

# Inhibition of return is at the midpoint of simultaneous cues

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**Abstract** When multiple cues are presented simultaneously, Klein, Christie, and Morris (Psychonomic Bulletin & Review 12:295–300, 2005) found a gradient of inhibition (of return, IOR), with the slowest simple manual detection responses occurring to targets in the direction of the center of gravity of the cues. Here, we explored the possibility of extending this finding to the saccade response modality, using methods of data analysis that allowed us to consider the relative contributions of the distance from the target to the center of gravity of the array of cues and the nearest element in the cue array. We discovered that the bulk of the IOR effect with multiple cues, in both the previous and present studies, can be explained by the distance between the target and the center of gravity of the cue array. The present results are consistent with the proposal advanced by Klein et al., (2005) suggesting that this IOR effect is due to population coding in the oculomotor pathways (e.g., the superior colliculus) driving the eye movement system toward the center of gravity of the cued array.

**Keywords** Attention · Eye movements · Inhibition of return · Saccade · Center-of-gravity effect

Whereas the capture of attention is a frequent consequence of a stimulus event in the visual periphery, Posner and Cohen (1984) discovered that an inhibitory aftereffect follows the removal of attention from a stimulated location. The resultant delay in responding to targets presented at previously stimulated peripheral locations is generally called *inhibition of return* (IOR). Posner and Cohen proposed that such

inhibition could serve to encourage orienting toward novelty. Klein (1988, Klein & MacInnes, 1999; see also Snyder & Kingstone, 2000; Tipper, Weaver, Jerreat, & Burak, 1994) later extended this idea by suggesting that IOR might facilitate visual search by discouraging reinspection of previously processed locations (for reviews, see Klein, 2000; Wang & Klein, 2010). Despite these well-ingrained ideas, the behavioral characteristics of IOR, and the boundary conditions thereof, are often contested (cf., e.g., Fecteau & Munoz, 2005, 2006, to Klein & Hilchey, 2011; Klein & Taylor, 1994; and Taylor & Klein, 2000).

Using stimulus arrays of one to four uninformative peripheral cues to generate IOR, and measuring it by having observers make simple manual detection responses to single target probes, Klein et al. (2005) confirmed the presence of a gradient of IOR around a singly cued location (Bennett & Pratt, 2001; Dorris, Taylor, Klein, & Munoz, 1999; Vaughan, 1984). Importantly, they also discovered that although IOR was present when multiple locations were cued simultaneously, contrary to earlier predictions (Posner & Cohen, 1984), it was not significantly present at the individually cued locations. Instead, IOR occurred for stimuli in the direction of the center of gravity of the cues. Indeed, when the center of gravity of the cue array was at the fixation point (e.g., two cues opposite each other), reaction times (RTs) to targets at peripherally cued and uncued locations were statistically indistinguishable. This pattern resolved a longstanding empirical discrepancy and answered a question that had interested the literature since 1985 (Maylor, 1985; Posner & Cohen, 1984; see also Tassinari & Berlucchi, 1993): When the visual system is confronted with multiple, simultaneously occurring cues, does IOR occur at each cued location, or does it occur at the midpoint of the cues, as might be expected if IOR is generated by the activation of the machinery responsible for orienting (Klein, Christie, & Morris, 2005)? In terms of the latter point, because a saccadic eye movement typically gravitates to the midpoint of simultaneously presented onset

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targets (Findlay, 1982), this account predicts that IOR should exist at the midpoint of simultaneously presented cues, and not at the individual cue locations.

Langley, Gayzur, Saville, Morlock, and Bagne (2011) recently replicated Klein et al. (2005) with a larger sample size. The one exceptional finding was that Langley et al. obtained a small (5-ms) but significant advantage for uncued targets following multiple cues whose center of gravity was at fixation. In other words, they found some evidence for IOR at each of the individually stimulated locations, but the magnitude of the effect was relatively small and in the range of the original Klein et al. finding.

