Saccadic distractor effects: The remote distractor effect (RDE) and saccadic inhibition (SI): A response to McIntosh and Buonocore (2014)

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We (Walker & Benson, 2013) reported studies in which the spatial effects of distractors on the remote distractor effect (RDE) and saccadic inhibition (SI) were examined. Distractors remote from the target increased mean latency and the skew of the distractor-related distributions, without the presence of dips that are regarded as the hallmark of SI. We further showed that early onset distractors had similar effects although these would not be consistent with existing estimates of the duration of SI (of around 60–70 ms). McIntosh and Buonocore (2014) report a simulation showing that skewed latency distributions can arise from the putative SI mechanism and they also highlighted a number of methodological considerations regarding the RDE and SI as measures of saccadic distractor effects (SDEs). Here we evaluate these claims and note that the measures of SI obtained by subtracting latency distributions (specifically the decrease in saccade frequency—or dip duration) are no more diagnostic of a single inhibitory process, or more sensitive indicators of it, than is median latency. Furthermore the evidence of inhibitory influences of small distractors presented close to the target is incompatible with the explanations of both the RDE and SI. We conclude that saccadic distractor effects may be a more inclusive term to encompass the different characteristics of behavioral effects of underlying saccade target selection.

Introduction

We would like to take this opportunity to respond to the issues raised by McIntosh and Buonocore (2014) in relation to our recent paper (Walker & Benson, 2013) on the remote distractor effect (RDE) and saccadic inhibition (SI), and in doing so we hope to reconcile researchers investigating saccade distractor effects (SDEs). McIntosh and Buonocore (2014) have usefully reported a simulation showing how an inhibitory mechanism, consistent with the time course of saccadic inhibition (SI), can produce skewed latency distributions without producing visible dips (that are typically regarded as the hallmark signature of SI). We consider that they have however misrepresented our position and in their critique they have conflated the remote distractor effect (RDE) with measures of saccadic reaction time (SRT) and SI with the distributional analysis approach, and in criticizing measures of SRT they attempt to undermine previous studies of the RDE. The claims made regarding ipsilateral distractor effects has further led them to conclude that the term remote distractor effect is no longer appropriate, but this fails to acknowledge the spatial limits of the RDE and is incompatible with the underlying neurophysiological explanations of both the RDE and SI. A potential source of misunderstanding is that the term SI, as originally conceived, refers to an observable behavioral phenomenon (a decrease in saccade frequency), but the term is increasingly used to imply a specific underlying mechanism and this apparent duality can be confusing. Here we further examine some of these issues and propose that saccadic distractor effects (SDEs) can be studied using either approach and encourage oculomotor researchers to apply a range of methodologies to elucidate the underlying mechanisms behind these behavioral effects.

Brief overview of Walker and Benson (2013)

In our study we set out to examine both the RDE (increase in SRT) and measures of SI (decrease in...
saccade frequency—Dip_{max} and time course of inhibition) observed under conditions in which the spatial location of the distractor was manipulated. The first experiment manipulated the eccentricity of distractor onsets presented simultaneously with the target—the rationale being that if the modulation of SRT reflects SI (an inhibitory mechanism starting 60–70 ms after distractor onset, peaking at around 90 ms, with a duration of ~60 ms, c.f. Buonocore & McIntosh, 2012, 2013) then this effect should be revealed by an analysis of latency distributions. The distractor-related latency distributions did not reveal the presence of a visible dip (no evidence of bimodality) usually regarded as the hallmark signature of SI (McIntosh & Buonocore, 2014), but instead showed a pronounced increase in skew. The average SRT and decrease in saccade frequency (ΔDip_{max}) increased as distractors approached fixation, as would be expected. We noted that the measures obtained by subtracting across latency bins do not provide conclusive evidence of SI: “Thus, the increase in skew observed with simultaneous onsets may reflect SI (a short-lasting effect) or could potentially be attributed to more than one inhibitory process” (Walker & Benson, 2013, p. 6). The simulation reported by McIntosh and Buonocore (2014) is informative in showing that this mechanism can increase the skew of a distribution, without evidence of a visible dip but further modeling is required to show whether other mechanisms can have similar effects and if these can account for the effects of early distractor onsets.

