 600–1,000 ms onset asynchrony after which two of the four placeholder locations are cued (for 50 ms). The period from the onset of the cue to the onset of the target is called the cue-target onset asynchrony (CTOA). Note that in the current figure this includes the Cue On and the Cue Off period. This makes the total CTOA 600–800 ms (50 ms plus 550–750 ms). The gray and black ring in the last frame represent the target and distractor, respectively. They are either both presented at the cued locations (relevant cue condition; upper frame), or both at the locations that were not cued (irrelevant cue condition; lower frame). The elements are not drawn to scale. See the online article for the color version of this figure.

black ring) appeared. The locations of the target and distractor ring were randomly selected from the four placeholders, meaning that they stand either at diagonally opposite locations ( $\sim 1/3$  of trials), or at two adjacent locations on the imaginary square ( $\sim 2/3$  of trials). Depending on the condition, either, the (future) target and distractor location were cued (*relevant cue condition*), or the two locations where no rings would appear were cued (*irrelevant cue condition*).

**Procedure.** Observers were instructed to fixate the central fixation dot until the dark-gray and black ring appeared. Observers were also asked to minimize blinking between the onset of the placeholder rings and the completion of each trial. To decrease the predictability of the upcoming trial we did not just vary positions, but also the timing of the onset of cue and later target and distractor. After an onset asynchrony sampled randomly between 600 and 1,000 ms, the two cues (red rings) appeared around two of the four placeholders (randomly selected) and were removed from the screen after 50 ms. Following the cue onset, there was a 600 to 800 ms cue target onset asynchrony (CTOA) after which the target and distractors appeared either (both) at the previously cued locations (relevant cue condition) or both at the uncued locations (irrelevant cue condition). This means that based on the cue, observers can anticipate that the relevant elements will appear either both in the cued placeholders or both in the noncued locations. We did this to obtain a situation analogous to typical IOR experiments where two placeholders are placed left and right of fixation. In such a situation, like in the current experiments, the observer can divide the stimulus into a cued and uncued part, and any attentional control settings will be similar to those experiments.

Observers were instructed to make a speeded saccade toward the target as soon as it appeared. They indicated that they had localized the target by pressing the “zero key” on the numerical keypad. The experiment consisted of two blocks of 250 trials separated by a small break ( $\sim 5$  min). Within each block, trials of the relevant cue

condition (125 trials) and irrelevant cue condition (125 trials) were randomly intermixed.

**Apparatus and eye movement analysis.** Eye movements were recorded using an SR-Research EyeLink II system at a sampling frequency of 500 Hz. The observer’s head was placed in a chinrest, at a viewing distance of 64 cm. Images were viewed binocularly, but eye movements were recorded from the left eye only. Eye movement data were collected for off-line analysis. Saccades were detected at a velocity of 20 deg/s, after which start and endpoint were found by searching back and forth until the velocity was 2 *SDs* higher than the velocity during fixation (as in Smeets & Hooge, 2003). First, saccades smaller than 1.5 degrees were removed and, subsequently, any fixations shorter than 50 ms were discarded from further analysis.

To avoid including trials where the observer incorrectly fixated during the presentation of the cues or did not correctly aim for either the target or distractor, we applied five exclusion criteria: trials where the observer’s initial fixation was not within 1.5 degrees of the fixation dot (occurrence: 0.9%); trials where a movement larger than 1.5 degrees was found during the period from the trial onset till the target-distractor onset (6.4%); trials where the saccade latency was either shorter than 60 ms or longer than 600 ms (0.4%); trials where the eyes did not land within 3 degrees of a placeholder (4.3%); and finally, trials where neither the target nor distractor was selected (1.8%). The combination of these criteria led to an exclusion of 11.8% of the trials.<sup>2</sup> Note that this percentage is smaller than the summation of the above percentages as more than one criterion could be violated on a single trial.

**Statistical analysis.** The critical variables of the observer’s behavior are the destination (to the target or not) and the response

<sup>2</sup> The omission of these trials does not change the outcome of the experiment.

latency. To model these response variables, we have chosen a logistic regression: As the dependent variable is binary (the observer either successfully selected the target, or not), a logistic function with saccade latency as an explanatory variable can be used to fit the current trial data.<sup>3</sup> As such, the probability of success for each trial ( $\theta$ ) of each observer ( $i$ ) can be modeled as follows:

$$\theta_i = \frac{1}{1 + e^{-(\alpha_i + \beta_i * latency)}}$$

here  $\alpha_i$  represents offset and  $\beta_i$  slope of the performance with increasing latencies. To now model the difference in performance between the irrelevant and the relevant cue condition a single offset parameter  $\Delta\alpha_i$  can be added, giving us:

$$\theta_{i,irr} = \frac{1}{1 + e^{-(\alpha_i - \Delta\alpha_i/2 + \beta_i * latency)}}$$

$$\theta_{i,rel} = \frac{1}{1 + e^{-(\alpha_i + \Delta\alpha_i/2 + \beta_i * latency)}}$$

for the irrelevant cue condition and the relevant cue condition, respectively. Keeping  $\alpha_i$  and  $\beta_i$  constant over the conditions, they represent the average performance over all trials. Introducing  $\Delta\alpha_i$  allows for shifting the function laterally to fit the potential difference between conditions.

If we return to the outline of our hypotheses in Figure 1, we see that for the VTD hypothesis (Figure 1B) we predict a lateral shift in the accuracy curve, in line with the difference in latencies between the irrelevant (baseline) condition and the relevant cue condition. For the SR hypothesis we expect that with longer latencies, performance increases in line with the same curve (Figure 1C). Thus, for the SR hypothesis we would expect the average  $\Delta\alpha_i$  to be 0, as there should be no shift in the curve. For the VTD hypothesis we would expect the average  $\Delta\alpha_i$  to account for the lateral shift in line with the delay in latencies. However, because in the logistic function latencies are multiplied by  $\beta_i$ ,  $\Delta\alpha_i$  is not expressed in terms of milliseconds, directly. Rather, because the latencies are multiplied by slope parameter  $\beta$ , so should the difference in milliseconds between the conditions to find the  $\Delta\alpha$  that corresponds to the correct shift in latencies for the VP hypothesis. To summarize, the SR hypothesis predicts that  $\Delta\alpha_i = 0$ , and the VTD hypothesis predicts that  $\Delta\alpha_i = l$ , where  $l$  is dependent on the latency difference between the relevant and irrelevant cue condition.

Now that we have laid the groundwork for our expectations, the next question is how to obtain parameter estimates and compare the hypotheses. As the frequentist approach to statistics only allows us to reject the SR hypothesis, we rely on a Bayesian approach. Using Jags (implemented in R using the RJags package Plummer, 2019; and utilizing R2Jags; Su & Yajima, 2015) we can estimate the parameter distributions. The complete model including all parameters is depicted graphically in Figure 3.

Even though we deviate from the frequentist approach, our approach is closely related to mixed effects models advocated in recent literature (Baayen, Davidson, & Bates, 2008; Jaeger, 2008) and used for the analysis of eye movement or psychophysical data with *time* as a predictor variable (De Vries et al., 2018; Fabius, Fracasso, & Van der Stigchel, 2016). In the current model we allow for observer variability by relating individual parameters, to

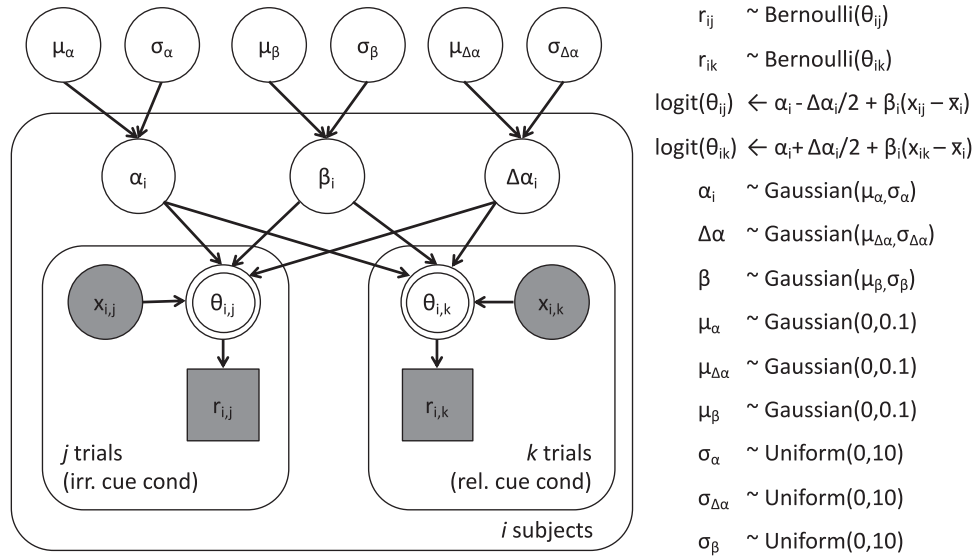
hyperparameters  $\mu_{\alpha}$ ,  $\mu_{\beta}$ , and  $\mu_{\Delta\alpha}$  that estimate the overall means over the observer dependent  $\alpha_i$ ,  $\beta_i$ , and  $\Delta\alpha_i$  (and  $\sigma_{\alpha}$ ,  $\sigma_{\beta}$ , and  $\sigma_{\Delta\alpha}$  representing the respective standard deviations). The latencies, expressed in milliseconds (represented by  $x$ ), are mean-centered by subtracting the mean latency ( $\bar{x}_i$ ) for each observer from the latency of each individual trial. Model priors for each of the parameters can be found in Figure 3. These were chosen to be sufficiently uninformative, that is, not to bias toward any specific outcome. This is achieved by utilizing normal distributions with a low precision. As such we limit bias while also avoiding the cutoffs that would be introduced by a pure uniform distribution. In the current case we have sufficient data as to minimize the influence of the prior: the selection of any other reasonable prior is unlikely to influence the shape of the posterior. For a more elaborate explanation of Bayesian parameter estimation using MCMC sampling see (Dyjas, Grasman, Wetzels, van der Maas, & Wagenmakers, 2012; Lee & Wagenmakers, 2014). Once parameter distributions have been obtained, we calculate Bayes Factors to determine evidence for one hypothesis over the other (Jeffreys, 1961). The difference between our conditions can be captured solely in the mean of the  $\Delta\alpha_i$  parameter:  $\mu_{\Delta\alpha}$ , which we will refer to as simply  $\Delta\alpha$  from here on. As explained above, the SR hypothesis is straightforward as we expect the fitted function to be the same for both conditions, hence  $\Delta\alpha$  is expected to be 0. The value of  $\Delta\alpha$  corresponding to the VTD hypothesis is obtained by multiplying the latency difference between the irrelevant and relevant cue condition by the estimate for the  $\beta$  parameter. More precisely, this value is calculated by multiplying the median of the estimate for  $\mu_{\beta}$  by the difference in median latencies (over all trials for all observers) between the two conditions.