For the present article, we sought to determine whether the same telling results would be obtained when the key methods of Klein et al. (2005) were repeated using saccadic eye movements to measure the effect of IOR, instead of simple manual detection responses. This manipulation is interesting for several reasons. One reason is primarily empirical: to determine whether the previous results would generalize to a different response modality. Because a variety of manual/saccadic dissociations are present in the IOR literature (for a review of the important dissociations of cause, effect, and representation, see Klein & Hilchey, 2011), it is not entirely clear what we should expect from such a change in response mode. For example, fixation removal at the time of target onset reduces the magnitude of the IOR effect when it is measured by way of oculomotor but not keypress localization responses. A corresponding finding is that reducing target luminance decreases the magnitude of the IOR effect when it is measured by keypress but not oculomotor responses (Hunt & Kingstone, 2003). In the same vein, when IOR is generated by S-cone stimuli, it is obtained when manual, but not when saccadic, responses are made to targets (Sumner, Nachev, Vora, Husain, & Kennard, 2004). Another reason would be to test a prediction that follows from Klein et al.'s proposed explanation of their pattern of results. Building on previous findings of Maylor (1985), they suggested that IOR is generated by "population coding in neural systems mediating overt or covert orienting." In other words, the cue's elements generate an orienting response (saccade preparation and/or shift of attention) toward the center of gravity of the cue array, and this is the location that is inhibited. If the population coding hypothesized by Klein et al. is implemented within the oculomotor pathway, then we ought to see the same, or a similar, pattern of IOR when saccades rather than manual responses are made. Importantly, if we were to find a qualitatively different pattern of results when saccadic responses were used to measure IOR (as might be predicted on the basis of dissociations like those reported by Hunt & Kingstone, 2003, Sumner et al., 2004, and others), this would provide strong evidence against any theory in which the codings of skeletal-motor and oculomotor IOR depend on a common representation of space.

Although we would be repeating the stimulus sequences used by Klein et al. (2005) while changing the task from simple detection with a manual response to saccadic localization, we chose not to repeat the analyses used in that study. Klein et al. analyzed their data in several nonoptimal ways in order to converge on the conclusions described above. Although we believe that the conclusions are correct, by improving on their analytic techniques, we would be able to generate findings with a clearer focus and to endorse them with greater confidence. Klein et al. focused their analyses on the difference in direction (vector angle) between the target and the center of the cue array. Their use of analyses of variance necessarily turned this continuous variable into a categorical one, and their use of regression was done without considering that the data came from separate participants (see Klein et al., 2005, note 3). Finally, other than noting that the small difference in RTs between cued and uncued targets (following cue arrays with a substantial net vector) was not significant, they performed no analysis of the effect of the distance between the target and the nearest cue element on uncued trials. Therefore, an important test of the alternative hypothesis, that the individual elements generate a local IOR effect, was missing.

For the present analyses (see the [Methods of data analysis](#) section below for a thorough description), we used multilevel modeling to properly analyze the regression of the continuous dependent variable (RT) on the predictor variable of major interest: the distance between the target and the center of the cues. This was done separately for cued and uncued targets, because they spanned different ranges and because, with uncued targets, a model comparison could be made between the distance of the target to the center of the cues and the distance of the target to the nearest cue, in order to see which of these factors better explained the data. Finally, to permit a comparison of our findings with saccadic responses to those of Klein et al. (2005) with manual responses, we reanalyzed their raw data using the same methods that we applied to the new data generated in the present experiment.

## Method

### Participants

Of the 12 Dalhousie undergraduate students who participated in this study, 11 were female. Their ages ranged from 18 to 25 years, and two of them were left-handed. They were compensated \$10 Canadian for their time.

### Apparatus and stimuli

All participants were tested in a dimly lit room, and all stimuli were presented against a black background. The stimuli were