In the second experiment distractors appeared 60 ms before, simultaneously with, or 60 ms after the target. The +60-ms delay condition was considered ideal for maximizing the visible SI using the approximation used in other studies, (baseline mean = 148 ms – 90 ms = ~60 ms: c.f. Buonocore & McIntosh, 2008, 2012). Importantly for McIntosh and Buonocore’s (2014) proposal that the term remote distractor effect may no longer be appropriate, the effects of small ipsilateral distractors (presented inside and outside the critical 20° RDE spatial window) were examined (see later section: Ipsilateral distractor effects and the spatial limits of the RDE). Early onset ipsilateral distractors close to the target axis facilitated latency (see also Edelman & Xu, 2009), while remote ipsilateral and contralateral distractors (on axis 45° from target) increased the skew of the latency distributions as reflected by the increase in SRT and Dip_{max}. The observed RDE with early onset remote distractors is interesting and may require additional assumptions regarding the SI mechanism as noted by McIntosh and Buonocore (2014). A third study investigated the effects of contralateral distractors presented at three delays after target onset based on the method as used by Edelman and Xu (2009), so the average of the delays was around 90 ms after target onset. The largest effect on SRT and the Dip_{max} measure of SI occurred at the shorter 30-ms delay period with distractors at fixation, whilst the effects of those at 2° and 4° decreased. The influence of distractor eccentricity on SRT and Dip_{max} was much less pronounced with the longer 60 and 90-ms distractor delays. We discuss the possibility that distractors at fixation may exert a greater inhibitory effect when presented after a short delay by reactivating neurons that had been active during fixation of the central cross prior to target onset.

The main conclusions were that the increase in SRT and generalized increase in skew for the distractor-related distribution may be attributed to the time course of an SI mechanism, but may also involve other, possibly longer lasting inhibitory, influences. Thus, the Dip_{max} measures of SI, obtained by the bin-by-bin subtraction of distributions, is as susceptible to a potentially broad range of inhibitory and facilitatory influences that change the overall shape of latency distributions, as is SRT. It is worth stressing that the original conception of SI (Reingold & Stampe, 2000; 2002) emphasized the time at which inhibition started to influence the latency distribution (around 60–70 ms later) with the maximum inhibition peaking at around 90 ms. The 60–70-ms estimate for the start of inhibition has proved to be highly reliable across observers and studies. This timing is entirely consistent with estimated neural transmission rates for visual stimuli to activate neurons in the superior colliculus, where inhibitory interaction effects between target and distractor are thought to occur. This is entirely plausible and will apply to all visual distractors with some variation arising due to stimulus salience. What is less clear is whether saccadic distractor effects (SDEs) reflect a transitory automatic inhibitory effect alone, or if these inhibitory processes may be longer lasting than this and could involve both automatic and sustained influences. Studies of SI have not, to date, examined the effects of early onsets (due to the focus on eliciting visible dips in the distribution) and so the estimated duration of SI may actually be longer than has previously been thought, as our results would suggest. A further consideration is that the inhibitory influence of a distractor may not be constant across SOA as the inhibitory effect may decrease over time as the target-related activity has become more established. It has been shown, for example, that the SI effects are greater with less potent saccade-goals (as in the memory-guided situation Edelman & Xu, 2009) and distractors may be less effective when presented after longer delay periods when the target-related activity has had time to develop.

**Methodological considerations**

McIntosh and Buonocore (2014) describe a number of methodological factors that could improve the
stability of the time course of the resulting SI measures such as the timing of the distractor onset to reflect the participants’ baseline median SRT. We note, however, that in our experiment 3 the SOA used was estimated from the average median SRT of the participants in control conditions, using the procedure from other studies of SI (Buonocore & McIntosh, 2008, 2012; Edelman & Xu, 2009) and the +60 ms delay used in our experiment 2 was ideal for revealing SI as a dip in the latency distribution. One implication of the reported simulation of SI is that measures of SI can be obtained across any SOA—irrespective of the presence of the SI signature dip. If this is the case then there is no need to optimize the distractor delay in order to maximize the visible effects on the distractor-related distribution and SI can be examined with early onset distractors as can the RDE.