Once we have obtained the parameter estimates we still need to test whether they should shift our prior belief toward one hypothesis over the other hypothesis (remember that we start unbiased). To this end, we use Bayes Factors as they are a measure of to what extent our relative beliefs should change in light of the data. To compare the models, for each hypothesis we calculate a Bayes Factor ( $BF_{VTD}$  and  $BF_{SR}$ ) individually, using the Savage-Dickey ratio (Dickey, 1971). To see how the belief has shifted from unbiased to one hypothesis over the other, we divide  $BF_{SR}$  through  $BF_{VTD}$  to provide us with a Bayes Factor that compares the relative evidence between the two hypotheses.

## Results

**Inhibition of return.** Before evaluating selection, it is important to verify that IOR was properly established in the double cueing paradigm. For this, we plot the average median latency for saccades for the irrelevant and relevant cue condition in Figure 4A. As expected, the latencies in the relevant cue condition are longer than in the irrelevant cue condition, with a latency difference of 20.9 ms,  $t(9) = 4.30$ ,  $p < .005$ ; Cohen's  $d = 1.04$ . The experiment was designed with the assumption that when two locations are cued simultaneously, IOR is induced at *both* locations. However, this assumption can be questioned based on previous reports that

<sup>3</sup> For this article we ran all our analyses using the logit link function. Another method based on a specific speed-accuracy trade-off function (see Wickelgren, 1977) is a good alternative that should be considered in future work.



**Figure 3.** Graphical model of observer accuracy for the irrelevant and relevant cue condition. Rounded nodes represent continuous variables, while rectangular nodes represent discrete variables (response  $r$  can either be 0 or 1). Shaded nodes are observed values ( $x$  for latency and  $r$  for the response). The double borders (surrounding  $\theta$ ) indicate that the parameter is deterministic, that is, defined in terms of other variables. The inner plates represent the trials for each condition ( $j$  for trials from the irrelevant cue condition and  $k$  for trials from the relevant cue condition). The outer plate the observers;  $\alpha$ ,  $\beta$ ,  $\Delta\alpha$  are estimated per observer. The nodes at the top of the figure are the estimates of the means and standard deviation over all observers. Prior distributions for the parameters are displayed on the right of the figure, as well as the calculation of the deterministic variables. To have unbiased priors one option is to use a uniform distribution. However, as it is difficult to determine a proper range a priori, we have chosen normal distributions as priors of the different means. In this manner there is minimal bias toward one outcome or the other. Note that the second parameter for the Gaussian is the precision and not the standard deviation (a precision of 0.1 equals a standard deviation of  $\sqrt{10}$ ). For more information on the graphical model see (Lee & Wagenmakers, 2014).

find IOR at the center of gravity of multiple cues, rather than at individual locations (Christie, Hilchey, & Klein, 2013). For our experiment it is possible that IOR was not properly established at the cued placeholders, but at a location *in between* the cues. For instance, in the case where two locations directly opposite of the fixation dot are cued, the center-of-gravity lies at the fixation dot, and as such, IOR could even be nonexistent at the cued locations. We have previously run into the question of *where* IOR is established when presenting two cues simultaneously (De Vries et al., 2016) and took this issue into account in planning our statistical tests. As such, to verify whether IOR was properly established at the cued locations in all cases, we planned a separate  $t$  test for comparing only the subset of trials where the target and distractor were placed directly opposite one another. Evaluating latencies by including only trials where the two cued locations stood at opposite corners of the imaginary square (see Figure 4B), we again obtain a significant effect of latency (latency difference: 17.9 ms;  $t(9) = 3.61$ ,  $p < .01$ ; Cohen's  $d = 0.82$ ). With a slightly smaller latency difference than when cues are not opposite with respect to fixation, it is still possible that the global configuration of the cues influences IOR. Another possibility is that the current requirement to distinguish the target from a distractor elevates the importance of individual locations compared with studies showing a center-of-gravity effect (Christie et al., 2013; Klein, Christie, & Morris, 2005). As such it is possible that when cued locations do not need

to be segmented, IOR is found at the center-of-gravity, while here IOR *is* established at the cued locations individually. Important here is that saccade latencies in the relevant cue condition are longer than in the irrelevant cue condition, irrespective of the cue position.

**Selection performance.** Now that we have established that IOR is properly induced, we evaluate how selection accuracy is affected. We sketched two possible scenarios in Figure 1: one where only visual target discrimination is delayed (Figure 1B; Visual Target Discrimination—VTD hypothesis), and one where only saccade readiness is reduced (Figure 1C; Saccade Readiness—SR hypothesis). Figure 5 shows that performance as a function of latency (averaged over observers) is in line with the SR hypothesis; performance is highly similar for both the relevant cue and the irrelevant cue condition. As outlined above, we estimated the parameters of a logistic function with  $\Delta\alpha$  representing the difference between the irrelevant cue condition and the relevant cue condition. To calculate the Bayes Factor comparing the two hypotheses, we created two priors that match our initial belief in the VTD and SR hypothesis. The priors used are Cauchy distributions centered on the prediction for their respective hypotheses and with a scale of 0.707. Typically, such a prior is used when the data has been scaled to have unit variance (Rouder, Morey, Speckman, & Province, 2012). In our case, the normalization of the data would not have led to a normalization of the  $\Delta\alpha$  parameter.

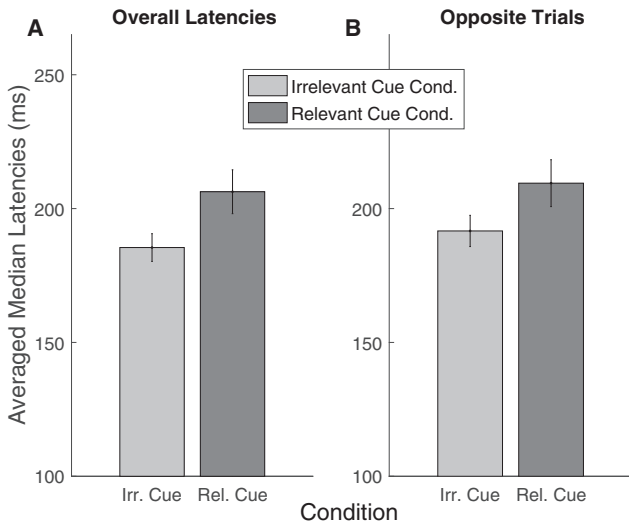


Figure 4. Latencies for the irrelevant and the relevant cued condition. (A) Median latencies are calculated for each observer and condition, and are subsequently averaged. The light gray bar represents the irrelevant cue condition, while dark gray bar represents the relevant cue condition. (B) Latencies for the subset of trials in which the two cues were presented at opposite locations with respect to the central fixation dot. Despite having the center-of-gravity at the central fixation dot, still a clear latency difference is found. Error bars represent SEM.

Therefore, the choice of the scale parameter is somewhat arbitrary. However, it is important to note that because of the nature of the calculation of our final Bayes Factor the scale parameter does not affect its value and our statistic would have been the same if we applied a different scale. In Figure 6A we plot both the prior distributions for the VTD Hypothesis and the SR Hypothesis, as well as the posterior distribution for the  $\Delta\alpha$  (representing the difference in intercept between the two conditions). Note that these prior distributions for the two parameter estimates representing the two hypotheses are unrelated to the uninformative model priors used to estimate the posterior distribution and serve solely to compare the two different hypotheses. The vertical dotted lines are drawn at the two points of interest. One at 0 for the SR hypothesis and the other at  $\sim -1.15$  representing the VTD hypothesis. Based on the intersections of these lines and the priors and posteriors (gray points) we can utilize the Savage-Dickey ratio (Dickey, 1971; Wagenmakers, Lodewyckx, Kuriyal, & Grasman, 2010) to calculate the Bayes factor for the VTD hypothesis against its prior and for the SR Hypothesis against its prior. For the former we find a Bayes factor of approximately  $5.0 \times 10^{-5}$  and the latter a Bayes Factor of 4.9. Dividing the Bayes factor for the SR hypothesis by the Bayes factor of the VTD hypothesis results in a Bayes Factor of  $9.7 \times 10^4$ , showing the evidence strongly favors the SR hypothesis over the VTD hypothesis.

### Discussion of Analysis Choices

**Prior choice.** A common critique of the Bayes Factor is that it heavily depends on the choice of priors. These priors are assumed to reflect initial beliefs, where we should note that this refers to the priors that we used to calculate the Bayes Factors, not

the priors that were used to estimate the parameters with MCMC sampling. Considering we use two prior distributions with the same shape—keeping all parameters equal except for the mean—this eliminates any potential influence of the shape of the prior distribution. The calculation of the Bayes Factor for the SR hypothesis over the VTD hypothesis is simply the height of the posterior at the predicted value for the SR hypothesis, divided by the height of the posterior at the predicted value for the VTD hypothesis. Or, in other words, because we were originally unbiased toward either hypothesis, the change in belief is solely dictated by the relative difference between the point estimates for the SR and VTD hypotheses.