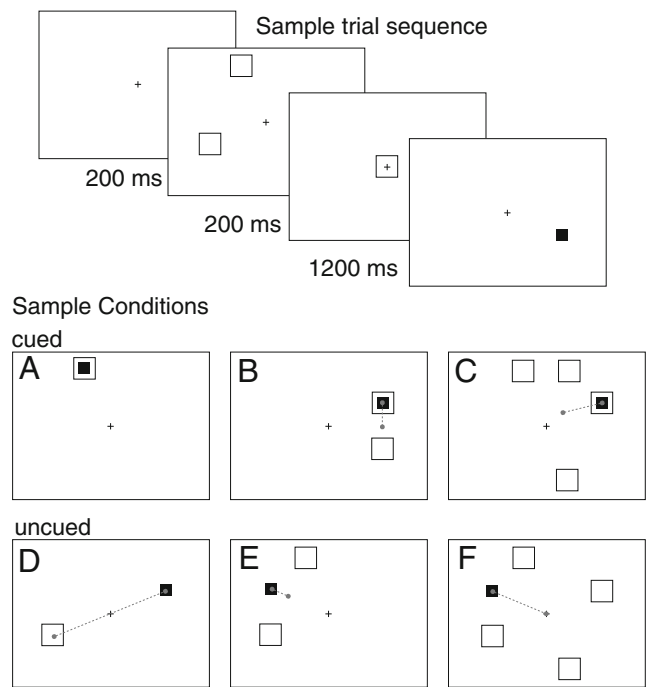
presented on a 19-in. ViewSonic Optique Q95 CRT monitor (Q95-3) connected to an Apple Mac mini with an Intel Core Duo processor, at a viewing distance of 57 cm. An EyeLink II video-based eye-monitoring system was used to monitor eye movements from the initiation of a drift correction phase, which ensured the accuracy of the calibration parameters at the beginning of the trial. The EyeLink headset was connected to a host computer, using an Intel Pentium 4 processor, which projected online gaze coordinates to a secondary monitor that was obscured by a black curtain during experimentation. After participants had performed a nine-point calibration procedure to determine and validate the precision of the eyetracker within a half degree of visual angle, the host computer provided accurate information about gaze position approximately once every 4 ms. A Python program written by J.C. was used to coordinate stimulus presentation with the eyetracking equipment.

The fixation stimulus was a white cross measuring  $0.5^\circ \times 0.5^\circ$ ; the cues were white, unfilled squares measuring  $2^\circ \times 2^\circ$ ; and the target was a white, filled square measuring  $1^\circ \times 1^\circ$ . The possible cue and target locations were eight equally spaced positions along the circumference of an imaginary circle with a radius of  $8^\circ$ . The positions started centered on the perimeter of the circle at a  $22.5^\circ$  angle from dead right, and then proceeded evenly spaced by  $45^\circ$  angles around the implied circle. Sample stimuli and displays are illustrated in Fig. 1.

Typically, we presented participants with 750 trials, which were randomly selected without replacement. Two participants experienced more trials (913 and 825) while we were exploring the number of trials that they could reasonably be expected to complete. All of their data were analyzed. Accepting only the first 750 trials from the participants who subsequently responded to additional trials did not affect our conclusions.

### Procedure

At the beginning of every trial, a white fixation stimulus appeared at the center of the computer screen. A manual spacebar response was required when the observer's subjective experience was that of having successfully fixated the fixation cross. This drift correction phase validated the calibration parameters and, when stable fixation had been achieved, one to four cues appeared simultaneously for 200 ms at randomly selected locations along the circumference of an imaginary circle. Participants were informed that these cues were irrelevant, to-be-ignored onsets, and they were further instructed to maintain fixation until the presentation of the target stimulus. Upon termination of the peripheral cue display, a central cue appeared at the center of the screen for another 200 ms in order to summon attention away from the peripheral cue(s). This cue-back was immediately followed by a single target stimulus, to which participants



**Fig. 1** Sample displays, with contrast reversal for readability. The upper sequence of panels depicts a typical trial, in this case with two cues and an uncued target. The lower six panels show some sample conditions. The cues and targets did not appear simultaneously, but are shown in this way for illustrative purposes, as are the gray dashed lines and dots, which depict the distance (lines) between the center of gravity of the cues (dots) and the target. Cued targets are illustrated in the top three panels, following one (a), two (b), and four (c) cues. Uncued targets are illustrated in the bottom three panels, likewise following one (d), two (e), and four (f) cues. Panel F illustrates one of several cue configurations for which the center of gravity of the cue array is at fixation

were instructed to make a speeded saccadic eye movement. The target appeared onscreen for 1,200 ms. Breaks could be taken at any point by refraining from initiating a trial.

