Inhibition of return: An information processing theory of its natures and significance

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Accepted for publication in the Special Issue “Cognitive and Motor Processes in Visuospatial
Attention” at Cortex

Article DOI: 10.1016/j.cortex.2020.11.009

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This work was possible due to the support of NSERC CGS and Killam Doctoral Scholarships to RSR, HSE Internal funding (Vision Modelling Lab) to WJM, and an NSERC Discovery Grant to RMK.

ABSTRACT

Inhibition of return (IOR) is an inhibitory aftereffect of visuospatial orienting, typically resulting in slower responses to targets presented in an area that has been recently attended. Since its discovery, myriad research has sought to explain the causes and effects underlying this phenomenon. Here, we briefly summarize the history of the phenomenon, and describe the early work supporting the functional significance of IOR as a foraging facilitator. We then shine a light on the discordance in the literature with respect to mechanism—in particular the lack of theoretical constructs that can consistently explain innumerable dissociations. We then describe three diagnostics (central arrow targets, locus of slack logic and the Psychological Refractory Period, and performance in speed-accuracy space) used to support our theory that there are two forms of inhibition of return—the form which is manifest being contingent upon the activation state of the reflexive oculomotor system. The input form, which operates to decrease the salience of inputs, is generated when the reflexive oculomotor system is suppressed; the output form, which operates to bias responding, is generated when the reflexive oculomotor system is not suppressed. Then, we subjected a published data set, wherein inhibitory effects had been generated while the reflexive oculomotor system was either active or suppressed, to diffusion modelling. As we hypothesized, based on the aforementioned theory, the effects of the two forms of IOR were best accounted for by different drift diffusion parameters. The paper ends with a variety of suggestions for further research.

Keywords: *inhibition of return; orienting; drift diffusion modelling; visuospatial attention*

Inhibition of return (IOR) is described as an inhibitory aftereffect of visuospatial orienting (Posner & Cohen, 1984; Posner, Rafal, Choate & Vaughan, 1985). IOR is typically observed experimentally as slower responding to a target that appears in a location toward which an observer had previously oriented. This effect has stimulated a broad spectrum of research across various domains of cognitive neuroscience in attempts to determine its cause and effect, nature and function and neural implementation. Perhaps the most noteworthy stimulus to the myriad of research on this topic is the proposal about the functional significance of IOR. For some time, it has been believed that there are two forms of inhibition, one that operates on the accrual of information from the inhibited location and one that operates as a response bias. We will review the evidence for these two forms, and show that the form generated depends on the activation state of the reflexive oculomotor system. We conclude by implementing a drift diffusion model to simulate the reaction time distributions and accuracies of the two types of IOR. Our model suggests that input and output IOR are best represented by different functional parameter sets.

1. THE MODEL TASK

IOR is typically explored experimentally with the spatial cueing paradigm (Figure 1 - left). The typical spatial cueing paradigm requires an observer to fixate some central stimulus on a screen. This central stimulus is usually flanked by two (or more) equidistant peripheral placeholder boxes. Some time after the start of a trial, a brief stimulus (typically 50-300ms in duration) occurs at one of the placeholder boxes. This onset could be a brightening of one of the boxes or the appearance of some stimulus within one of these boxes. This onset (also referred to as a cue), is uninformative as to the location of any subsequent stimuli. Some duration after the cue (cue-target onset asynchrony; CTOA), a target appears in one of these boxes that requires some response. Various response types have been used to explore the effect, such as manual detection (e.g., Posner

& Cohen, 1984; Maylor & Hockey, 1985), manual localization (e.g., Rafal, Egly, & Driver, 1994; Fischer, Pratt, & Neggers, 2003; Avery, Cowper-Smith, & Westwood, 2015), manual discrimination (e.g., Hartley & Kieley, 1995; Lupianez, Milan, Tornay, Madrid, & Tudela, 1997), temporal order judgments (e.g., Posner et al., 1985; Maylor, 1985), and saccadic eye movements (e.g., Vaughan, 1984; Taylor & Klein, 2000; Lim, Eng, Janssen & Satel, 2018).

The results that are obtained from these paradigms are typically biphasic (Figure 1 - right) - when the CTOA is short (<300ms), responses to targets that appear at the same location as the cue tend to be fastest. This effect is suggested to occur as a result of attention being captured by the cue (Lupianez, Milliken, Solano, Weaver, & Tipper, 2001, but see MacInnes & Bhatnagar, 2018). When the interval between the cue and target is longer (>300ms) and there is sufficient time for attention to return to fixation, responses to targets that appear at the same location as the cue tend to be slowest. This effect has been shown to be long-lasting both temporally (lasting up to 2-3 seconds post-cue; Samuel & Kat, 2003) and spatially (persisting across 6-7 sequentially cued locations; Snyder & Kingstone, 2000), and is suggested to occur as an attentional bias against previously attended locations. This inhibitory effect was first discovered by Posner and Cohen (1984), and subsequently named inhibition of return (IOR; Posner et al., 1985).

2. AN HISTORICAL REVIEW OF THE PHENOMENON

Posner and Cohen (1984) attributed the cause of the inhibition to be any peripheral stimulus and suggested that the effect was to reduce the efficiency of target detection in the vicinity of this stimulus. However, in different variants of the model task Posner et al. (1985) identified oculomotor activation as the cause and a motor bias as the effect. Different causes and resulting effects between these two patterns of findings beg the question as to whether or not they are

actually reflecting the same mechanism (for a more thorough review of the seminal distinctions, see Hilchey, Klein & Satel, 2014; Klein & Redden, 2018).

Figure 1. (LEFT) Sequence of events in the model spatial cueing task. (RIGHT) Prototypical pattern of response times as a function of CTOA in the model task. Responses to targets at the cued location are represented with black circles, and responses to targets at uncued locations are represented with white circles (redrawn from Klein, 2000).

2.1 - Functional Significance: Inhibition of Return During and After Search

Posner and colleagues (1984; 1985) proposed that IOR was a bias that favoured orienting to novel locations. Posner et al (1985) extended this idea by proposing that “such a bias would have obvious advantages in scanning for visual targets.” Klein (1988) tested this “foraging facilitator” proposal in a prototypical search task. Following the logic proposed by Treisman and Gelade (1980), Klein used popout and serial search trials, which according to Treisman and Gelade (1980) are done pre-attentively and attentively, respectively. Klein’s hypothesis was that if inhibitory tags are left behind as a consequence of disengaging attention during serial search, then these tags ought to exist in serial, but not in popout, search. By presenting a simple detection probe “On” or “Off” a location where a search array item had just been, Klein could test whether having

attended to items in an array was sufficient to generate IOR. The findings were precisely in line with this hypothesis: when probes were presented at a location where a serial search item had been presented, observers were slower to detect the probe relative to when the probe was presented at a location where no search stimulus had been. However, when probes were presented subsequent to a popout search trial, there was no difference in probe detection performance for probes that were presented “On” or “Off” a search item. Inhibitory effects on reorienting behaviour have since been observed in both covert (e.g., Mühler & von Mühlenen, 2000; Takeda & Yagi, 2000) and overt (e.g., Klein & MacInnes, 1999) search paradigms so long as the scene is not removed before the probe for IOR is delivered (for a review, see Wang & Klein, 2010). Although there are some who disagree with the foraging facilitator hypothesis for IOR (e.g., Hooge et al, 2005) the weight of the evidence strongly favors it.