**Dividing Bayes Factors.** To demonstrate that our final Bayes Factor can be obtained directly by dividing the height of the posterior at the prediction for the SR hypothesis by the height of the posterior at the VTD prediction, we can turn to the definition of the Bayes Factor. The Bayes Factor is defined as the ratio of the likelihoods. In the following formula that means the ratio of the posteriors is equal to the ratio of the priors multiplied by the Bayes Factor:

$$\frac{posterior_{SR}}{posterior_{VTD}} = \frac{prior_{SR}}{prior_{VTD}} \times \frac{likelihood_{SR}}{likelihood_{VTD}} = \frac{prior_{SR}}{prior_{VTD}} \times BF_{SR-VTD}$$

In essence, the Bayes Factor answers the question to what extent our prior belief ratio should be shifted in light of the new data to obtain the posteriors. Because our prior expectation for each hypothesis was the same, the ratio of the priors is 1. This means that in the current case the Bayes Factor is equal to the ratio of the posteriors:

$$\frac{posterior_{SR}}{posterior_{VTD}} = 1 \times BF_{SR-VTD} = 1 \times BF_{SR-VTD}$$

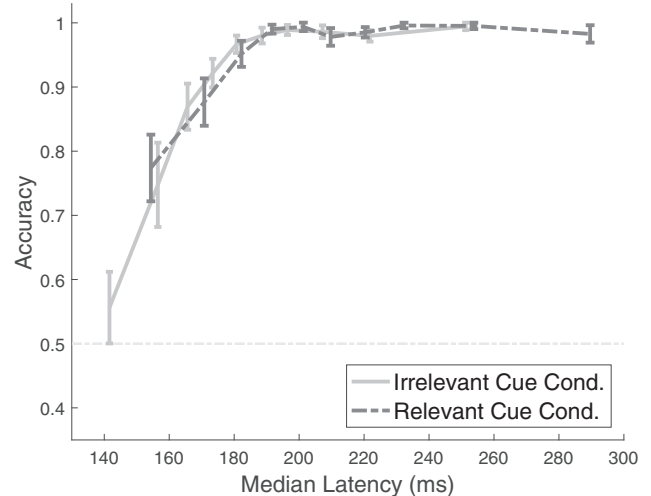
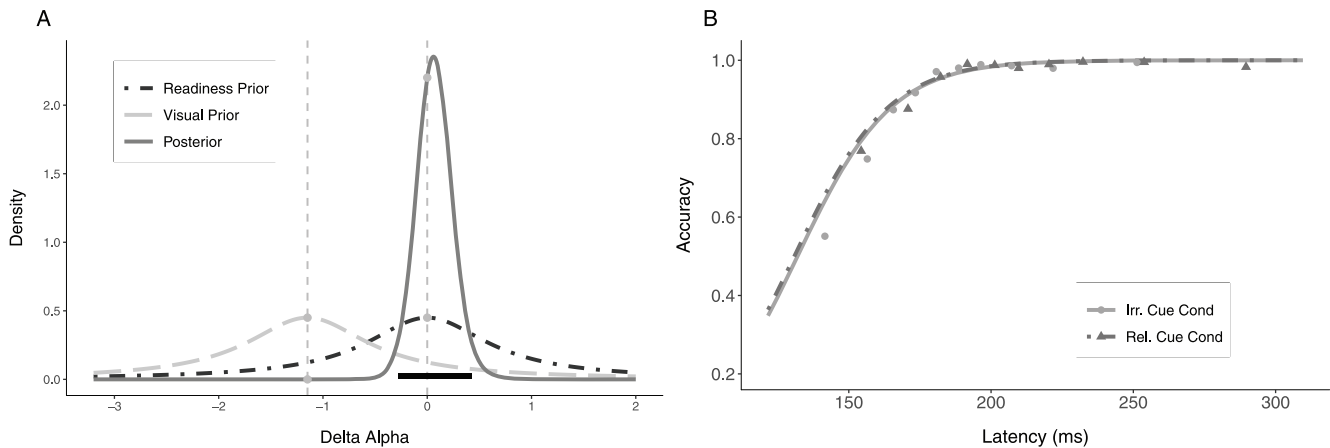


Figure 5. Accuracy as a function of latency in Experiment 1A. Trials are ordered based on latency and divided over 10 bins for the irrelevant cue condition, relevant cue condition, and each observer, separately. Mean latency and proportion correct are calculated for each bin and averaged over observers. The light gray line represents accuracy in the irrelevant cue condition and the dark gray dotted line represents accuracy in the relevant cue condition. Error bars represent SEM.





**Figure 6.** Model fits. (A) Prior distributions for the visual target discrimination and saccade readiness hypothesis are displayed in *dotted*, light-gray, and *dash-dotted* dark-gray, respectively. In *solid* mid-gray the updated posterior for the  $\Delta\alpha$  parameter is plotted. The black horizontal bar below the posterior distribution represents the 95% credible interval (by determining the highest density interval). Vertical dotted lines are placed at the center of both values of interest. The intersections between the respective prior and the posterior are represented by gray dots. These intersections are used to obtain the Bayes Factor utilizing the Savage-Dickey ratio calculation (see text for more details). (B) Fitted prediction from the logistic model based on all parameter estimates as produced by the Gibbs sampler. The light gray solid line represents performance for the irrelevant cue condition and the dark gray dotted line represents the fit for performance in the relevant cue condition. The fits are based on raw trial data; data points are included only for illustrative purposes.

Thus, dividing the height of the posterior at the prediction for the SR hypothesis, by the height of the prediction for the VTD hypothesis we obtain the same result, without dividing the two Bayes Factors. However, to keep the work accessible to the less specialist reader we wanted to stay close to the examples in the cited work (e.g., Dyjas et al., 2012; Lee & Wagenmakers, 2014; Lodewyckx et al., 2011). Therefore, we include the extra steps in the calculation of the Bayes Factor above.

**Comparative factor.** Bayesian analysis is relatively new to evaluate hypotheses in this type of research. Not only is there a debate between proponents of the Bayesian approach and those who favor frequentist analysis, there is also debate on the best way to perform model comparison in the field of Bayesian analysis. Bayes Factors are a comparative measure of (proportional) change in beliefs based on the priors and the presented evidence. A shortcoming of being a comparative measure is that the Bayes Factor can only tell us how much more likely one model is over another, but does not provide evidence for a model per se. Or in other words, one could obtain a high Bayes Factor while comparing two models neither of which has any validity. In the current case a comparison between two factors is what we are interested in. As described above, we have broadly divided the preparation of a visually guided saccade in two components: The need to process visual input to determine a target and the need to prepare a saccade. Considering the broad definition, we do not expect either to be exactly true. However, in cases where neither model is true the Bayes Factor has been shown to ultimately favor the model that is closest to the true model (Chatterjee, Maitra, & Bhattacharya, 2018). Furthermore, while evidence for one hypothesis over the other does not necessarily provide absolute proof for the specific hypothesis per se, for the current purpose it allows us to distinguish exactly what we want to.

It is important to note that such shortcomings are by no means limited to Bayes Factors. A common misconception about null hypothesis significance testing (NHST), held by students as well as lecturers, is that it provides evidence for the alternative hypothesis (Haller & Krauss, 2002). In reality NHST only allows one to reject the null hypothesis and does not provide any direct evidence for the proposed alternative hypothesis. As such it also leaves open the possibility that any other alternative model fits the data better. The current analysis is actually very similar to a frequentist approach using a generalized linear mixed effects model where the logit is used as a link function. Ultimately, the main difference is that we use a Bayesian approach for estimating the parameters (distributions) of the functions. And because this provides us with a credibility distribution on the parameters, it allows us to compare the likelihood of our two hypotheses.

**Credibility intervals.** With the Bayes Factor being limited to comparing the two hypotheses it is important to understand that for the comparison to be meaningful we also take into account the posterior distribution on  $\Delta\alpha$  in general. For a hypothesis to have any validity, the corresponding prediction should at least fall within the 95% credible interval (CI) of the posterior. In Figure 6 the black horizontal bar below the posterior represents the 95% CI (based on the highest density interval). Here we can see that the posterior distribution is centered around the prediction of the SR hypothesis. At the same time the prediction corresponding to the VTD hypothesis falls well outside of the 95% CI and is ascribed a near zero probability. As such there is little reason to believe that an alternative analysis would result in different outcomes. The shape of the posterior suggests that our results are best explained by a reduction in saccade readiness.

**Number of observers.** Bayesian analysis, unlike frequentist analysis, is not rooted in a (theoretical) repetition of experiments.

As such, an official power analysis for Bayesian methods does not exist. Yet, it is still important to verify that the current number of observers provides a reliable estimate for the posterior and, consequently, the calculated Bayes Factors. Essentially, we want to exclude the possibility that the current outcome is dependent on the number of observers we ran. To investigate this possibility, we evaluate how the posterior behaves as a function of the number of observers. This allows us to see to what extent the data depends on the number of observers (by removing observers from our analysis). As such, for the following analysis we create a number of permutations of the observer order (e.g., 3, 1, 7, 8, 4, 2, 10, 9, 6, and 5) and rerun the analysis adding one observer at a time in the given order. We repeat this process with a number of different permutations. The resulting posteriors are plotted in Figure 7. First, to assess the convergence of the posterior and the reliance on the observer order we look at how the 95% CI (by means of calculating the highest density interval; HDI). The thick bars indicate the average 95% posterior that is found to converge as the number of observers increases. However, more important than the average are the errorbars, as they represent the maximum spread of the posterior over the different observer orders. For instance, inspecting the errorbar at Observer 5 in this figure tells us that regardless of which five observers we include, the 95% CI never overlaps with the prediction corresponding to the VTD hypothesis. We can also see that after seven observers the variation in the posterior estimate becomes minimal and regardless of which three of our 10 observers are not yet entered into the analysis, there is barely any effect on the posterior estimate. As such, we deem it highly unlikely that the addition of more observers would have changed the current outcome. Nevertheless, we did not know beforehand whether 10 participants were suitable for the current analysis. This and other

small limitations outlined below led us to rerun a similar version of this experiment in Experiment 1B that includes a fresh set of 10 observers.