### Methods of data analysis

We performed several steps in data preparation before analyzing the saccadic reaction times (SRT). Eye movements that started within 20 ms of target onset were immediately discarded as impossibly fast (here, blinks were not differentiated from other kinds of eye movements). Eye movements were recorded as correct if the angle of the initial trajectory fell within  $12.5^\circ$  on either side of the target's direction. Given a skewed and sparse long tail on the SRT distribution and many fast SRTs, an assessment of the SRT distribution was undertaken using 10-ms bins to determine upper and lower SRT cutoffs that were based on trends in accuracy. We found that acceptable accuracy (88 %) wasn't reached until 90 ms, with chance, or poorer, performance at shorter times. Consequently, all SRTs shorter than 90 ms were labeled anticipations and removed from further analysis. Long SRTs were also examined, and we found that,

given a decline in accuracy and the small amount of data at later SOAs, about 450 ms was a judicious cutoff. This trimming based on distribution and accuracy removed 5.1 % of the trials, the majority of which were anticipations, with only 0.5 % of the total being longer than 450 ms. The accuracy of the remaining trials was so high (99.5 %) that a meaningful analysis of accuracy was not possible. The analyses that follow are based on the correct remaining SRTs.

When the resulting distribution was assessed with Box–Cox (Box & Cox, 1964) transformations, we discovered that the distribution of the inverse of SRT ( $1/\text{SRT}$ ) approximated a normal distribution better than the untransformed SRTs. As a consequence, analyses were performed on  $-1/\text{SRT}$ , but for the purpose of portraying the results, the data were back-transformed to SRTs in milliseconds when this could be done reasonably. It is useful to note that, although we did back-transform the data, the only justification was convention. The inverted score can simply be interpreted as the number of eye movements that could be made per second.

The analysis was conducted using the lme4 package (Bates, Maechler, & Bolker, 2011) in R (R Development Core Team, 2012) using linear mixed-effects regression. The analysis is reported primarily like regression results, with  $b$  indicating the slope of the predicted line. This is a linear mixed-modeling approach that doesn't have agreed-upon degrees of freedom for statistical tests of the fixed effects. Nevertheless, for a study such as ours, any  $t$  value greater than 2.0 can be considered significant, because the values of the degrees of freedom are related to the number of observations—which was in the hundreds for our model with the fewest SRTs—and not just to the numbers of conditions and participants (Baayen, 2008, pp. 269–270).

## Results

The analyses are presented in two parallel sections. The first contains just the analysis of the present data, and the second contains a reanalysis of the data from Klein et al. (2005) using the techniques presented here.

We first examined trials with a single peripheral cue and analyzed SRTs as a function of the Euclidean distance between the cue and the target. The effect of distance was found to be significant and to reasonably approximate a straight line,  $b = -0.487$ ,  $SE = 0.0426$ ,  $t = 11.43$ . This can be seen in the left-hand panel of Fig. 2 as the black line and black circles. A substantial IOR effect of over 30 ms emerged here when cued targets (cue center of gravity – target distance = 0) were compared to targets at the opposite location from the cue (distance = 2.0).

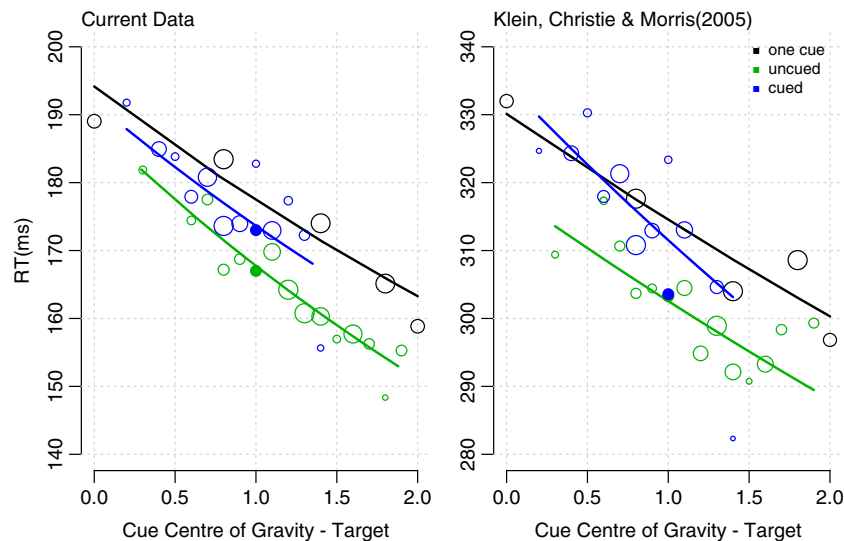
Trials with multiple cues for which the center of gravity of the cued array fell at least  $1.7^\circ$  from fixation were subjected to separate analyses, depending on whether the target fell on