2.2 - A phenomenon without consensus on definition or theoretical framework

Dukewich and Klein (2015) explored the diversity of perspectives researchers endorse for the phenomenon of inhibition of return. The results from a survey of over 60 IOR experts revealed little agreement on the phenomenon, with varying perspectives on causes, mechanisms, effects and components. For instance, whereas 43% of the experts agreed that IOR is a general term for similar looking effects, the remaining 57% conversely supported the idea that IOR could not be explained as a single, unitary construct.

Much research has proposed that a single mechanism can account for IOR effects across sensory and response modalities. For instance, adaptive gain models of IOR have been proposed to suggest the phenomenon operates as a supramodal habituation response to orienting (Dukewich, 2009; Sereno, Lehy, Patel, & Peng, 2010; Rutherford, O’Brien, & Raymond, 2010). Supporting

its supramodal nature, IOR has been observed between successive responses to stimuli presented from all pairings of vision, audition and touch (Spence, Lloyd, McGlone, Nicholls & Driver, 2000). Mathot, Dalmaijer, Grainger and van der Stigchel (2014) conceptualized IOR as a habituation to visual inputs, and demonstrated the size of an individual's IOR effect correlates with the pupillary light response. Differences in the time course of IOR between effectors (Briand, Larrison & Sereno, 2000) have also been interpreted in the context of the premotor theory of attention (Klein, 1980; Rizzolati, Riggio, Dascola & Umiltà, 1987). Cowper-Smith, Harris, Eskes and Westwood (2013) argue in support of a unitary inhibitory mechanism across effectors when comparing pointing responses to oculomotor responses. Studies using multiple stimuli to measure the influence of the center of gravity of the cueing array have also suggested a unitary inhibitory phenomenon affecting both manual and saccadic responses (Christie, Hilchey & Klein, 2013; MacInnes, 2017).

Alternatively, numerous dissociations support the hypothesis that there are (at least) two qualitatively different inhibitory cueing effects. Sumner and colleagues (2004) used a mixture of cue stimuli that did (S-Cone stimuli) or did not (traditional luminance stimuli) bypass the superior colliculus to examine the influence of the subcortical structure on IOR when measured with manual and saccadic responding. They found that when manual responding was required, both cue types generated IOR. However, when saccadic responses were required, typical luminance cues generated IOR whereas S-Cone cues did not. Investigating the effect of sequences of eye movements planned independently or in parallel, MacInnes, Kruger and Hunt (2015) found saccadic IOR only after sequences of independently programmed eye movements, but manual IOR after both independent and parallel sequence conditions (see also Sereno, Jeter, Pariyadath & Briand, 2006). IOR seems to be readily encoded in an object-based reference when manual

responses are required (Tipper, Driver & Weaver, 1991; Tipper, Weaver, Jerreat, & Burak, 1994; Weaver, Lupianez & Watson, 1998; Tipper, Jordan & Weaver, 1999; Theeuwes, Mathot & Grainger, 2014; Smith, Ball, Swalwell & Schenk, 2016), but when saccadic responses are required, IOR may (Abrams & Dobkin, 1994; Tas, Dodd & Hollingworth, 2012; Swalwell, 2019) or may not (Abrams & Pratt, 2000; Senturk, Greenberg & Liu, 2016; Redden, Hilchey & Klein, 2018) be object-based. Contrary to Cowper-Smith et al. (2013), Pratt and Neggers (2008) argue that separate inhibitory mechanisms influence pointing and oculomotor responses. Hunt and Kingstone (2003) asked their participants to make manual or saccadic localization responses to targets in alternate blocks while orthogonally manipulating target luminance and whether or not the fixation stimulus was removed at the time of the target. Their experiment revealed a double-dissociation: when saccadic responses were required IOR interacted with fixation removal but not with luminance, and when manual responses were required IOR interacted with luminance but not with fixation removal (but see, Michalczyk & Bielas, 2019).

Regardless of whether one ascribes to a unitary or dualist theory to explain IOR, neuroscientific studies of non-human primates (Dorris, Taylor, Klein & Munoz, 1999; Dorris, Klein, Everling & Munoz, 2002; Mirpour, Arcizet., Ong, & Bisley, 2009), and patients with impairments in cortical (Bourgeois, Chica, Migliaccio, de Schotten, & Bartolomeo, 2012; Bourgeois, Chica, Valero-Cabre, & Bartolomeo, 2013) and sub-cortical (Gabay, Henik, & Gradstein, 2010; Smith, Rorden & Jackson, 2004) brain regions support the hypothesis that the neural systems involved in eye movements play a key role in the nature of IOR's effect(s).

2.3 - Two Forms Proposed

Taylor and Klein (2000) conducted a parametric investigation into the phenomenon of IOR to systematically explore the relative contributions of input and output mechanisms. They did so by assessing the relationships between mixed central arrow and peripheral signals across response modalities. By counterbalancing the response required to a spatially uninformative first signal (ignore, manual, saccade) and second signal (manual, saccade) over six experimental sessions, 24 unique conditions were created (Figure 2). The results showed that when observers were not required to generate eye movements during a trial (Figure 2: cells 1 & 2), slower responding at cued locations was only found when the second signal was a peripheral event. Because this inhibitory effect could be generated by a centrally-presented arrow, these results preclude any sensory cause for the resulting effect as the central arrow and peripheral luminance signals do not

Figure 2. Results matrix (Cued RT - Uncued RT) from Taylor & Klein (2000). The large rows and columns represent the stimulus-response ensemble (numbered in the center of each panel). The small rows and columns within them represent the signal types. The conditions purported to elicit output-based effects are the black panels, while input-based effects are grey panels. Solid circles depict statistically significant effects.

overlap in location. Furthermore because inhibition can only be measured in responses to targets presented at the peripheral locations suggests that the effect exists at the spatial location and manifests on input mechanisms. In striking contrast, when observers were required to engage the oculomotor system at any point during a trial (Figure 2: cells 3 - 6), equivalent inhibition to both types of second signal was found, suggesting that this inhibitory effect operates on output processes, and manifests as a bias against responses spatially compatible with the first signal. Taylor and Klein posited the dissociation as evidence for two forms of IOR: when eye movements are made, the output form was generated; when eye movements are not made the input form was generated. As we will show, there are two forms, but the association (circa 2000) of the two forms of IOR simply with the response modality (an attribution made by many IOR scholars), was mistaken.