### Experiment 1B

In Experiment 1A inducing IOR results in a reduction in saccade readiness; yet, there are some caveats. One could argue that the results of Experiment 1A are specific to short-term cueing effects, rather than IOR in general. First, the cue-target onset asynchrony at 600–800 ms is short compared with many studies that use CTOAs around 1,000 ms. Second, while the cue and target obviously do not overlap temporally, they do overlap spatially. This could facilitate forward masking, compared with typical IOR studies that often do not include this direct spatial overlap (Lupiáñez, Martín-arévalo, & Chica, 2013; Posner & Cohen, 1984; Sapir et al., 2013; Sapir, Soroker, Berger, & Henik, 1999). Moreover, it has been argued that the early cueing effect (inhibitory cueing effect; ICE) has to be distinguished from oculomotor IOR (Hilchey, Klein, et al., 2014). To evaluate whether the findings of Experiment 1A pertain to IOR in general, we ran a second experiment. In Experiment 1B we include both a short and a long CTOA. We also removed the direct overlap between cue on the one hand, and target and distractor on the other. Moreover, the number of observers was based on numbers used in our previous studies that relied on a similar IOR manipulation, but did differ considerably otherwise. The fact that the posterior distribution of interest converges over observers and large Bayes Factors are obtained in Experiment 1A is a strong indication that the number of observers was (more than) sufficient. Nevertheless, an internal replication

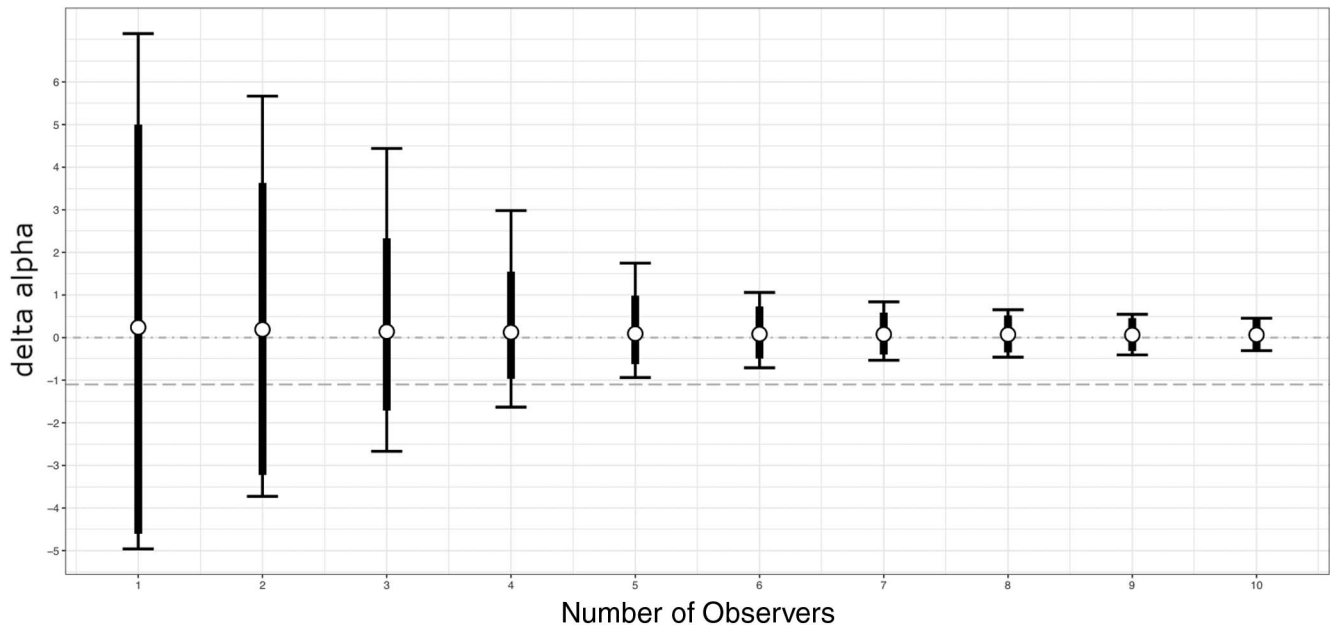


Figure 7. Posterior convergence. We show the 95% credible interval (CI) as it evolves with the addition of observers. Each bar indicates the estimate for the given number of observers (on the  $x$ -axis). The thick part of the bar represents the average 95% CI, while the errorbars represent the extremes in the 95% CI (min and max range) over the 100 permutations that we ran.

will provide additional evidence that the number of observers is indeed sufficient for its purpose.

The choice of the target and distractor properties in Experiment 1A gave rise to two other smaller issues. First, for some observers in Experiment 1A performance was close to ceiling level. This means that for these observers the predictions for the respective hypotheses were very similar for the middle and longer latencies. Second, clearly different conspicuity levels for the target and distractor were used. There is considerable debate about why a conspicuous distractor attracts more saccades than a less conspicuous target. Some argue that this is because top-down processes have little effect on the destinations of such saccades (e.g., Theeuwes, 2010; van Zoest & Donk, 2010). Furthermore, to ensure that sufficient visual target discrimination underlies saccade selection, we distinguished target and distractor solely by polarizing their luminance contrast. Both target and distractor had equal contrast, however, they could be distinguished on the basis of their polarity. The target was of a positive polarity, while the distractor had contrast in the negative polarity.

## Method

While the general paradigm of Experiment 1B was the same as in Experiment 1A, it was run on a different experimental setup and many specific parameters were different. Below we have outlined the differences.

**Observers.** Observers were again recruited through a public website and mailing lists. *None* of the current observers participated in Experiment 1A. Based on the convergence analysis and the large Bayes Factors from Experiment 1A we reasoned the previous number of observers should be sufficient and, again, 10 observers were included (7 female; aged 18–35).

**Stimulus.** Placeholders (diameter: 0.90 degrees, with a dot of 0.1 degrees at its center) were again placed at the corners of a randomly oriented imaginary square now each at a distance of 5.1 degrees from fixation. The target and distractors' diameter were 1.53 degrees and these rings had a thickness of 0.45 degrees.

**Procedure.** To evaluate whether the effect also holds for longer CTOAs this adapted version of the experiment includes two conditions: a short CTOA of 600 ms, and a longer CTOA of 1,000 ms. The latter is more common in IOR studies. Cues appeared after a cue onset asynchrony of 500 to 800 ms. To prevent the cues from spatially overlapping with the target and distractor, rather than using a ring cue, we changed the color of the placeholder disks from white to red for 50 ms. In an attempt to keep performance below ceiling level, we removed the fixation dot upon stimulus onset because it is known that this shortens saccade latencies (Saslow, 1967). To make the task more difficult and ensure a minimal contribution of any stimulus-driven processes, we also used a target and distractor with limited contrast. Finally, to minimize intertrial effects, we prevented any overlap between placeholders from trial to trial, by forcing an angular separation between any placeholder in a previous trial compared with the next of at least 22.5 degrees. The experiment was preceded by 20 practice trials, 125 trials were included per condition, resulting in a total of 520 trials per observer. The experiment was run in a single session.

**Eye movement analysis and apparatus.** For Experiment 1B, stimuli were presented on an Asus PG278Q 27" LCD monitor at a

resolution of  $2560 \times 1440$  with a frame rate of 100 Hz. Eye movements were recorded using an SR-Research EyeLink 1000 system at a sampling frequency of 1000 Hz. The observer's head was placed in a chin- and headrest so that the eyes were stable at a viewing distance of 70 cm. Images were viewed binocularly, but eye movements were recorded from the left eye only. A 13-point calibration procedure was executed before the start of the experiment. We again applied saccade detection as described in Smeets and Hooge (2003) using the same parameters of Experiment 1A. Rather than pressing the spacebar to initiate a trial, online detection of the refixation of the fixation dot was used to initiate the next trial; observers were also no longer required to press a button to initiate or finalize each trial. This procedure was established by detecting when the eye position returned to a position within 0.9 degrees of the fixation dot for an uninterrupted period of at least 150 ms. To prevent fatigue and establish the reliability of the calibration, every 20 trials a drift correction requiring a spacebar press was included. Alternatively, if observers wanted to force a break, they were told to simply shift their gaze to a corner of the screen. Finally, we applied the same five exclusion criteria as described in the methods section for Experiment 1A, with the exception that the maximum distance of the saccade landing point from any placeholder was reduced from 3 to 2 degrees. This reduction was based on the assumption that with the reduced target/distractor eccentricity the deviation in saccade landing point would also decrease. We later checked this by inspecting the data from the experiment. We note that while we do find the deviation of landing points to decrease, it is not as strong as we expected. When looking at the minimum range that includes 95% of all landing points per observer, we see that the deviation in Experiment 1B is reduced by 24% as compared with Experiment 1A.

Overall, we report the following violation rates: fixation distance criterion: 2.6%; latency criterion: 0.9%; saccades landing further than 2 degrees from target or distractor: 5.8%; saccades not directed at either target or distractor: 1.4%; movement greater than 1.5 degrees during cue presentation: 1.5%. Combined percentage of trials excluded: 7.9%.

## Results

In Figure 8 we plot the latencies for the irrelevant cue condition and the relevant cue condition for the 600 and 1,000 ms CTOA, separately. As in Experiment 1A, we see that saccade latencies in the relevant cue condition are longer than saccade latencies in the irrelevant cue condition (short-CTOA: 29.2 ms;  $t(9) = 6.28$ ,  $p < .0005$ , Cohen's  $d = 1.18$ ; long-CTOA: 20.1 ms;  $t(9) = 4.81$ ,  $p < .001$ , Cohen's  $d = 0.89$ ). Overall latencies are longer in the 600 ms CTOA condition compared with the 1,000 ms CTOA condition. This corroborates studies that evaluate how expectation of upcoming saccade targets reflects the initial latency (e.g., Oswald, Ogden, & Carpenter, 2007).