a cued (e.g., Fig. 1b) or an uncued (e.g., Fig. 1e) location, and then to a combined analysis.

For targets that fell at uncued locations, both the distance from the center of gravity of the cue array and the distance from the nearest cue were modeled as predictors for the inverse SRTs. This allowed for a comparison of the hypothesis that the center of gravity of the cues would be responsible for any IOR effect found with the hypothesis that the actual stimulated locations would be responsible. Given that these two predictors are correlated, three models were calculated: one with distance from the center of gravity to the target (global) as the predictor, one with distance from the nearest cue to the target as the predictor (local), and one using both distances as predictors in order to estimate their unique effects. A check of collinearity between the two predictors was low enough that they could both be entered into an analysis at the same time (tolerance = 0.45).

Comparison of the three models was done using an information criterion (AIC) approach that is similar to likelihood ratio testing, while penalizing more complex models for their additional numbers of parameters (Akaike, 1974; Symonds & Moussalli, 2011). Using this method, the model with the lowest AIC was considered the best (absolute AIC values are meaningless). The local-effect-only model could be excluded from consideration, with its  $\Delta\text{AIC}$  being 17 greater than that of the global-effect-only model—indicating that the global effect was a substantially better predictor of SRTs than the local effect. An evidence ratio (ER) calculation showed the full model to be 3,935 times more likely than the local-effect-only model. The full model with both the local and global predictors had the lowest AIC, 3 lower than that of the global model,  $\text{ER} = 4.7$ . The unique effects of distance from the center of gravity (the global effect) and nearest stimulus (the local effect) were determined from the full model. Although the unique contribution of the global effect,  $b = -0.459$ ,  $SE = 0.092$ ,  $t = 4.968$ , was larger than the unique local effect,  $b = -0.246$ ,  $SE = 0.086$ ,  $t = 2.86$ , the significance of the latter value, and the lower AIC for the full model, still suggested some contribution of the stimulated location. To summarize, following multiple cues, and for targets presented at a location that did not contain a cue element, the global effect was the prime contributor of the IOR found, with a smaller unique contribution coming from the local effect. The slope of the uncued line in the left panel of Fig. 2 was taken from the center-of-gravity-only model,  $b = -0.654$ ,  $SE = 0.062$ ,  $t = 10.55$ .

A simpler analysis was performed on the multiple-cue data when the target appeared at a previously cued location because, for these trials, the distance to the nearest stimulus was always 0, and therefore IOR could only be observed as deviations from the center of gravity. As with the uncued



**Fig. 2** Reaction times (RTs) as a function of the distance between the center of gravity of the cue(s) and the location of the target (plotted on the x-axis in units of the radius of the cue array). The size of a circle is proportional to the number of trials, and best-fitting linear functions were computed using linear mixed-effects analysis. The data plotted in black are from trials with a single cue. The cued and uncued lines and the corresponding open circles come from trials with multiple cues whose center of gravity was substantially away from fixation. “Uncued” represents data from trials for which the target was presented

at a previously uncued location, whereas “cued” represents data for which the target was presented at a previously cued location. The solid circles represent data from symmetrical cue arrays whose center of gravity was centered at fixation. The data from Klein, Christie, and Morris (2005) are presented in the right panel using the same conventions as just described for the present saccadic task. In other words, the means and regression lines were calculated using methods similar to those in the present study, to allow for easier comparisons to the prior results

targets, the evidence for a negative slope was strong,  $b = -0.545$ ,  $SE = 0.91$ ,  $t = 6.02$ , as is illustrated by the cued line in the left panel of Fig. 2.