McIntosh and Buonocore (2014) also place emphasis on scaling the change in saccade frequency measure of SI (that reflects distractor potency) so it takes into account the underlying baseline frequency. Although the resulting ratio measure can improve the stability of the proportional change measure, it has been reported that these measures are actually comparable (Buonocore & McIntosh, 2012). The similarity of these two measures can be confirmed by a direct comparison of the change in frequency (Dip_max = distractor distribution − baseline) and the ratio (Dip_max/R = (distractor distribution − baseline)/baseline) using data from our experiment 2 as shown in Figure 1 below (note scales on y axis). Figure 1 shows a consistent pattern of change in saccade frequency for both of these measures across distractor conditions and SOA. A smaller reduction is apparent for ipsilateral distractors close to the target (0° axis) and a larger effect for remote ipsilateral and contralateral distractors. The ratio measure consistently mirrors the percentage frequency change measure with the exception of contralateral distractors in the delayed onset (+60 ms SOA) condition. We agree that the ratio is most likely to be a more stable measure, but the differences between these measures is often small and using it would not have changed the conclusions we made.

Is SI a more sensitive measure of saccadic distractor effects (SDEs)?

McIntosh and Buonocore (2014) further suggest that SI may be more sensitive to oculomotor inhibition than median latency, although they do not provide evidence to support this claim. It is the case that the distributional analysis provides more information than does the RDE but that does not make SI a more sensitive measure. Both the increase in median SRT and the maximum decrease in saccade frequency (Dip_max) can be taken as measures of distractor strength and both measures will be susceptible to changes in the shape of the distractor-related distributions and are highly correlated, e.g., the correlation between median SRT and Dip_max from our experiment 1 is: r(50) = −0.631, p < 0.001, see Figure 2. We examined the suggestion that the decrease in saccade frequency (Dip_max) is a more sensitive measure of distractor inhibition than central tendency using the data from our experiment 1. A two-factor analysis of variance (ANOVA), Target Eccentricity (2) × Distractor Eccentricity (5), was performed on mean and

Figure 1. (a)–(c). Comparison of the change in the percentage of saccades (Dip_max = distractor − baseline) and ratio (Dip_max/R = distractor − baseline/baseline) measures of SI using data from Walker and Benson experiment 2 for: (a) −60 ms SOA, (b) 0 ms SOA, (c) +60 ms SOA. It can be seen that the two measures of SI are broadly comparable across distractor spatial location and SOA. The one case where the ratio measure departs from the percentage change is for the delayed onset (+60 ms) condition and it remains to be seen if this difference between the measures is a robust finding.
Ipsilateral distractor effects and the spatial limits of the RDE