In Figure 9 we plot performance as a function of latency (as in Figure 5). Performance for the short CTOA condition again seems highly similar as a function of latency in both the relevant cue and the irrelevant cue condition (comparing results in Figure 5 with Figure 9A). In Figure 9B, performance for the long CTOA also looks in line with the hypothesis that saccade readiness is affected, even though the result is not as clear cut as it is for the short CTOA condition. We calculated a Bayes Factor using the posterior dis-

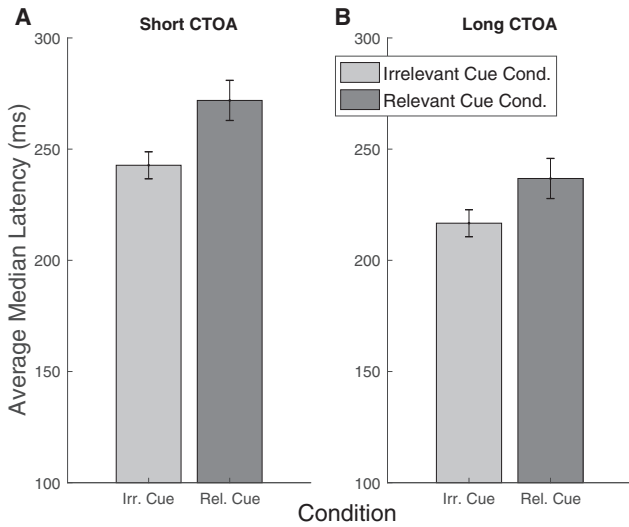


Figure 8. Saccade latencies Experiment 1B. (A) Latencies for the short cue-target onset asynchrony (CTOA) condition. The light gray bar represents the latencies for the irrelevant cue condition; the dark gray represents the latencies for the relevant cue condition. Error bars represent the standard error of the mean. (B) As in (A), but now for the long CTOA condition.

tributions estimated by the Gibbs sampler (as in Experiment 1A). In the current experiment we apply the analysis for both the short CTOA condition and the long CTOA condition, separately. Estimates for the  $\Delta\alpha$  parameter are plotted in Figure 10. The top row (Figure 10A and 10B) shows the fits for the short CTOA condition. In the bottom row (Figure 10C and 10D) the same is plotted for the long CTOA condition. For the short CTOA condition we again

find that the SR Hypothesis is much more likely than the VTD Hypothesis (BF:  $6.0 \times 10^3$ ). For the long CTOA condition we also find the evidence in favor of the SR Hypothesis (BF: 78.1). Clearly, the Bayes Factor for the short CTOA, again highly favors the SR hypothesis over the VP variant. In the long CTOA condition the Bayes Factor is considerably smaller, yet overall a Bayes Factor of 78 is *very strong* evidence (Jeffreys, 1961) in favor of the SR hypothesis over the VTD hypothesis. At the same time, it is important to note that the median and 95% CI for  $\mu_{\Delta\alpha}$  in the long CTOA condition is shifted in the direction of the prediction for the VP Hypothesis, and with a smaller latency difference in the Long CTOA condition, the difference in predictions corresponding to each hypothesis are closer together. As the posterior is shifted toward the prediction corresponding to the VTD hypothesis we cannot exclude the possibility that some delay in visual target discrimination has an effect on the latency delay in the long CTOA condition. Notwithstanding this, the prediction corresponding to the SR hypothesis still falls within the 95% CI and the VTD prediction still falls outside this range. That is, the evidence still favors the SR hypothesis over the VTD hypothesis.

### Experiment 2

The results of Experiments 1A and B suggest that the *readiness to execute* a saccade is reduced by inducing IOR, while *visual target discrimination* remains mostly unaffected. If this is indeed the best way to view IOR, we should be able to make predictions based on this finding. For example, *when* saccade readiness is reduced, we expect saccades that rely least on visual target discrimination, to be most affected by inducing IOR. The destination of very short-latency, so called express saccades (Fischer & Ramspurger, 1984), can even be predicted based on neural activity in the superior colliculus before stimulus presentation alone (Marino

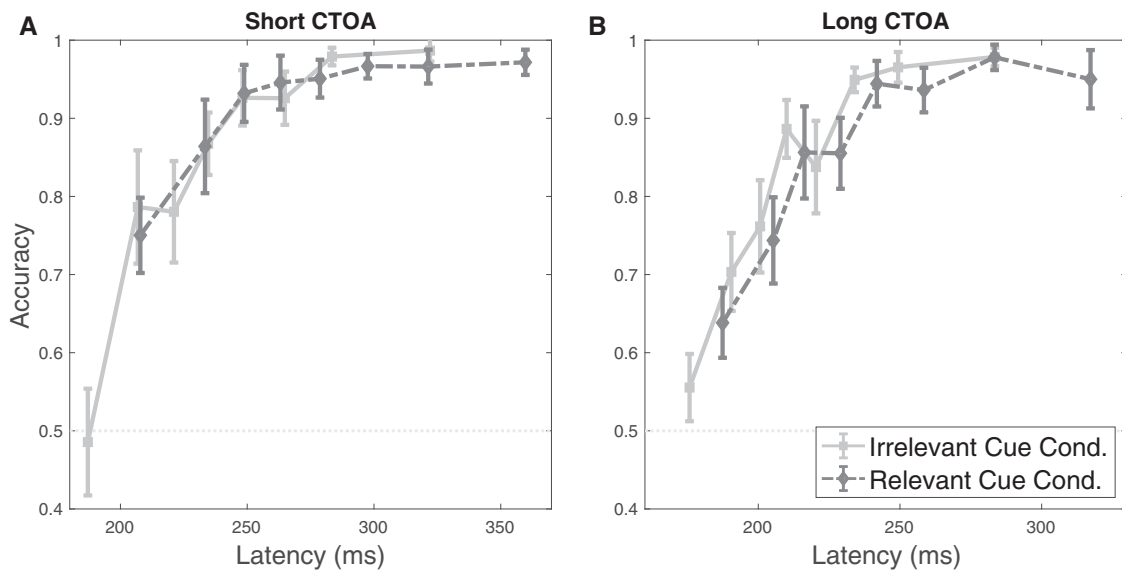
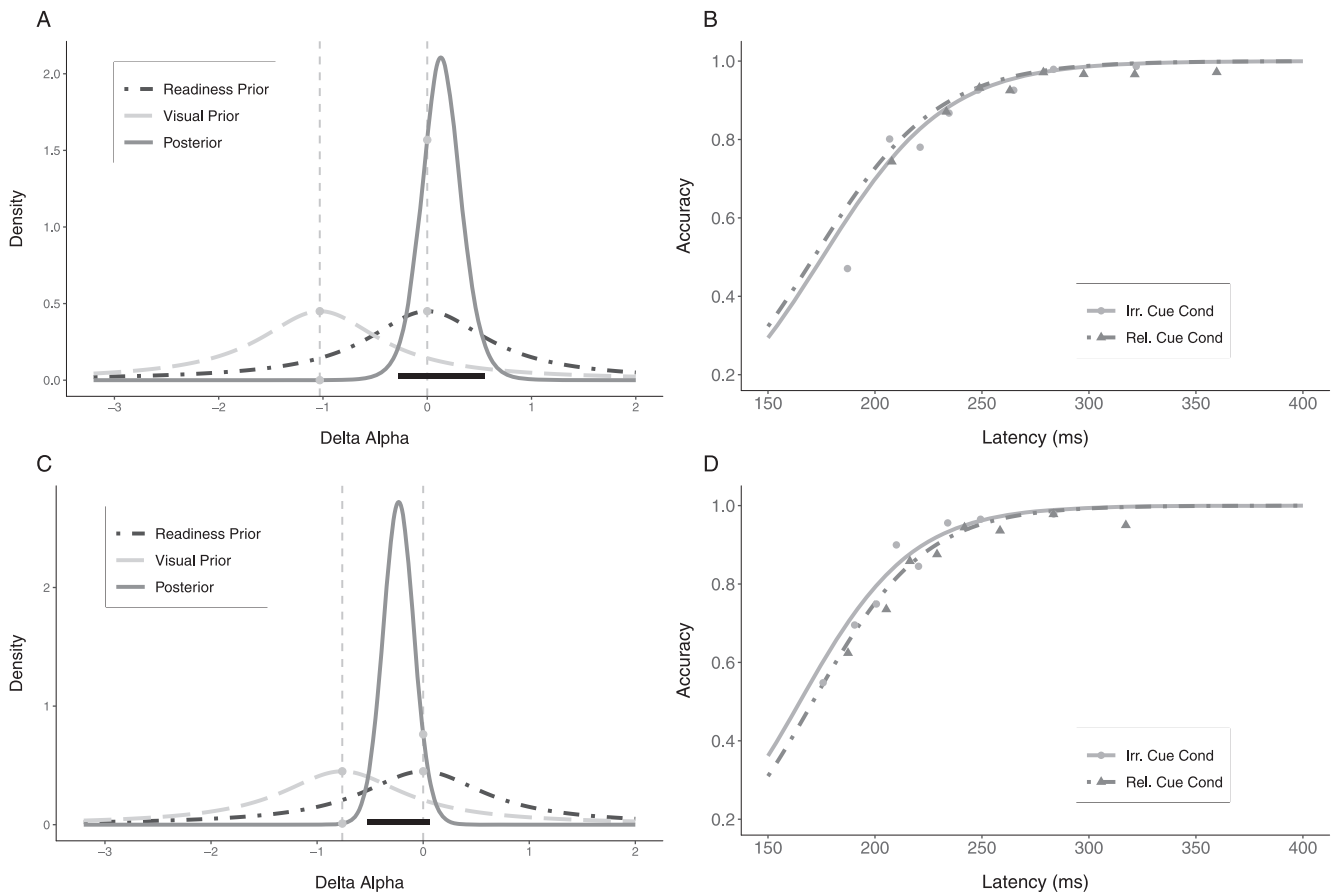


Figure 9. Accuracy as a function of latency for Experiment 1B. Bins are calculated as in Figure 5; again, the light gray solid line represents performance for the irrelevant cue condition and the dark gray dotted line represents performance for the relevant cue condition. (A) Results for the short cue-target onset asynchrony (CTOA) condition and (B) results for the long CTOA Condition. Error bars represent SEM.