The main effect of cueing on these multiple-cue trials with a center of gravity substantially away from fixation can now be explored. As can be seen in Fig. 2, cued targets tended to fall closer to the center of gravity of the cue array. Given that we found that the center of gravity has an effect, it behove us to assess whether a cueing effect was present, by comparing cued and uncued trials while taking the global effect into account. Therefore, we ran a model comparing cued and uncued trials with centers of gravity that substantially deviated from 0, while also including the global effect. This analysis essentially showed a main effect of cueing (5.4 ms;  $t = 4.67$ , 95 % confidence interval [CI95%] = [3.1, 7.8 ms]). Put another way, the heights of the cued and uncued lines in Fig. 2 differ significantly.

The final analysis was conducted on trials for which the center of gravity of the cue was at fixation (in other words, trials on which the net vector of the cue was zero), just as Klein, Christie, and Morris (2005) did. This happened for trials on which two peripheral cues were exactly 180° apart or four cues were symmetrically placed around fixation (e.g., Fig. 1f). Although our estimate of the SRTs on these trials was faster for targets presented at uncued (167 ms) than at cued (173 ms) locations, our range of likely possible differences ( $t = 1.77$ , CI95% = [−0.9, 11.8 ms]) included 0. These values are the filled circles in Fig. 2.

#### Klein et al. (2005) reanalysis

The results of Klein, Christie, and Morris (2005) were reanalyzed and are depicted in the right-hand panel of Fig. 2. The initial data cleaning, including removing trials with eye movements and trimming RTs, was done exactly as was reported by Klein et al. One of the first substantial deviations from the original analysis was that a participant was dropped due to too few usable observations (17). For the remaining participants, between 98 and 358 trials were included. Another substantial deviation was that inverse RTs were analyzed, as in the present study. These were closer to normal in distribution than were the actual RTs, and time measured as a rate has an ease of interpretation roughly equivalent to that of time measured in milliseconds. What follows parallels the results reported in that article.

Rates of responding on trials with a single peripheral cue were analyzed as a function of the Euclidean distance between the cue and the target. The effect of distance was found to be significant and reasonably approximated a straight line,  $b = -0.15$ ,  $SE = 0.031$ ,  $t = 4.90$ . This can be seen in the right-hand panel of Fig. 2 as the black line and black circles. A substantial IOR effect of over 30 ms emerged here when cued targets were compared to targets at the location opposite from the cue.

Trials with multiple cues for which the center of gravity of the cued array fell at least 1.7° from fixation were subjected

to separate analyses, depending on whether the target fell on a cued or an uncued location.

For targets that fell at uncued locations, both the distance from the center of gravity of the cue array and the distance from the nearest cue were modeled as predictors for the inverse SRTs. Comparison of the three models—local effect only, global effect only, and both—was again done using an information criterion (AIC) approach. The local-effect-only model could be excluded from consideration, with a  $\Delta\text{AIC}$  7 greater than the global-effect-only model. Contrary to the new saccade data presented above, the global-effect-only model was better than the full model,  $\Delta\text{AIC} = 5$ . Therefore, again, the global effect was a stronger predictor of RTs than was the local effect, but in this case we found no evidence of a local contribution. The unique global and local effects were determined from the full model. Only the global effect,  $b = -0.19$ ,  $SE = 0.07$ ,  $t = 2.67$ , was significant, and the unique local effect was in the opposite direction and very small,  $b = 0.03$ ,  $SE = 0.07$ ,  $t = 0.45$ . The slope of the uncued line in the right panel of Fig. 2 was taken from the center-of-gravity-only model,  $b = -0.166$ ,  $SE = 0.047$ ,  $t = 3.55$ .

A simpler analysis was performed on the multiple-cue data when the target appeared at a previously cued location; as with the uncued targets, the evidence for a negative slope was strong,  $b = -0.22$ ,  $SE = 0.07$ ,  $t = 2.97$ , as is illustrated in the cued line in the right panel of Fig. 2.