3. THREE DIAGNOSTICS FOR INPUT & OUTPUT EFFECTS

As reviewed above (Section 2.2), there is little empirical or theoretical agreement in the IOR literature. With that in mind, we propose that perhaps a major factor in the discordant literature is that researchers have, in fact, been measuring (and ultimately conflating) two distinct effects: an input form of IOR degrading the quality of information recruited from the inhibited location, and an output form of IOR influencing the criterion at which responses are executed. In the following section, we will describe three diagnostics used to determine whether an effect is operating at the input or output level. Furthermore, we will summarize the research using each of these diagnostics, including how the findings converge with the theory that there are two forms of inhibition of return, and how the form observed in any experimental context is contingent upon the activation state of the reflexive oculomotor system.

3.1 - 1—Central Arrow Targets

Inhibition measured by responses to a peripheral onset target can be attributed to output and/or input processes as the cue and target overlap spatially. Using centrally-presented arrows as targets was first pioneered independently by Rafal, Egly, and Rhodes (1994) and Abrams and Dobkin (1994). As previously stated, a central arrow target following a peripheral onset allows the evaluation of a motoric (output) contribution to the inhibition, as there is no repetition of the sensory pathway from the cue relative to the target (e.g., Fischer, Pratt & Neggers, 2003). When

Figure 3. How the pattern of results when central arrow and peripheral onset targets (depicted schematically on the x-axis) are randomly intermixed can be used to infer whether an input effect (LEFT) or output effect (RIGHT) has been generated.

arrow targets are used in conjunction with peripheral onset targets, one can discern whether the inhibitory effect generated by the cue is operating on inputs or outputs with the following logic: If the inhibitory effect is influencing the quality of information at the cued location, then one would observe slower RTs for cued peripheral onsets (relative to uncued), but no effect on arrow targets since there is no spatial overlap between the cue and arrow target (as illustrated in the left panel of Figure 3). However, if the inhibitory effect is only influencing responding, then RTs will be slower to cued peripheral onsets and to arrows in the direction of the cue (as illustrated in the right panel of Figure 3). It is noteworthy that we have already highlighted this diagnostic in the previous “Two Forms” section when presenting Taylor and Klein’s (2000) methods and findings (see Figure 2).

Rafal, Egly and Rhodes (1994 - Experiment 4) had observers execute an eye movement in the direction of a central arrow presented after a spatially uninformative peripheral onset. Supporting a motoric effect, they concluded that “because the go-signal never appeared at the cued location, any inhibition of return in Experiment 4 would not be attributable to an inhibition of detection (pp. 293).” Abrams and Dobkin (1994) found uninformative peripheral onsets inhibited saccadic responses for both central arrows *and* peripherally-presented targets, however to a greater extent for peripheral onset targets than central arrows. They proposed that two additive components comprise IOR: an attentional component, that under our interpretation would be an effect that would delay input processing, and a motoric component. They suggest central arrow targets were only sensitive to measuring the motoric component, whereas both components contributed to the inhibition for peripheral targets.

Abrams and Dobkin’s pattern of results was contradicted by Taylor and Klein’s (2000) findings in the same condition (see Figure 2 - Cell 4). Hilchey, Klein and Ivanoff (2012) noted that a key methodological difference between Abrams and Dobkin’s (1994) static display experiments

and those of Taylor and Klein (2000) was that Abrams and Dobkin implemented a between-subjects design to evaluate the effect of the different target diagnostics, while Taylor and Klein implemented a within-subjects design with cue and target types completely intermixed. While Abrams and Dobkin showed different magnitudes of inhibition between target types, Taylor and Klein (2000) showed statistically indistinguishable inhibition between target types in each cell in which the output form of IOR was generated (Figure 2, cells 3-6). Hilchey et al. hypothesized that when target types are blocked, observers could instantiate different spatial attentional control settings (ACS) — observers might more effectively filter out the uninformative peripheral cue in blocks with central arrow targets because the cue never appears in task-relevant space. This would not be the case when targets are only peripheral onsets, or randomly intermixed between peripheral onsets and central arrows because the uninformative cue appears in a task-relevant location. Hilchey et al. directly compared this within/between blocks distinction and showed that when target types were randomly intermixed, there was equivalent inhibition for each target type. However, when target types were implemented in separate blocks, IOR only occurred with peripheral targets. Hilchey et al. thusly refute Abrams and Dobkin's two component model for IOR and explain the pattern in Abrams and Dobkin's static display experiments as caused by a difference in spatial ACS.

Hilchey, Dohmen, Crowder and Klein (2016) measured manual localization responses to central arrow targets following either a pro- or anti-saccade to a peripheral cue. On prosaccade trials, they found that responses to central arrows in the direction compatible with the cued location were slower than those compatible with the uncued location—consistent with an output effect in the cued direction. However, when antisaccades were required to the cue there were no discernable differences between responses to central arrows compatible with either the location of the cue or

the direction of the eye movement—inconsistent with an output effect in either direction, but rather precisely the result that would be predicted for an input effect at the cued location. These results suggest that the output form is not elicited by an eye movement per se, because both groups were required to make eye movements. Rather, the important distinction is whether the system responsible for reflexive eye movements is suppressed or not, since one must suppress the reflexive eye movement tendency in order to generate an antisaccade (Everling, Dorris, Klein, & Munoz, 1999; Ignashchenkova, Dicke, Haarmeier, & Thier, 2004).

3.2 - 2—PRP & Locus of Slack

The psychological refractory period refers to the delay in the processing of the second of two sequentially presented targets when the interval between them is relatively short (cf Pashler, 1998). When “structural” interference can be eliminated as the cause (because there is no overlap in the input modality or responding effectors for the two tasks), it is generally assumed that the delay is caused by a central processing stage (often called a central bottleneck) that can only perform some mental operation(s) for one task at a time. When processing of one task reaches this central bottleneck, processing of the subsequent task cannot usurp the central bottleneck until processing of the first event has completed this stage. As illustrated in Figure 4, when the second task is delayed by some manipulation, such as IOR, it is possible to use the pattern of performance when the interval between the stimuli for the two tasks is varied to distinguish whether the manipulation was affecting early (pre-bottleneck) or later (bottleneck or post-bottleneck) stages of processing.

Figure 4. Prediction of a central bottleneck model (as described by Pashler, 1998) when the interval (TTOA) between the onset of two stimuli, S1 and S2 requiring speeded responses, is relatively short (A) and relatively long (B). The bottleneck stages of processing for both tasks are shaded in grey. A baseline condition, for which Task 2 does not suffer from IOR, is presented in the upper portion of each panel, whereas in the lower portion, Task 2 suffers from IOR. This results in the prolongation of a task 2 stage of processing (represented by the solid horizontal arrows). On the left side a pre-bottleneck stage of processing has been prolonged. Compared to the baseline condition, so long as the TTOA is long enough to avoid any overlap of the bottleneck stages of processing (B) the full effect of the manipulation that prolonged processing in Task 2 is manifest in RT2 (dashed double-sided arrow); but when the TTOA is short (A), the prolonged early stage of processing is absorbed into the period of slack and no effect of IOR is seen in RT2. On the right side it is assumed that the manipulation slows the bottleneck stage of processing (the predictions are the same if a post-bottleneck stage is delayed). In this case, the response time to complete Task 2 is prolonged by identical amounts (dashed double-sided arrows) whether the TTOA is short (A) or long (B). (Redrawn from Klein et al., 2019).