**Figure 10.** Model fits Experiment 1B. (A) Priors for the visual target discrimination and saccade readiness hypothesis are displayed in *dotted light-gray* and *dash-dotted dark-gray*, respectively. In *solid mid-gray* the posterior for the  $\Delta\alpha$  parameter is plotted as estimated for the trials of the short CTOA condition. Again, the horizontal black bar below the posterior distribution indicates the 95% credible interval (using the highest density interval). Light gray dotted vertical lines are placed at the center of both values of interest. The intersections between the respective prior and the posterior are represented by gray dots and used in the Savage-Dickey calculation for the Bayes Factor. (B) Fits from mixed-effects model are based on the parameter estimates from the Gibbs samplers. The light gray solid line represents performance for the irrelevant cue condition and the dark gray dotted line represents the fit for performance in the relevant cue condition. The fits are based on raw trial data; data points (as from in Figure 8A) are included only for illustrative purposes. (C and D) same as (A) and (B) for the long CTOA condition.

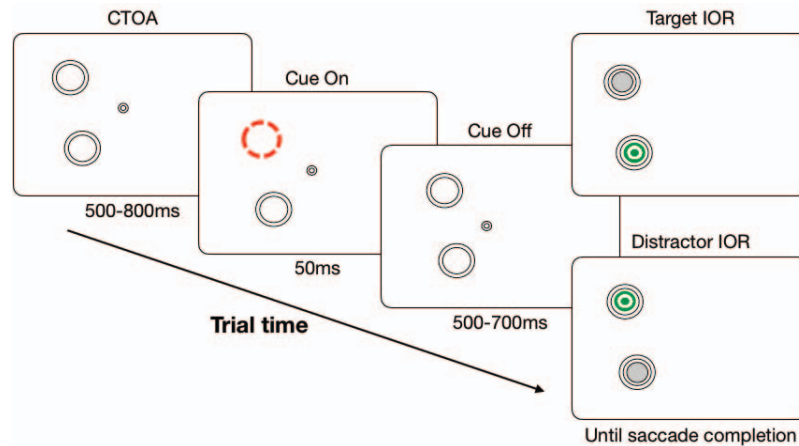
et al., 2015). As express saccades rely on minimal visual target discrimination, we expect the destination of such saccades to be affected most. Unfortunately, eliciting express saccades in humans is no easy task (Kingstone & Klein, 1993). Nevertheless, it is typically thought that shorter latency saccades in general are more stimulus-driven and rely on limited visual target discrimination as they are more likely to be attracted to salient distractors (e.g., de Vries et al., 2011; van Zoest & Donk, 2005), and sudden onsets (Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999). A reduction in saccade readiness is likely to affect the destination of such short-latency saccades most.

Here we introduce a saccade capture task where stimulus-driven saccades are frequent. We expect to only find differences between capture at the cued compared with the uncued location for the very short latency saccades.

## Method

**Observers.** Thirteen observers (9 female; ages 18–35) were recruited from the same pool as the previous experiments. We slightly increased the number of observers as we are also interested in a potential correlation over observers. Because of the different nature of the experiment, observers from the previous Experiments were allowed to participate.

**Stimulus and procedure.** Each trial started with two place-holder rings (diameter: 1.53 degrees; thickness: 0.09 degrees), placed on two randomly selected corners of a randomly oriented imaginary square standing at equal distance from fixation (5.1 degrees). Hence, they were either separated by a 90-degree or 180-degree angle with respect to the central fixation dot (see Figure 11 for the full chronology of a trial). The onset of the



*Figure 11.* Trial chronology in Experiment 2. Each trial starts with an onset asynchrony of 500–800 ms after which a red cue (here for illustrative purposes represented as a thick dotted ring) is briefly presented overlapping one placeholder (50 ms). After the onset of the cue, there is a 550–750 ms cue-target onset asynchrony, following which a target (gray disk) and distractor (green flash with a duration of 50 ms, here for illustrative purposes represented as a bull’s-eye) are presented. The observers are instructed to keep their eyes on the fixation dot until the target and distractor appear, upon which a saccade should be initiated as quickly as possible toward the target. The fixation dot either disappeared slightly before (200–70 ms) or slightly after (70–200 ms) the onset of the target and distractor (not represented in the current figure). See the online article for the color version of this figure.

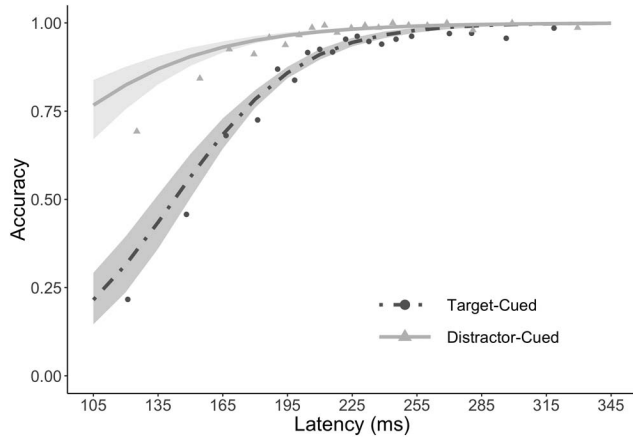
placeholders was followed by the presentation of a cue; one of the two placeholder rings was flashed by doubling the ring’s thickness (increasing the thickness to 0.19 degrees) and changing its color to red for 50 ms. After a cue-target onset asynchrony (550–750 ms), the target (a light gray disk) was presented simultaneously with a green distractor that disappeared after 50 ms. Each had a 1-degree diameter. The target was either presented within the previously cued placeholder and the distractor in the uncued placeholder (*target-cued condition*) or vice versa (*distractor-cued condition*).

As before, observers were instructed to maintain their gaze on the fixation dot from the presentation of the placeholders till the onset of target and distractor. Observers were told to saccade toward the gray target and made aware that a green flash would be presented in the other placeholder. The observers were instructed that an eye movement should be initiated as quickly as possible; it was explicitly stated that speed was more important than accuracy. To further facilitate speeded reactions, we manipulated the offset time of the fixation dot either slightly before the onset of the target (gap condition: 200–70 ms) or slightly after (overlap condition: 70–200 ms). It is known that introducing a gap leads to saccades with considerably shorter latencies (Saslow, 1967). Observers started with 20 practice trials followed by 260 trials for each of the two conditions intermixed, making it a total of 540 trials.

**Eye movement analysis and apparatus.** The set-up and analysis parameters were the same as for Experiment 1B. As in Experiment 1B, observers controlled the pacing of the experiment by refixating the central fixation dot and were only required to press the spacebar every 20 trials (or when a stable fixation could not be detected). Exclusion criteria were the same as in Experiment 1B, with the exception of the criterion that the eye movement had to aim for target or distractor, as in the current set-up these are the only possible options (there are no empty placeholders). This results in the following violation rates: fixation distance criterion: 4.0%; latency criterion:

2.4%; saccades landing further than 2 degrees from target or distractor: 6.9%; movement greater than 1.5 degrees during cue presentation: 0.6%. The combined percentage of trials excluded equals 10.2%.

**Statistical analysis.** Because observers will either correctly saccade toward the target or erroneously saccade toward a distractor, we again rely on a logistic regression. In Experiment 1 we used Bayesian methods for estimating the parameters of the mixed effects model. We made this choice for two main reasons. First, one of our hypotheses was associated with a null prediction for which frequentist statistics are not suitable. Second, Bayes Factors allow us to make a direct comparison between our two hypotheses. Ideally, for the sake of philosophical consistency, as well as allowing for easy replication, we would choose a similar analysis for the current experiment. However, because the previous experiment provided for a comparison between two very specific predictions, we were able to circumvent the difficulties of specifying an adequate prior. Unfortunately, in the current case we want to evaluate whether our parameters reliably deviate from zero and as such Bayes Factors require the specification of very accurate priors. Determining a reasonable prior for a logistic regression is a complicated issue that is not readily solved (e.g., Albert, 1988; O’Hagan, Woodward, & Moodaley, 1990; West, Harrison, & Migon, 1985). Given this issue we have opted to return to the frequentist paradigm to establish whether the regression coefficients reliably deviate from zero. More specifically, our model relies on a logistic link function where latency, condition and their interaction are included as fixed effects. Observers, on the other hand, are included as a random effect. The analysis was run using the package lme4 in R (Bates, Mächler, Ben, & Walker, 2015) where the above resulted in the following syntax: *correct ~ latency + condition + latency\*condition + (1|observer)*.



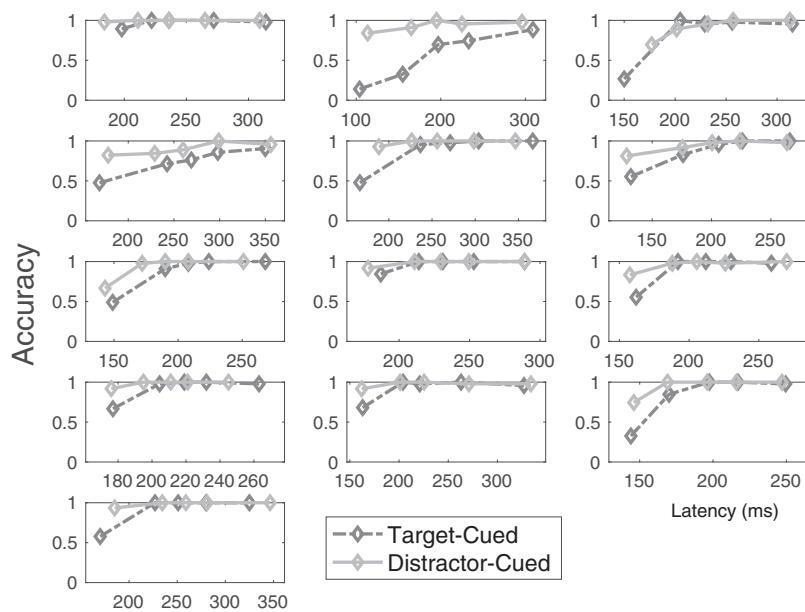
**Figure 12.** Accuracy as a function of saccade latency. A Generalized Linear Mixed Effects Model was estimated using a logit link function. The resulting lines are the fits for the Distractor-Cued condition (solid light gray) and Target-Cued condition (dotted dark gray), respectively. The shaded regions around the lines represent the bootstrapped 95% confidence intervals (5,000 iterations). Data points (filled dots for the Target-Cued condition, triangles for Distractor-Cued condition) are mean proportions and latencies for saccades with latencies split over 20 bins for each observer. Data points are purely for illustrative purposes and not the source of any analysis.