Further examining these multiple-cue trials with a substantial net vector revealed a main effect of cueing,  $t = 2.96$ ,  $\text{CI}_{95\%} = [2.9, 14.9 \text{ ms}]$ . The back-transformed RTs to targets presented at cued locations (310 ms) were longer than those to uncued locations (302 ms). This was not due to cued targets being close to the center of gravity, because the model that tested for this effect also included the center of gravity. Because this local effect did not occur for distances from the cue elements  $>0$ , we concluded that this local effect had no gradient. We note that this effect was 6 ms and not statistically significant in Klein et al.'s (2005) analysis.

The analysis of trials for which the center of gravity of the cue was at fixation yielded results similar to those of Klein et al. (2005), because the RTs were very similar: 303.6 ms for cued and 303.3 ms for uncued trials,  $t = 0.039$ ,  $\text{CI}_{95\%} = [-15, 16.6 \text{ ms}]$ . Note the much larger CI, despite the larger number of participants in this study. This was due partly to the fact that manual RTs are more variable than saccadic RTs, and partly to the fact that each participant had far fewer trials.

To summarize this section, Klein et al.'s (2005) conclusions were fundamentally supported by the new analyses. RTs could be predicted from the centers of the cue arrays, but not from the individual cue locations when those two variables were separated. An overall effect of cued versus uncued targets did occur, similar to what Klein et al. found (theirs being nonsignificant), but it did not appear to have a

gradient contributing to the magnitudes of RTs as they varied in distance from a cued location.

## Discussion

The pattern of results observed here with eye movement responses is very similar to the one generated by Klein et al. (2005) in a simple manual detection task. To provide an equivalent basis for comparison, we subjected their data to the same analytical strategy (importantly, with its focus on the center of gravity) used in the present study (see the right panel of Fig. 2). The similarities were remarkable:

1. For both saccadic and manual responses, whether IOR was measured from the location of a single cue or from the center of gravity of the array of cues, we found a similar gradient (slope of the RT function) of IOR. This center-of-gravity effect of the cue array was substantial ( $>25$  ms over uncued targets, and a similar effect for cued targets).
2. For both saccadic and manual responses following multiple cues with a center of gravity substantially away from fixation, a small disadvantage emerged for targets appearing at a location that had been cued relative to one that had not been (see Fig. 2).
3. For both saccadic and manual responses, when the cue array's center of gravity was at fixation, the RT difference between cued and uncued targets was not significant.

It should be noted that the local inhibitory effects (Finding 2) were relatively small (5–8 ms) whether they were accompanied by a small local gradient, as in the present study, or not, as in Klein et al. (2005). These direct effects of stimulation must be participating in the computation of the center of gravity. We cannot be sure why they are so small, but one possibility is that they are akin to the smaller retinotopic effects that are seen when an eye movement intervenes between a single cue and a target, as opposed to the spatiotopic effects seen more directly in IOR studies (Maylor & Hockey, 1985; Satel, Wang, Hilchey, & Klein, 2012). We believe that the retinotopic effect (which is between 5 and 6 ms) and our local effects (which are of a similar magnitude) may be represented in the colliculus. In contrast, we believe that the much larger spatiotopic effect, and our global effect, are computed cortically (see below).

A caveat is in order with regard to Finding 3, for four reasons. First, in the present study this result was statistically null in the presence of a 6-ms advantage for targets presented at uncued locations. Second, this advantage was roughly the same size as the advantage for uncued targets following multiple-cue arrays with substantial net vectors (Finding 2). Third, our analysis of the uncued data following multiple cues with substantial net vectors did reveal a significant contribution to IOR rooted in the distance between the target

and the nearest cue element. Fourth, as we noted above, using methods similar to those of Klein et al. (2005), but with many more participants, Langley et al. (2011) found a significant 5-ms advantage for a target presented at an uncued location following cues whose center of gravity was centered on fixation. Thinking meta-analytically, all of these findings suggest that, in addition to the much larger global effect that is represented by the slopes of the functions in Fig. 2, a small, but real, local effect exists for centers of gravity at fixation, and that, due to inadequate power and the particular random sample, Klein et al. missed this effect.

Notwithstanding the similarities noted above, one difference might merit further research into distinctions between the saccadic and manual response systems. In the present study, on uncued trials we found a small inhibitory contribution of the nearest cued location, over and above that of the center of gravity on uncued target trials. This was not found in the Klein et al. (2005) data, and the effect in that study was in the opposite direction.