Klein and colleagues (Kavyani, Farsi, Abdoli & Klein, 2017; Klein, Kavyani, Farsi & Lawrence, 2018) applied this logic to discern the stage at which the two forms of IOR may be

operating. They found that when participants were forbidden to make eye movements (Kavyani et al., 2017), the effect of the cue on T2 interacted with the delay between tasks—there was no observable IOR when the TTOA was short, but the effect emerged at longer TTOAs—suggesting that the inhibition was operating at a pre-bottleneck (sensory; input) stage, and thus would have been absorbed into the slack period when the delay between tasks was sufficiently short. However, when eye movements were required (Klein et al., 2018), the inhibitory effect was additive with the delay between tasks, suggesting that the inhibition on T2 was operating at a post-bottleneck (response selection/execution; output) stage of processing.

3.3 - 3—*Speed-Accuracy Space*

Ivanoff, Klein, Lupianez (2002) hypothesized how an inhibitory after-effect operating at early or late stages in information processing would influence performance in terms of speed and accuracy. Using this approach, a genuine decrease in performance (i.e., slower and less accurate response; Figure 5 - dotted arrows) would indicate input-based inhibition at the cued location, whereas output-based inhibition would be represented by a speed-accuracy trade off (Figure 5 - solid arrow). Ivanoff & Klein (2001) used a Go/No-Go task and found a speed-accuracy tradeoff (SAT) function at cued versus uncued locations when participants were instructed to keep their eyes at fixation during the experiment. Later Hilchey, Hashish, MacLean, Satel, Ivanoff & Klein (2014) examined the role of eye movements using the Ivanoff and Klein (2001) paradigm. Hilchey et al. (2014) used a go/no-go task like Ivanoff and Klein (2001), however, they provided real-time eye movement feedback on each trial in order to suppress oculomotor activation. They showed that actively suppressing the oculomotor system in a manual response task changed the form of IOR from output-based (e.g., Ivanoff & Klein, 2001; Ivanoff & Klein, 2003; Taylor & Ivanoff,

Figure 5: Illustration of the two theories of IOR in speed-accuracy space. All functions represent hypothetical rates of information accrual where improvement in the accuracy of performance as response time increases. If the RT delay associated with IOR is caused a genuine deterioration in performance this would result in a rightward shift of the function (as shown by a shift from the solid function to the less efficient dotted function, represented by the dotted arrows) or a change in slope of the function. Alternatively, observers may demonstrate slower responding, with the additional response time eliciting an improvement in accuracy, also referred to as a speed-accuracy trade-off or criterion shift (represented by the solid arrow). The dashed arrow illustrates the ambiguity of a pattern with increase RT and increased accuracy (see text for explanation)

2003; Ivanoff & Klein, 2004; Prime & Ward, 2006; Prime & Jolicoeur, 2009) to input-based (e.g., Cheal, Chastain & Lyon, 1998).

In addition, Chica, Taylor, Lupianez & Klein (2010) examined the two effects underlying IOR using a non-spatial two-alternative forced choice (2AFC) task with coloured targets. The results showed that when participants were instructed to maintain fixation, and on-line feedback

on unwanted eye movements was provided, the inhibition was input-based (degraded performance). On the contrary, when subjects successfully made a saccade to the cue and back to the original fixation before the final target, output-based inhibition (a speed-accuracy tradeoff) was observed. Chica et al. (2010) concluded that the motoric flavor of IOR elicited by oculomotor activation does not affect perceptual processing, and rather increased response time leads to more information accrual, vis more accurate responses.

This dissociation was reinforced by Redden, Hilchey and Klein (2016), whereby subjects were required to make either a prosaccade or antisaccade (instead of ignore, as in Chica et al.) in response to the cue, and execute a subsequent manual 2AFC response to targets. Observers who made a prosaccade to the cue showed slower but more accurate target responses (output effect), whereas observers who made an antisaccade to the cue showed slower and less accurate target responses (input effect). This pattern also reinforces the causal relationship between reflexive oculomotor activation and inhibitory effect reported by Hilchey, Dohmen, Crowder and Klein (2016) using the central arrow diagnostic. Furthermore, generating full SAT functions using the response-window method (Wickelgren, 1977) has clarified a possible ambiguity in SAT patterns. It is possible that an upward pointing arrow representing an SAT could be accompanied by a genuine change in performance (Figure 5 - dashed arrow), whereby the arrow starts on one function and ends on a less efficient one. However, using the response-window method has shown that when eye movements are discouraged (Ivanoff & Klein, 2006) performance for cued targets exist on a less efficient function than do uncued targets, but when eye movements are required to the cue (Redden, Hilchey, Aslam, Ivanoff & Klein, 2020) performance for cued and uncued targets exist on a single performance function (Figure 5 - solid arrow).

4. COMPUTATIONAL MODELS OF IOR

Inhibition of return has been the subject of numerous computational models with each exploring various combinations of neural, cognitive and functional aspects. For example, salience models (Itti & Koch, 2001; Walther, Itti, Riesenhuber, Poggio, & Koch, 2002; Park, Shin & Lee, 2002; for review, see Krasovskaya & MacInnes, 2019) have used IOR in its functional role by reducing activation at previously attended salient locations. In these models, bottom up salience is computed using gaussian pyramids and separate feature maps inspired by feature integration theory (Treisman & Gelade, 1980), but a mechanism is needed to prevent repeated fixations at the point of maximal salience. IOR is implemented on top of a leaky integrate and fire layer (Burkitt, 2006) to depress activation on the salience map to allow selection of new locations. The Superior Colliculus plays a role in IOR, and has been the source of multiple approaches to neural models of its expression. Dynamic neural field (DNF) models for example can represent IOR as short-term depression of the superior colliculus and have been used to simulate spatial cuing (Satel, Wang, Trappenberg & Klein, 2011), biphasic patterns of RTs at short and long CTOAs (Lim, Eng, Janssen & Satel, 2018), and in overt search (Wang, Satel, Trappenberg & Klein, 2011).