## Results

**Selection analysis.** Based on the finding that the readiness to execute a saccade is reduced toward the cued location, we predicted that only short-latency saccades would be biased away from

the previously cued location. In [Figure 12](#) we have plotted the proportion correct as a function of latency for both the target-cued and the distractor-cued conditions. Clearly, accuracy is lowest for the short-latency saccades and highest in the distractor-cued condition. We have fitted a generalized linear mixed-effects model to compare the two conditions. We find a clear effect of condition ( $\beta = 3.62$ ,  $SE = 0.457$ ,  $z = 7.94$ ,  $p < .0001$ ) and also an effect of latency ( $\beta = 5.16$ ,  $SE = 0.252$ ,  $z = 20.46$ ,  $p < .0001$ ). In line with our predictions, there is an interaction between latency and condition ( $\beta = -1.63$ ,  $SE = 0.370$ ,  $z = -4.40$ ,  $p < .0001$ ). While the overall analysis shows a gradual convergence of performance between the two conditions, evaluating individual observers shows an interesting trend. It demonstrates that for most observers the difference in performance is only present for the very short saccade latencies; for over half the observers the difference is only found for the first quintile of saccade latencies. These data of individual observers are plotted in [Figure 13](#).

**Additional analyses.** The main comparison which focusses on selection as a function of latency was executed as planned (see above). We did not plan a latency comparison for saccades toward the cued and uncued elements. This because, for a large proportion of saccades, we expected the effect of the cue to be spatial rather than temporal (we expected short-latency saccades to be biased away from the cue). As such, we did not expect a balanced set of saccades for the cued and uncued location. Nevertheless, as we do observe that a large majority of saccades aims for the target it is still interesting to evaluate the latencies for these saccades. A post hoc analysis shows that indeed latencies for saccades toward the uncued target are slightly shorter than toward the cued target: 9.1 ms (target not cued: 225.7 ms; target-cued: 234.8 ms;  $t(12) = 3.2635$ ,  $p < .01$ ). This difference is not as large as in the previous



**Figure 13.** Accuracy as a function of saccade latency for individual observers. Subplots represent individual observers. For each observer the proportion toward the target is plotted for the Target-Cued condition (dark-gray dotted line) and Distractor-Cued condition (light-gray solid line). For the majority of observers the difference in performance between conditions is only present for the short-latency bins.

Experiment 1A and 1B, which was to be expected as the spatial bias in the current Experiment meant that many saccades affected by IOR simply do not end up on the cued location.

Some interesting questions regarding other variations introduced in the experiment can also be answered. For instance, we introduced a gap manipulation where the fixation cross was removed before the appearance of the stimulus in 50% of the trials. Comparing the latencies for gap and no-gap trials we observed median latencies to be 28.4 ms faster (on average) in the gap condition (gap condition: 211.8 ms; no-gap Condition 240.2 ms;  $t(12) = 6.5929, p < .00005$ ). We also analyzed the difference in accuracy for the gap and no-gap trials and found accuracy to be higher in the no-gap trials by 5.9% (gap condition: 88.04%; no-gap Condition 93.97%;  $t(12) = 5.3902, p < .0005$ ).

Last but not least, the configuration of the elements may have had some effect. In the current setup, target and distractor either stood at a 180-degree angle (with respect to fixation;  $\sim 1/3$  of the trials) or at a 90-degree angle ( $\sim 2/3$  of the trials). Comparing these factors we find latencies to be slightly shorter in the adjacent condition with a difference of 5.9ms (adjacent trials: 223.5; diagonal trials: 229.4;  $t(12) = 2.8582, p < .05$ ). With these shorter latencies we also find the accuracy to be slightly lower in the adjacent trials for both the target-cued (adjacent trials: 85.28%; diagonal trials: 88.69%;  $t(12) = 2.3320, p < .05$ ) and the distractor-cued condition (adjacent trials: 94.88%; diagonal trials: 97.03%;  $t(12) = 2.4886, p < .05$ ).

We note that the analyses in the current section were post hoc and the result of questions we received after having run our planned comparisons. As we do not require all of these to be significant using an alpha of 0.05 could inflate the number of false-positives and a more stringent alpha of 0.0085 with Bonferroni correction for the six exploratory tests in this section would mean that the latter three tests pertaining to the configuration of the stimulus do not reach significance.

**Absolute latency and capture.** Typically, short-latency saccades are defined relative to the latency distribution of each observer individually. That is, one evaluates whether the shortest latency saccades of an observer are biased differently than the observer's longer latency saccades. Nevertheless, there is also the possibility that the absolute latency of an observer's saccades plays a role. For instance, studies that focused on express saccades over different observers found that while most naive observers made a number of express saccades, this does not hold for all observers (Fischer et al., 1993). Taking into account that express and short latency saccades are least influenced by higher order visual target discrimination, we expect saccade readiness to have a larger effect here. As such, observers that initiate their saccades in closer contingency to stimulus onset could have a stronger bias as a result of IOR than observers that take more time to initiate their saccade.

To this end, we analyzed error rates as a function of each observer's median latency for the target-cued condition only. A planned comparison of the error rate and median latency for each observer (Figure 14A) shows a nonsignificant correlation ( $\rho = -0.20, p = .55$ ). While perhaps one could argue that for such a correlation analysis, we should have included a slightly larger number of observers, considering the lack of correlation at the current level it is unlikely that more observers would have led to a significant result.<sup>4</sup> However, our expectation to find a negative correlation relies on the assumption that median latency is a

reliable indicator for whether a specific observer makes more short-latency saccades. In the case of express saccades, for instance, it is often seen that the latency distribution of an observer is bimodal, with one early peak for express saccades and a separate peak for regular saccades. From this perspective, the median latency may not be the best indicator of whether an observer made many short-latency saccades. Therefore, in a deviation from the planned comparison we reran the analysis using the median latency of only the first quintile of saccade latencies. The choice for the first quintile is somewhat arbitrary; however, it does ensure we are comparing roughly the same number of saccades for each observer. As shown in Figure 14B we find a much stronger, significant, negative correlation over our participants ( $\rho = -0.84, p < .0005$ ). Despite the lack of a correlation in our planned comparison this suggests that very short-latency, highly stimulus driven, saccades drive the current bias in saccade landing positions.

## Discussion Experiment 2

The purpose of Experiment 2 was to evaluate a prediction based on the findings that inducing IOR primarily affects the readiness to execute a saccade. In line with the prediction that short-latency, stimulus-driven, saccades are most affected by inducing IOR, we found that only the very short-latency stimulus-driven saccades were strongly biased away from the cued location. Goal-driven saccades were minimally affected, if at all. However, we should note that this experiment cannot completely rule out any effect on goal driven-saccades. The experiment pitted a clear target against a clear distractor. It is still possible that in cases where a target has to be distinguished from more similar distractors the biasing effect of the cue may extend to longer latencies. However, small biases in this hypothetical setup could still be explained by reduced saccade readiness for the target location. Importantly, the purpose of the current experiment was to directly contrast stimulus-driven with goal-driven saccades and we find a strong effect for short-latency saccades that is absent for longer latency saccades. To the best of our knowledge, this is also the first demonstration of a variation in spatial bias in IOR as a function of latency.

As explained in the method section we have opted to use a frequentist analysis over continuing the Bayesian approach from Experiment 1. Also, in Experiment 1 we did not strictly stick to Bayesian tests as we used  $t$  tests to compare the difference in latencies between conditions. Because the approaches are based on different philosophies such mixing could be argued to be undesirable. On the other hand, there are also advocates of combining the two approaches, see for instance (Dienes & Mclatchie, 2018) who propose to include Bayes Factors with all frequentist statistics. Still, in the current case, we neither adhere to a strict separation of methodologies, nor a strict combination. While we hope to have outlined good reasons for the choices made, and we believe that changing statistical procedures post hoc is a decision of last resort, we also believe that, future research is better off when the analyses are based on a more consistent approach.

<sup>4</sup> A power analysis with an optimistic expectation of an  $R^2$  of 0.64 combined with a power of 0.95 shows 11 observers would be required. A more conservative expectation of an  $R^2$  of 0.36 and a power of 0.8 leads to a minimum of 15 observers.



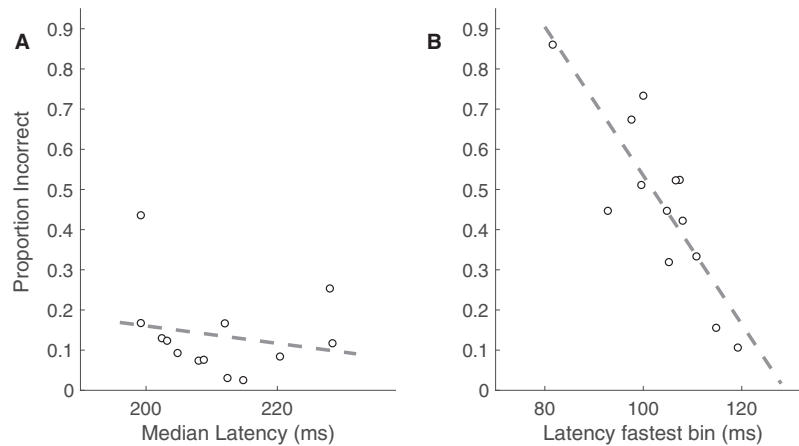


Figure 14. Relation between capture and latencies. (A) Percentage capture for each observer as a function of median latency for all trials of the target-cued condition. (B) Capture percentage as a function of the median latency for *only the first quintile* of the saccade latency distribution (the fastest latency bin in Figure 11) of the target-cued condition. Dotted line represents the linear regression line.

## General Discussion

In three experiments we have demonstrated how inducing IOR using peripheral cues affects the oculomotor decision process. Experiment 1A and 1B provide converging evidence that inducing IOR at peripheral locations affects the readiness to saccade toward these locations, while at the same time visual target discrimination proceeds unimpeded. Based on the finding that saccade readiness for cued locations is reduced, we predicted that the destination of short-latency, more stimulus-driven, saccades should be most affected in IOR (i.e. biased away from cued locations). In Experiment 2 we show that this is indeed the case: oculomotor capture is decreased for short-latency saccades when the capture location was previously cued. On the other hand, longer-latency, goal-driven saccades aim for the target, even when it appears at the cued location.