Our introductory remarks noted dissociations between IOR for saccadic and manual responses (Hunt & Kingstone, 2003; Sumner et al., 2004). In contrast to these saccade/manual dissociations, the present results demonstrate that for both manual and saccadic responses, IOR occurs at the center of gravity of simultaneously presented cues. The striking similarity of the findings from these two response modalities is consistent with the idea that both oculomotor (Klein & Hilchey, 2011) and skeletal-motor (Pratt & Neggers, 2008) IOR can be encoded in the same representation of space.

The data are consistent with the population-coding account described in the introduction and by Klein et al. (2005). Both the IOR effect (e.g., Dorris, Klein, Everling, & Munoz, 2002; Fecteau & Munoz, 2005; Posner, Rafal, Choate, & Vaughan, 1985; Sapir, Soroker, Berger, & Henik, 1999; Sereno, Briand, Amador, & Szapiel, 2006) and the center-of-gravity effect (e.g., Alahyane, Koene, & Pelisson, 2004; Glimcher & Sparks, 1993; Robinson, 1972; Schiller & Sandell, 1983; van der Stigchel, de Vries, Bethlehem, & Theeuwes, 2011; van Opstal & van Gisbergen, 1990) are closely linked to stimulus-driven activation of the oculomotor system. If common oculomotor pathways are responsible for (1) the IOR effect and (2) the center-of-gravity effect, it should come as no surprise that there would be center-of-gravity effects of IOR.

Despite the present and extant evidence suggesting that IOR and the center-of-gravity effect are implemented by shared oculomotor circuitry, it is worth noting that pathways outside the superior colliculus have been implicated in both of these effects. Cortical mechanisms must normally play a role, if not in IOR's generation, then at least in its maintenance over substantial periods of time (Samuel & Kat, 2003), its environmental coding in the face of eye movements (Maylor & Hockey, 1985), and its object coding in the face of movements of a cued

object (Tipper, Driver, & Weaver, 1991). This line of thinking has been bolstered in recent years by studies showing that parietal lesions (Sapir, Hayes, Henik, Danziger, & Rafal, 2004) and transcranial magnetic stimulation (TMS) to the right parietal cortex (van Koningsbruggen, Gabay, Sapir, Henik, & Rafal, 2010) disrupt the dynamic coordinate system of IOR, and that object-based IOR fails to cross the vertical midline in split-brain patients (Tipper et al., 1997). Similarly, cortical mechanisms have been suggested to play a role in saccade averaging (i.e., the center-of-gravity effect). Saccade averaging can also depend on the perceptual center of gravity (or center of area; Melcher & Kowler, 1999)—essentially a Gestalt perceptual representation of a given configuration of stimuli—and not on the component visible elements (McGowan, Kowler, Sharma, & Chubb, 1998; Melcher & Kohler, 1999).

## Conclusions

We have demonstrated that oculomotor IOR generated by multiple stimuli is primarily driven by the center of gravity of the cueing array and not by the individual cued locations. This extends the findings of Klein et al. (2005) and Langley et al. (2011), based on buttonpress responses. Therefore, irrespective of response modality, IOR occurs at the center of gravity of simultaneously presented cueing arrays. Thus, although many examples of response-based dissociations have appeared in the IOR literature (see Klein & Hilchey, 2011), here we have found a remarkable similarity in the effects of the center of gravity on IOR, whether measured by saccadic or manual responses. It is worth noting that local effects of the individual cue elements also occur, but that these effects appear to be much smaller in magnitude than the center-of-gravity effect of IOR. Finally, the extension of the center-of-gravity effect of IOR from manual to eye movement responses is consistent with the proposal that the center-of-gravity effect depends on “population coding in neural systems mediating overt or covert orienting” (Klein et al., 2005, p. 299). We suspect that the global effect that we have found in the generation of IOR may be similar in cause to the center-of-gravity effect when the target is composed of multiple items and saccade averaging is the result. Both effects might be rooted in the machinery responsible for oculomotor behavior—certainly the superior colliculus—and probably in some of the cortical networks that project to it.

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