Accumulator models have been a popular approach since they provide accurate simulation of response time distributions (Ratcliff & McKoon, 2008; Ratcliff & Van Dongen, 2011), but they also mirror neural activation in areas involved in IOR such as the lateral intraparietal area (Gold & Shadlen, 2003), the frontal eye fields (Hanes & Schall, 1996) and the superior colliculus (Ratcliff, Hasegawa, Hasegawa, Smith, & Segraves, 2009). Many accumulator models have also been used to infer underlying cognitive mechanisms through parameter changes needed to satisfy experimental conditions. For example, Ludwig, Farrell, Ellis and Gilchrist (2009) applied a Linear Ballistic Accumulator (LBA) to sequential saccades, and found inhibition of saccadic return was best accounted for with a reduction in information accumulation at previously fixated locations

Figure 6. (LEFT) Methods figure redrawn from Redden, Hilchey, and Klein (2016). (RIGHT) Table of cueing effects (RT and Accuracy) as a function of whether observers were required to generate a prosaccade or antisaccade relative to the onset of the spatially-uninformative cue.

and they interpreted this as shift in target desirability. However, Prinzmetal, Taylor, Myers and Nguyen-Espino (2011) applied the LBA to a spatial cueing task, and found IOR was best described as a change in decision threshold. Likewise, MacInnes (2017) used drift diffusion to model the spatial gradient of IOR (e.g., Vaughan, 1984; Hooze & Frens, 2000; Bennett & Pratt, 2001; Wang, Yan, Klein & Wang, 2017), and found that the gradient of inhibition for both manual and saccadic responses could be accounted for by a change in the amount of information needed to make a response. This was interpreted as evidence for similar underlying mechanisms for the phenomenon across effectors.

4.1 - Present Work

Here we describe a computational model of the findings from Redden, Hilchey and Klein (2016; see Figure 6). As described previously, in this study two groups of participants completed the same cueing task wherein an uninformative peripheral cue preceded a non-spatial discrimination target. The key experimental manipulation was the eye movement instruction at the

time of the cue: one group generated an eye movement to the cued location and back to fixation (prosaccade) prior to target onset, and the other generated an eye movement to the uncued location and back to fixation (antisaccade) prior to target onset (Figure 6 - Left). Importantly, while both groups showed slower responses to targets presented at the cued location, they showed markedly different performance with respect to accuracy. The antisaccade group showed a cost in accuracy at the previously cued location (i.e., genuine cost in performance; Figure 5 - dotted arrows), while the prosaccade group showed an improvement in accuracy at the previously cued location (i.e., speed-accuracy tradeoff; Figure 5 - solid arrow). These patterns are consistent, respectively, with the input attribution ascribed to IOR when the reflexive oculomotor system is suppressed, and the output attribution ascribed to IOR when the reflexive oculomotor system is not suppressed. By implementing drift diffusion modelling of these data, we hope to specify how various underlying computational decision components may be affected by these two inhibitory phenomena. Specifically, we hypothesize that different decision parameters will be affected by the eye movement instruction manipulation.

5. DRIFT DIFFUSION MODEL: INPUT AND OUTPUT IOR

5.1 - Parameters

The drift diffusion model was implemented in Matlab (2016a) and based on parameter learning from MacInnes (2017). The model parameters specified a 2AFC with separate but equal thresholds (A and 0) for the possible responses – the correct or the incorrect one for each trial. Starting bias and variance (Z ; $s(z)$) were not enabled in the model since the cues were not informative of the non-spatial response. The mean drift rate v ensured accumulation toward the correct threshold, but within trial variability $s(v)$ around that mean could result in accumulation to either threshold and at variable times (see Figure 7 for model parameters). Non-decision

Figure 7. Decision parameters for the accumulation of evidence over time toward one of two possible choice thresholds (A & 0). Starting points z and starting variances $s(z)$ represent bias to one of the choices. Drift rate v is a constant signal toward one (correct) of the two choices while within trial variance around that drift rate ($s(v)$) add further response choice and response time uncertainty. A response is made when accumulation crosses either threshold and the time to reach that threshold is recorded. Non decision components ($u;w$) are also added.

parameters u and w were combined to a single parameter. Of the parameters included in the model, single best fit parameter effects that would result in increased RTs are limited to: increased non-decision time ($u+w$), reduced drift rate (v), reduced within-trial variability ($s(v)$), and increased threshold ($A/0$). A reduction in drift rate (v) would elicit an associated cost in accuracy, while reducing within-trial variability ($s(v)$) or increasing threshold ($A/0$) would result in an associated improvement in accuracy. Increased non-decision time ($u+w$) would elicit no change in accuracy, as the evidence accumulation process is independent of these parameters.

5.2 - Method

We report how we determined our sample size, all data exclusions (if any), all data inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. Since our modelling is a re-analysis of previously reported data (Redden, 2020¹), the sample size, data inclusion/exclusion criteria, and all experimental manipulations/measures were determined by the original authors (Redden, Hilchey & Klein, 2016). As such, while no part of the present study was pre-registered in a time-stamped, institutional registry, all decision criteria were based precisely on the methods and analysis of the original study.

Best fit values for this model were learned using a genetic algorithm from MacInnes (2017) and matched to data from Redden et al (2016). Since we were interested in the change in parameter space for the different experiment conditions, the model was initially trained for a baseline condition with threshold fixed and freedom for all remaining parameters, then restricted to a single best fit parameter to describe the model change for experiment manipulations. The primary question was whether information accrual at cued locations would be best described as a change in accumulation rate or as a bias (change in threshold) as compared to uncued locations, and whether this best fit differed in the prosaccade and antisaccade condition. To this end, the full set of parameters of the initial model were initially trained to fit uncued prosaccade trials (uncued antisaccade trials could have also been used since these baselines were identical) using the process described next.

¹ Model code and data available at <https://osf.io/3wqtr/>.

Genetic algorithms begin with multiple sets of random values for parameter selection, and use some ‘fitness function’ to quantify how well the resulting parameters match against real world observation. We will call each set of random parameters ‘contenders’, and the initial set of contenders the first ‘generation’. For each contender, a set of responses were generated so that the contender’s performance could be statistically compared to the true human response distribution. For all tests and comparisons, the human data for each condition was treated in its entirety, meaning that individuals were not modelled separately. Comparison initially used three statistical tests: a t-test of the percentage errors found for the contender and for the human participants, a z-test of human vs model RTs, and two Kolmogorov-Smirnov (KS) tests (Weber, Leemis & Kinkaid, 2006) to compare the human and contender RT distributions for both correct and incorrect responses. The t-test and z-test required multiple samples, so means for multiple simulated subjects were generated for a given parameter set. Optimizing multiple values for a single fitness function is a known problem in machine learning (see Konak, Coit, & Smith, 2006 for a review) and in practice often combined to a single ‘fitness score’ to evaluate each contender and provide the best fit for both correct and incorrect responses. We did try a number of weighted formulas to combine speed and accuracy optimization, but our best results were found with the following two stage process using pareto optimality (Konak et al, 2006). A vector of three separate statistics [KS, t, z] were kept for the parameter set belonging to every contender. A contender’s vector was said to dominate that of another if any of the statistics improved without the others in the vector getting worse. A pareto optimal solution (or solutions) is one that is not dominated by any other solution. For each generation, our fitness function attempted to find the best known pareto optimal set for that generation, meaning contenders that were not dominated within that generation. We additionally placed a restriction rule that any pareto optimal solution must not differ significantly

for the z and t test when comparing human and model data. So the minimal KS statistics would dominate, but only if the other tests dismissed the hypothesis that the human and model rates were different.

$$\text{If } T(acc) < 2.0 \ \& \ Z(corrRT) < 1.7 \quad F() = KS(inc) * KS(corr)$$

$$\text{Else} \quad F() = 1.0$$

The parameter space was optimized through 10,000 iterations in stage one, but was followed by a second optimization regime to prioritize the correct accuracy KS test, since the relatively fewer incorrect responses may have biased the fitness toward that statistic in the first stage. Using the parameter space from stage one as the starting point, the genetic algorithm was run a second time with 5000 iterations with only accuracy and KS test for correct responses in the fitness function.

$$\text{If } T(acc) < 2.0 \quad F() = KS(corr)$$

$$\text{Else} \quad F() = 1.0$$

This allowed a refinement of the stage one parameter space toward a better fit on correct responses, but hopefully with parameters still near the incorrect KS-test space if such a solution existed.