A puzzling claim made by McIntosh and Buonocore (2014) is that the term remote distractor effect may no longer be a useful concept. This, they argue, is because ipsilateral distractors (at the target location) can produce inhibitory effects “and we have recently shown that these inhibitory effects can be even stronger than those of remote distractors (Buonocore & McIntosh, 2012).” In their discussion of ipsilateral distractor effects McIntosh and Buonocore do not make clear the important distinction between remote, and near, ipsilateral distractors, which is conflated in their study by the use of large rectangular distractors presented at the target location. Buonocore and McIntosh (2012) examined the influence of contralateral and ipsilateral distractors, presented at the same eccentricity (5°) as the saccade target. The rectangular distractors varied in size from 1°–16° vertically and appeared after long (fixed) SOAs of either 120–130 ms after the target. With this configuration distractors greater than 3.5° vertically would fall both inside and outside the 20° spatial window of the RDE (Walker, Deubel, Schneider, & Findlay, 1997). Thus, distractor size and spatial relationship to the saccade target were conflated, and this could account for the nonlinear relationship they report. In their experiment 2 a weak SI inhibitory effect was observed with ipsilateral distractors that increased with distractor size (consistent with the spatial modulation of the RDE). The finding of a stronger ipsilateral distractor effect was observed only with the larger distractors as they note: “Ipsilateral events are more distracting than contralateral events, at least at larger distractor sizes > 4°” (Buonocore & McIntosh, 2012). Critically for McIntosh and Buonocore’s argument a small SI effect (a decrease in saccade frequency) was observed with small 2° distractors, and the effect was similar in magnitude to that produced by contralateral distractors at the same eccentricity (see Buonocore & McIntosh, 2012, figures 2C and 3C). The finding that a distractor, appearing at the target location, can induce SI contrasts with the findings of Edelman and Xu (2009) who presented small ipsilateral distractors on an axis 22° from the horizontal (thus outside RDE window) or at the location of the saccade goal (inside RDE window) in a memory-guided paradigm. Only distractors at 22° from the target axis produced an SI effect, while those presented at the saccade goal did not (an increase in the frequency of short latency express saccades was observed). Similarly Bompas and Sumner (2011) reported no evidence of SI with small ipsilateral distractors at the target location (“we found virtually no effect of late distractors appearing at the location of the target,” p. 12509). Furthermore, the presence of SI with a distractor at the target location is incompatible with the neurophysiological explanations of both SI and the RDE (Bompas & Sumner, 2011; Buonocore & McIntosh, 2008, 2012; Casteau & Vitu, 2012; Edelman & Xu, 2009; Reingold & Stampe, 2002; Walker et al., 1997; Walker, Kentridge, & Findlay, 1995). To summarize, studies using small ipsilateral distractors presented within the RDE spatial window have not revealed evidence of inhibition on measures of SI (Bompas & Sumner, 2011; Edelman & Xu, 2009) or

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<td>14.9**</td>
<td>6.94**</td>
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<td>Tar × Dist (4,16) =</td>
<td>0.78</td>
<td>0.81</td>
<td>1.82</td>
<td>0.69</td>
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Table 1. F-statistics from a two-factor ANOVA (T-Target (2), D-distractor (5)) evaluating median SRT, mean SRT, Dipmax, and Dipmax/Ratio measures using data from five participants from Walker and Benson’s (2013) Experiment 1. * sig. $p < 0.05$, ** sig. $p < 0.001$. “
SRT. The stronger SI effect observed by Buonocore and McIntosh (2012) was for the larger ipsilateral distractors and this is not evidence against the remote distractor effect. Although McIntosh and Buonocore (2014) state they prefer simple explanations to account for SDEs their own account has included additional endogenous attention components, for example: “Ipsilateral events are more distracting than contralateral events, at least at larger distractor sizes (>4). A plausible account of this size difference would be that endogenous attention allows strong top-down inhibition of the distractor-related activation, provided that the distractor is spatially removed from the target” (Buonocore & McIntosh, 2012, p. 38). The inclusion of an “endogenous attention” mechanism in addition to SI (which is regarded as an automatic inhibitory effect) raises additional questions about the interpretation of behavioral effects.

Implications and conclusions for studies of saccadic distractor effects (SDEs)

Studies of SDEs typically examine the effects of a specific distractor manipulation (such as salience, size, spatial location, etc.) on SRT or the measures of SI. McIntosh and Buonocore’s (2014) simulation of median SRT and the change in saccade frequency (Dipmax) as shown in their figures 1abc shows that the inhibitory influence of the distractor was constant (as it was modeled to be) across all SOAs, the implication being that the SI profile (and Dipmax) does not have to be studied using behavioral paradigms with long distractor delays optimized in order to observe a visible dip. Delaying distractor onset may be required to observe the maximum dip, but the change in saccade frequency measure (Dipmax) may actually be invariant of SOA. It is likely that the SI measures will be less stable (more susceptible to noise) when the distractor is timed to influence only a small proportion of saccades (as with long SOAs). There is no compelling reason to accept the assumption that the SI measures may provide a more sensitive measure of distractor effects when comparing the effects of a specific distractor manipulation (such as luminance, size, spatial location, etc.) or that these are more robust than the modulation of SRT, as long as the experimental conditions are optimized for the measure being used. What the analysis of distributions can reveal, that is not obtained from SRT, is of course information about the time-course of the distractor effect.