Few studies have reported a spatial bias in selection (e.g., Boot et al., 2004; Posner et al., 1985; Theeuwes & Godijn, 2004). The strongest case appears to be presented in Boot and colleagues (2004) where, after completing a sequence of four saccades, a choice between a novel location and a previously visited location had to be made. When the instruction was to saccade toward *either* location, a strong bias away from previously visited locations was found, with the effect being most prominent for the last visited location. In a paradigm resembling that of Boot et al., Fabius and colleagues (2016) also found a bias away from previously fixated locations, but *only* when observers were instructed to search, and, *only* for the last visited location. In contrast to Boot et al. (2004) the bias was completely absent in the free viewing condition. Our Experiment 2 can potentially explain the differences between the two studies: we found that *only* stimulus-driven saccades are strongly biased away from the cued location. In Boot et al. the upcoming targets were presented during the saccade, while in Fabius et al. (2016) the targets were presented with a delay after landing. Therefore, it is likely that in Boot et al. (2004) new targets appearing at saccade offset resulted in more stimulus-driven responses, hence a stronger bias away from the previously visited location. The results of Fabius et al. (2016) may be more repre-

sentative of regular scanning saccades, as there was ample time to establish fixation and anticipate the upcoming targets. Theeuwes and Godijn (2004) reported a reduction in capture saccades for locations that served as either target or distractor earlier in the same trial. This is in line with our results of the second experiment as it shows that stimulus-driven saccades are affected by IOR. While stimulus-driven saccades are often found in simple search tasks, saccade destinations during search of natural scenes appear to be minimally influenced by conspicuity (Einhäuser, Rutishauser, & Koch, 2008; Goschy, Koch, Müller, & Zehetleitner, 2014; Henderson, Brockmole, Castelano, & Mack, 2007). When Hinde and colleagues removed the search component and fully engaged observers by having them watch famous movie clips they found no evidence of capture by periodically occurring onset distractors (Hinde, Smith, & Gilchrist, 2017). Saccade destinations while searching natural scenes are likely determined by extensive visual target discrimination and while a reduction in saccade readiness may increase fixation durations, it could be insufficient to affect the destination of saccades.

It has been argued that the destinations (or landing points) of shorter latency saccades are less influenced by higher-order levels of processing than the destinations of longer latency saccades. For the very short latency express saccades it has even been demonstrated that their destination can be predicted on the basis of activity in the superior colliculus before any visual stimulation (Marino et al., 2015). In Experiment 2, we found that short latency saccade destinations are strongly influenced by the peripheral cue, which provides further evidence that saccade readiness is reduced with inducing IOR. On the other hand, longer latency saccades aim for the target, regardless of which location was cued. A post hoc analysis of the data of Experiment 2 reveals that the observers who initiate saccades after the shortest latencies (in the absolute sense) have a stronger bias away from the cued location than observers whose shortest latency saccades are longer. The fact that the bias relies mostly on very short latency saccades adds to the evidence that IOR is the result of a reduction in readiness to execute a saccade.

The current results offer insight into how the oculomotor decision process is affected by inducing IOR. A well-known brain structure that plays a key role in the oculomotor decision process is the superior colliculus (SC). It receives input from the retina, visual cortex, and other important areas. The superior colliculus projects directly to the brainstem's reticular formation where burst neurons innervate extraocular motor neurons that are required for moving the eye (e.g., Scudder, Kaneko, & Fuchs, 2002). Because of its intricate role in saccade generation, it has been described as an agent of the *readiness* and the *selection process* (Wurtz & Mohler, 1976). Notwithstanding this, it has been argued that it is unlikely that the SC itself is the locus of IOR. Using direct stimulation of neurons in the intermediate layers of the SC, Dorris and colleagues (2002) found that saccades were initiated faster, rather than slower, through stimulation of sites that were previously stimulated by the presentation of a cue. The fact that the SC itself is not responsible, stands in an apparent contrast with the notion that a reduction in saccade readiness underlies IOR. However, potentially depressed inputs to the intermediate layers of the SC *can* explain the reduction in readiness to execute a saccade. Yet, in contrast to what has previously been suggested, the depression would have to be selective: The current behavior could be explained if only signals in the exogenous pathways are depressed as the result of a cue, while signals via the endogenous pathway progress unimpeded. The suppression in the exogenous pathways will lead to a reduced initial activation at cued locations, a form of reduced saccade readiness as more input is required to trigger the saccade toward this location. While endogenous signals arrive unimpeded, it will take longer for a saccade to be triggered. The greater weight from endogenous pathway will mean the resulting saccade will have a higher probability of being directed toward elements resembling the target. Therefore, with the delay in initiation, saccades become more accurate. We should note that there is a shift in the direction of the visual discrimination hypothesis for longer cue-target onset asynchronies (Experiment 1B), which could still indicate that with longer delays, inputs from higher order processing areas can also become depressed. That is, shortly after the cue only the exogenous pathway would be affected, but after a longer period the depression could spread to inputs from higher order processing areas.

Obviously, this is not the first modeling attempt to understand what underlies IOR. Previously, the parameters of linear accumulators were fit to tease apart the basis of the delay in saccade initiation (e.g., Ludwig, Farrell, Ellis, & Gilchrist, 2009; MacInnes, 2017). While there are important differences between the linear accumulators, they typically share the property that when evidence accumulation reaches a specific threshold a saccade is triggered. Fitting a linear ballistic accumulator, Ludwig and colleagues found that IOR is best represented as a change in evidence accumulation rate, rather than a change in threshold. Ludwig and colleagues emphasize that the envisioned decision unit in their model is a *motor structure*. In the current context this can be considered as closely aligning with our description above, where we suggest inputs from the exogenous pathway may be suppressed. Looking at the spatial gradient of IOR, however, MacInnes (2017) reported that in his Diffusion Model the best way to represent IOR is by adapting the starting point variance. In the case of Ludwig et al. (2009) this would correspond with a difference in threshold rather than

accumulation rate. As suggested by MacInnes (2017) the discrepancy could be the result of the method for inducing IOR. While MacInnes induces IOR with a cue, in Ludwig et al. (2009) guided saccades are used to induce IOR (often also referred to as inhibition of saccadic return; see Hooge & Frens, 2000). Both the models by Ludwig et al. and MacInnes are process models. We decided not to present a process model as there are a number of open questions regarding what exactly drives short-latency saccades toward salient distractors. Therefore, the current findings cannot directly contribute to the accumulation rate versus threshold debate.

The fact that IOR is also found for previously fixated locations (Vaughan, 1984) is a key finding underlying the hypothesis that IOR serves a functional role in search: IOR is thought to bias future saccades away from previously cued locations to prevent unnecessary refixations and facilitate a more efficient search (often referred to as the foraging hypothesis; Klein, 1988). As we only induced IOR by using peripheral cues, we cannot draw strong conclusions as to whether our results will generalize to inhibition of saccadic return. However, in recent IOR studies much emphasis was placed on whether IOR should be described as input-based or output-based (Hilchey, Dohmen, Crowder, & Klein, 2015; Hilchey, Hashish, et al., 2014; Redden et al., 2016). In those studies, it was found that the response delay as a result of a peripheral cue, without any involvement of the oculomotor system, is the result of input-based effects. On the other hand, when saccadic responses are required, the oculomotor system is activated and output-based effects are found. Our results are in line with output-based effects. This was to be expected because in our experiments there is strong emphasis on the observer's task to initiate a saccade as quickly as possible. Several of the aforementioned studies also use discrimination tasks where observers are asked to discriminate a target using key presses. Similar to the current finding, the studies show that, after making a saccade toward a cue, (manual) discrimination responses for targets at the cued location have longer latencies than at the opposite location, but also increased accuracy (e.g., Redden et al., 2016).

From here, we find it tempting to suggest that the results generalize to saccadic IOR and, as such, the saccade readiness hypothesis may explain why there is little evidence that saccades in search are biased away from previously visited locations. To draw any strong conclusion, however, a corroboration of the results of Experiment 2, where IOR is elicited using saccades rather than peripheral cues, is necessary. If decreased input from the exogenous pathway is the source of the delay in inhibition of saccadic return it is still possible that IOR functions to bias observers from previously attended locations. However, rather than foraging all locations during search, it may just prevent the refixation of salient locations and events that have previously attracted attention. This way, locations that would else recurrently attract attention (and potentially saccades) do not continuously interfere with the search process.

## Summary

Our experiments provide converging evidence for the notion that in the oculomotor decision process the role of IOR can best be seen as a reduction in the readiness to execute a saccade. Previ-

ously, many studies have focused on what aspects of processing are affected when inducing IOR. Most of these studies focus on an individual aspect in isolation (e.g., whether the visual discrimination speed is affected by inducing IOR). What makes the current study unique is that we evaluated how inducing IOR affects the preparation and destination of the upcoming saccade. In Experiment 1 visual target discrimination appears to mostly progress unimpeded for previously cued peripheral locations. As such, the notion that IOR stems from a general depression in visual signals seems unlikely. Nevertheless, selective depression in the exogenous pathways leading to a reduction in readiness to saccade toward the cued location is a possible explanation. Interestingly, the finding that saccade readiness is reduced, allowed us to predict when saccades are biased by a cue. In Experiment 2 we found that only saccade destinations most affected by saccade readiness (short-latency, stimulus-driven saccades) were biased away from cued locations. As stimulus-driven saccades appear less common in search of natural scenes (e.g., Anderson, Ort, Kruijine, Meeter, & Donk, 2015; Einhäuser et al., 2008) it is not surprising that refixation rates in search of natural scenes are typically high. With this, the current findings likely explain why the delay in inhibition of return is found consistently, while studies on the spatial bias often stand in apparent contrast.

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Received February 13, 2019

Revision received July 5, 2020

Accepted July 24, 2020 ■