For each iteration and contender, the vector of values listed above were recorded as a similarity score for fitness function that reflected the goodness of that contender as compared to human data. Contenders in the first generation were then sorted according to whether they were dominated by other contenders, with up to five contenders satisfying pareto optimality being selected to move on to the next generation. If fewer than 5 solutions were currently pareto optimal,

the best KS statistic among dominated solutions were added to keep the number consistent at each generation. In addition to the best contenders, the next generation was also populated with variations of these winners including: mutations that had a single parameter randomly changed; and crossovers that received parameters from two different top contenders from the previous generation. Five additional contenders with random parameters rounded out the set of contenders for the next generation. This process was repeated recursively for following generations until the similarity score was seen to asymptote. KS statistic reached asymptote after 400 generations, but the algorithm was tested up to 10000/5000 to ensure that a global maximum was reached.

Once best-fit parameters were obtained for the uncued pro-saccade condition, a modified search algorithm was run to determine which single parameter best produced the change in results caused by a cued target, separately for the prosaccade and antisaccade conditions. The genetic search only allowed a single parameter to mutate from the uncued prosaccade parameter set to determine which single parameter best fit that experiment manipulation. Although allowing multiple parameters to mutate would have certainly produced a better mathematical fit, our objective for this model was to determine the single best fitting parameter to inform how the

Figure 8. Human and model density distributions of reaction time for correct responses (LEFT). On the right, correct (blue) and incorrect (dark grey) distributions together, for model (TOP; yellow background) and human (BOTTOM; light grey background) performance. All densities are set for the area under the curve to integrate to one separately for the correct and incorrect responses.

experiment manipulation changed underlying information processing. Since the presence/absence of speed accuracy tradeoffs are critical in the input/output theory of IOR, the fitness function was modified to test the accuracy of the resulting vector in speed-accuracy (SAT) space (Redden et al., 2016). In particular, the fitness function was the inverse of the difference in angular vector between human and model data in SAT space. This allowed us to promote RT and accuracy equally and test for the parameters predicted by the speed accuracy tradeoff. Note that while we did not include KS statistic as part of the fitness function for the cued data, we still tested these results for model evaluation.

5.3 - Results

Figure 9. Results from drift diffusion modelling (top and bottom panels) of the human data from Redden, Hilchey, and Klein (2016; middle panels). Model results from two separate simulations of the model. Both simulations are fit by a 7.5% reduction in drift mean (top left and bottom left) for antisaccade data and display the expected drop in performance (slower and less accurate; red arrows). Prosaccade data, however was equally fit by a 6% increase in threshold (bottom right) and a 10% reduction in trial noise (top right) with both resulting in the observed speed accuracy tradeoff (slower but more accurate; green arrows). Error bars represent Fisher's least significant difference for the effect of cueing.

We compared the resulting simulated distribution of the initial parameter (after the complete two-stage process) set against human data from the uncued/pro-saccade condition. With

the KS test, we could not dismiss the null hypothesis that the human and model data are from the same distribution ($K=.03$, $p = .57$, and see Figure 8). Likewise for incorrect responses, we could not dismiss that distributions were the same ($K=.14$, $p = .31$). Note that the small number of incorrect trials makes fitting the KS statistic easier despite the better visual fit of the correct distribution.

Likewise, human-model t-tests of the reaction times ($t < 1$, $p = .84$) and errors ($t < 1$, $p = .63$) do not reject the null that human and model are the same.

For results testing the changes needed for the cued data, our primary hypothesis focused on the direction of the speed accuracy tradeoff. Cued trials in the antisaccade condition were consistently well modelled by a 7.5% reduction in drift mean suggesting a pure performance cost at the location of the cue that slows RTs and reduces accuracy rates. Model simulations with the drift mean adjusted for antisaccade cue were not seen as different from human data for neither RT ($t < 1$, $p = .59$) nor accuracy ($t < 1$, $p = .99$). Prosaccade trials, however, were equally well modelled by two different parameter changes. As predicted, simulations with a 6% increase in threshold for cued as compared to uncued prosaccade trials (Figure 9) resulted in RTs ($t < 1$, $p = .94$) and

Figure 10. Density distributions for correct responses for prosaccade cued trials when shifting noise parameter (top left) and threshold parameter (top right). Likewise, model (yellow) and human (light grey) distributions for correct (blue) and incorrect (dark grey) for Noise (bottom left) and threshold (bottom right) adjustments. All densities are set for the area under the curve to integrate to one separately for the correct and incorrect responses.

accuracies ($t < 1$, $p = .99$) similar to human data. But we saw equally well-fitting simulations with a 10% reduction in trial noise for cued pro-saccade data with RT ($t < 1$, $p = .98$) and accuracy ($t < 1$, $p = .85$) not dissimilar from human results. Both trial noise (Figure 9 - TOP) and threshold (Figure 9 - BOTTOM) match the critical speed accuracy trade off (slower, more accurate) that we observe in human data.

Although cued data were not trained specifically on reaction time distributions, we decided to test the two contending parameters for the pro-saccade findings to see if either held an advantage (Figure 10). Simulated results for both parameters were indistinguishable from human data according to the KS test (Threshold KS = .027; $p = .70$; Noise KS = .033, $p = .41$). The only minor diagnostic that preferred one parameter fit over the other was comparing the standard deviations of 20 simulated results compared to standard deviations of human data. Threshold results were seen as different from human data ($t(19) = 5.7$, $p < .001$) whereas Noise data was not ($t(19) = 1.4$, $p = .18$). Whereas this difference may point to diagnostics that may disentangle these two parameters in the future, we will not read too much into this post-hoc result given the excellent fit of both parameters on the other key metrics. Moreover, as will be discussed below, there are logical reasons based on the other diagnostics described earlier that favour the change in threshold.