In our analysis we emphasized the presence/absence of visible notched dips as the signature of SI. This is not surprising given that the majority of published studies of SI use visualization of dips in distributions as evidence for the presence of this effect and they also ensure that the timing of the distractor onset is idealized to maximize these dips. The simulation described by McIntosh and Buonocore (2014) shows that the SI mechanism can produce an increase in the skew of the simulated distributions without evidence of a dip across any distractor delay. This is a useful demonstration and from this it may be inferred that the change in distractor distributions can reflect the proposed SI mechanism but further modeling along these lines would be informative to show whether other potential mechanisms would produce similar effects.

One implication of the simulation is that there is no need to visualize the SI signature dip as evidence of SI. However, in terms of the change in saccade frequency measures, obtained from subtracting across latency bins, these will be influenced by whatever mechanism is responsible for the change in shape of the distractor-related distribution, as is a median or mean. Future research should focus on using the measure, or measures, that are most suitable for the research question under investigation.

McIntosh and Buonocore (2014) suggest that distributional analyses have the capability to reveal temporal differences that would be incompatible with SI, such as a monotonic shift in the whole distribution. In a previous study (Benson, 2008) that compared the RDE for bilateral versus unilateral target and distractor presentation, a shift in the whole distribution was observed such that the RDE effect of an increase in latency for distractor related trials compared to single target trials occurred across the whole duration of the distribution. The effect of predictable (location-based) targets resulted in a faster distribution overall compared to a latency distribution for unpredictable (location-based) targets for single-target trials and for distractor trials. Central distractors at fixation had a greater effect than peripheral distractors across the whole latency distribution for a predictable target location condition, while peripheral distractors had a greater effect with unpredictable target locations. A detailed analysis using a vincintizing procedure examined the effects of distractors across the whole distribution and revealed a consistent pattern across each latency bin for all distractor types (see figure 1b, Benson, 2008). The consistent shift observed across all latency bins (from 200–300 ms) is potentially incompatible with a short-lasting inhibitory mechanism.

To conclude, we include a comment from an anonymous reviewer who noted that: “Studies of human behavior should focus on elucidating basic mechanisms, not on ‘studying psychophysical tasks.’” We agree that the debate regarding SI and the RDE is unhelpful and that more theoretically interesting
questions regarding saccadic distractor effects remain to be resolved. We would not want to appear evangelical over the use of SRT as the preferred measure of saccadic distractor effects and agree that the SI measures can provide additional useful information about the time course of oculomotor inhibition depending on the question being asked. Both the RDE and SI are behavioral measures and both terms lack formal definition and their neurophysiological underpinnings remain to be revealed. Neither the median SRT nor SI should be regarded as being sensitive to only one potential source of inhibition. We welcome further work, including modeling, that takes into account what is already known about saccadic distractor effects in order to develop our understanding of the underlying processes involved in saccade target selection.

Keywords: remote distractor effect, saccadic inhibition, superior colliculus, lateral interaction effects, oculomotor inhibition, saccade target selection

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Footnotes

1 Note we reported the change in percentage of saccades measure as used by Buonocore and McIntosh (2008, 2012) rather than the ratio measure advocated by McIntosh and Buonocore (2014) as these two analysis methods are actually highly consistent (Buonocore & McIntosh, 2012).

2 Reingold and Stampe (2002) note that neural transmission rates for visual stimuli to activate buildup neurons in the intermediate layers of the SC are around 60–70 ms. Although this is suggestive of a role of the SC in distractor-related inhibition, the transmission rates of visual signals reaching other potential oculomotor structures—such as the frontal eye fields and lateral intraparietal sulcus (LIP) are not dissimilar (FEF 45–130 ms, LIP 70–200 ms, see Figure 1—O’Shea, Muggleton, Cowey, & Walsh, 2006). In this regard we have shown that patients with parietal damage and unilateral neglect, without visual field defects, do not show the normal RDE (Benson, Ietswaart, & Milner, 2012; Walker & Findlay, 1996).

References