6. DISCUSSION

We have presented a diffusion model with excellent fit to human error and reaction time data in a choice reaction task. Further, supporting our hypothesis, we have demonstrated that the two forms of IOR are clearly best fit by adjusting different parameters from the baseline response model. Diffusion parameters are often thought to reflect different underlying cognitive effects (Smith & Ratcliffe, 2004). We, therefore, propose that this adds to the growing evidence for the two forms - input and output - of IOR. As expected, IOR generated with an antisaccade was best modelled by a drift rate decrease reflecting a pure performance decrement. IOR generated by a prosaccade, however, was equally fit by two parameter shifts, though it should be noted that both of these possibilities are quite different from the drift rate result of the antisaccade condition. The hypothesised increase in the threshold parameter did match human results as predicted, but so too did a decrease in the trial noise parameter. Although there was little difference in these parameters

in simulated results, we believe the bulk of the evidence, as we describe next, currently supports the threshold parameter as the cause of the speed accuracy tradeoff of the output form of IOR.

Whereas a reduction in trial noise provided an equally good fit to these SAT data as the threshold parameter, we believe the trial noise cannot explain the various output effects observed using the other diagnostics: central arrow targets and the PRP method. A reduction in trial noise can be considered an improvement in signal-to-noise ratio (SNR) as a consequence of signal strength remaining unaffected while noise is reduced. This effect results in an SAT in speed-accuracy space since both noise and signal contribute to RT (vis slower RT with equivalent “signal” but reduced “noise”), and reduced noise elicits fewer errors. It is unknown to us how such an influence on the decision process (reduced SNR) could also account for inhibited RT to central arrows presented at fixation (i.e., a target sharing no stimulus overlap with the cue). Nor is it clear how a reduction in SNR as a consequence of the cue could account for the additive-with-TTOA pattern observed in the PRP design when output IOR is generated, thought to be a result of

Figure 11. An information processing theory of the two forms of inhibition return described in the text (with the input form represented in red and the output form represented in green). a) Which form is generated depends on the state of the reflexive oculomotor system (ROMS: – indicates it is suppressed; + indicates it is not suppressed). b) A classic information flow diagram simplified from Attneave, 1959. Inputs flow through the perceptual machinery (P) and lead to perceptual experiences at varying levels of abstraction at a central processing system (H). Outputs from this system, corresponding to voluntary behavior, give rise to actions at various levels of complexity. The red and green polygons represent the locus of operation of the two forms of inhibition of return (this component of the figure is adapted from Klein & Redden, 2018). It is important to note that for present purposes we have greatly simplified Attneave’s original figure which included feedforward and feedback signals, reflexes and habits that bypass (H) and the possibility for affective (evaluative) modulation. c) How the two forms of IOR affect processing as represented in a diffusion model, with the input form slowing the accumulation of evidence (decrease in drift rate) and the output form operating as a bias against responding (an increase in the threshold of evidence required to initiate a response). The rectangles above the “time” lines represent the effect upon RT generated by the two forms of IOR. The possible effects upon accuracy are not illustrated here (see text for explanation).

prolonged queueing of T2 response demands. However, the threshold parameter account neatly converges with the patterns observed in these other paradigms: an increase in response threshold

in the direction compatible with the cue would also inhibit localization responses to central arrows², and produce the additive-with-TTOA pattern in the PRP task.

The information processing theory we are proposing for the two forms of IOR is represented in Figure 11. Here we have embedded, into an information flow diagram adapted from Attneave (1959), illustrations of the diffusion parameters we assume to be responsible for the ubiquitous delays in reaction time that are the hallmark of IOR. As reviewed above, the reduced drift rate associated with the input form will result in slower and often less accurate responding whereas the increase in threshold associated with the output form will result in slower but more accurate responding (a speed-accuracy tradeoff).

Computational models can be seen as mathematical instantiations of theories and have the advantage of forcing us to be specific about theory components that are often missing in verbal theories (Broadbent, 1987; Guest & Martin, 2020). Generative models in particular are well suited since they are able to recreate (vis simulate) distributions of responses that are similar to those produced by human participants. The diffusion model, for example, was able to match human responses in distribution of correct responses, distributions of incorrect responses, percentage of errors, the overall vector in Speed-Accuracy trade-off space and (to a degree) the response variability. Relative to other computational models of IOR, ours is the only accumulation approach to focus on error rates in addition to reaction time distributions. Whereas RT distribution shape is an important factor in determining parameter contribution (Ludwig, 2009), the rate and latencies of errors on 2AFC tasks is often a defining feature of key theories.

² A pattern observed directly by Redden, Hilchey, Aslam, Ivanoff and Klein (2020), when intermixing central arrow and peripheral discrimination targets following a prosaccade.

Perhaps the most interesting aspect of a good model is its ability to suggest new hypotheses for testing (van Rooij & Baggio, 2020). In this regard, while our model results converge theoretically and empirically with a substantial amount of IOR research, the findings are not precisely consistent with modelling work on neurophysiological phenomena. Reviews of neural models of speed-accuracy tradeoffs (i.e., when the observer opts to trade speed for accuracy) implicate a change in baseline—rather than a change in decision threshold—as the mechanism underlying the SAT in several neural substrates shown to be associated with IOR, such as the lateral intraparietal (Hanks, Kiani & Shadlen, 2014), frontal eye fields (Heitz & Schall, 2012), and the superior colliculus (Ratcliff et al., 2009). Computationally, a reduction in baseline as a result of IOR would equate to an increased decision threshold since both result in a change in distance from starting point (z) to the response (A or O), however it is believed that there are differences in how the start and decision boundary shifts are represented neurally (Bogacz, Wagenmakers, Fortmann & Nieuwenhuis, 2010). We chose to focus on threshold changes since our task manipulation of interest was non-informative as to the correctness of response. While a change in threshold can increase the information needed for either (correct or incorrect) response equally, the change in starting point (z) is a true bias with a reduction in distance for one response coming at the expense of an increase in the other.

Whereas we have argued in the Introduction for our two forms conceptualization over various theoretical and empirical accounts of IOR, work remains to determine the extent to which our constructs can account for other expert's frameworks for the phenomenon. In particular, Lupianez and colleagues (Lupianez, 2010; Lupianez, Martin-Arevalo, & Chica, 2013) have shown inhibition can be observed in the absence of facilitation at short SOAs, and as such describe IOR as an onset-detection cost—manifesting as a function of similarity between cue and target stimuli,

with increasing similarity eliciting greater costs—rather than a consequence of the attentional disengagement from the cue stimulus. The prosaccade/antisaccade paradigm that provides the foundation of our model does not afford the measurement of attentional facilitation, since the time it takes to generate the requisite eye movements to the periphery and back to fixation in this task (~300ms) is longer than the time course of most facilitatory effects of an uninformative peripheral onset (Lupianez et al., 2001). As such, the degree to which either or both forms of IOR co-exist with attentional facilitation is heretofore unanswered (but see Hilchey, Klein & Satel, 2014). Additionally, in the empirical work leading to Lupianez and colleagues’ framework, a shift of attention as a result of the cue would have been implied (since there were no explicit oculomotor instructions relative to the cue), whereas in our experiments, the shifts of attention were explicit (as overt eye movements were required). Lupianez’s experiments did not employ eye monitoring, so the state of the reflexive oculomotor system for observers in those studies, the importance of which to the form of IOR was emphasized by Hilchey, Hashish et al (2014), is ambiguous. Lastly, as described above, the onset-detection cost framework proposes IOR is manifest as a function of similarity between cue and target stimulus. In our paradigm, the same cue and target stimuli were used to elicit qualitatively different effects: a genuine performance cost, and an SAT. As such, whereas the onset-detection cost framework may or may not map on to either form of IOR (see Hilchey, Klein & Satel, 2014, for further discussion of this point), it is unclear how this framework would completely account for the present dissociation and various other dissociations across our three diagnostics (e.g., Hilchey, Dohmen, Crowder & Klein, 2016) without further conditionals to the theory³.

³ This same logic can serve to critique the habituation account of IOR (Dukewich, 2009). While habituation may serve as an explanatory mechanism of one of the two forms we propose, without additional parameters it cannot explain the numerous dissociations we have summarized across our three diagnostics.

Additionally, our theoretical representation of two dissociable inhibitory phenomena provides a framework to begin addressing other areas lacking consensus—the neural implementation, and the object-based representation of IOR. Whereas patient data has been informative in implicating the brain regions involved in some form of IOR, to our knowledge no patient studies have employed a non-spatial decision task to measure both RT and accuracy. Thus, the results are ambiguous as to the particular form of IOR that was generated, or impaired, in these special populations. Moreover, Martin-Arevalo, Chica and Lupianez (2016) reviewed the literature on IOR using event-related potentials (ERPs), and found no single component reliably indexed the various behavioural effects reported across studies. However, perhaps the lack of consensus stems from the insensitivity to the two forms construct, and researchers may have been measuring both forms simultaneously—either between trials or between subjects (see, e.g., Satel, Hilchey, Wang, Story & Klein, 2013, for an ERP study sensitive to the two forms). By applying the prosaccade/antisaccade methodological injunction to generate the two forms separately, it is conceivable that more reliable patterns may be gleaned due to a reduction in inter- or intra-subject variability resulting from the conflation of two inhibitory processes.

This same approach could serve to address the lack of consensus on the degree to which IOR is encoded in an object-based reference. Inhibitory cueing effects appear to be most readily encoded in object-based reference under conditions akin to when the input form of IOR would have been generated: when observers are instructed to ignore the cue and generate a manual target response (Figure 2 - Cell 1; Tipper, Driver & Weaver, 1991; Tipper, Weaver, Jerreat, & Burak, 1994; Weaver, Lupianez & Watson, 1998; Tipper, Jordan & Weaver, 1999; Theeuwes, Mathot & Grainger, 2014; Smith, Ball, Swalwell & Schenk, 2016). However, under conditions wherein the output form is thought to be generated (i.e., when saccadic responses are required; Figure 2 - Cells

3-6), it is less certain whether IOR is (Abrams & Dobkin, 1994; Tas, Dodd & Hollingworth, 2012; Swalwell, 2019) or is not (Abrams & Pratt, 2000; Senturk, Greenberg & Liu, 2016; Redden, Hilchey & Klein, 2018) object-based. Moreover, while the input form is sensitive to the presence of placeholder objects in the traditional cueing paradigm, the output form is not (Hilchey, Pratt, & Christie, 2018). Regardless of which form may have been generated, object-based IOR effects tend to be smaller than those observed in more traditional cueing paradigms (e.g., Tipper, Driver & Weaver, 1991; Abrams & Dobkin, 1994). To this end, it has been posited that IOR (at least in dynamic displays) may in fact not be encoded in an object-based referent, rather that object-based effects are artefacts of a commonplace methodological flaw (Redden & Klein, 2019): “There is a potential confound implemented in many investigations employing the moving boxes paradigm—the motion (if/when it occurs) always occurs in the same direction. Even though the spatial cue is uninformative regarding subsequent target locations, the direction in which the cued object will move is typically predictable. If observers are using the cue and/or motion in some temporal attentional control setting in order to prepare for the target onset, then the shift of spatial attention elicited by the cue onset may be biased (albeit slightly) toward the region of space in which the cued object would eventually terminate. This bias in the allocation of spatial attention might actually result in an inhibitory, location-based gradient ... spreading disproportionately into the location of the cued object relative to the uncued object due to its asymmetry with the cued axis, which would masquerade as an object-based effect.” Explicitly generating the two forms in a variant of the moving boxes paradigm wherein the motion direction is not predictable would provide clarity to this end.

Future research ought to discern which of the two forms of IOR is operating in search—in particular because IOR in search is one of the more ubiquitous findings in the literature (see Wang

& Klein, 2010, for a review), and is thought to empirically represent the functional significance of the phenomenon. Whereas, as suggested by Klein & Redden, both forms of IOR could operate in service of search—one reducing the salience of previously attended inputs, the other biasing responses from previously attended locations—currently the evidence in the literature is ambiguous. Klein and MacInnes (1999) argued that the inhibitory tags generated during overt search are encoded in the visual representation of the scene (IOR encoded at the input level), since there was no inhibitory effect on performance when the scene was removed; a pattern reinforced in the spatial cueing paradigm by Redden, Klages and Klein (2017). However, Boot, McCarley, Kramer and Peterson (2004) demonstrated that saccadic inhibition persists at a location, even when previously fixated stimuli have been removed (IOR encoded at the output level). The relative activation level of the reflexive oculomotor system may in fact offer some insight into these different patterns. In the study conducted by Klein and MacInnes (1999), observers were instructed to freely search a complex visual scene for a target, a search strategy that may or may not be guided by the reflexive oculomotor system. Boot et al. (2004), however, had observers track onsets as they were presented sequentially, an injunction that is certain to engage the reflexive eye movement system. Determining the degree to which the reflexive oculomotor system is involved in any given search behaviour ought to clarify this ambiguity, and may serve to explain the various patterns observed when different tasks (and objectives) are employed (Dodd, van der Stigchel & Hollingworth, 2009).

In conclusion, we have presented a framework that can account for numerous divergent patterns observed in the IOR literature. While work remains to address outstanding components of our framework (i.e., object-based representations, mechanisms influencing visual search, neural implementation), empirical dissociations across three converging diagnostics—central arrow

targets, PRP method and locus of slack logic, and consideration of performance in speed-accuracy space—and the present computational evidence support our hypothesis that there are two distinct forms of inhibition of return, with the activation state of the reflexive oculomotor system influencing which form is observed. Importantly, both forms perform the functional role of biasing the organism toward novelty, as ascribed originally by Posner—they just do so differently. We propose the input form operates on a saliency map (Figure 11 - Red), serving to influence the quality of information received from previously cued objects/locations, whereas the output form operates on a priority map (Figure 11 - Green), serving to influence the selection of responses relative to prior orienting behaviours.

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