

Temporal dynamics of saccadic distraction

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The saccadic distractor effect, in which irrelevant stimuli delay saccades to target stimuli, is a popular tool for investigating saccadic competition. Here, we outline the main components of a competition framework to account for the temporal dynamics of the distractor effect, inspired by race models of saccade generation. We first test a key prediction of this framework: the degree of interference should depend upon the degree of temporal overlap of target and distractor signals in the competition stage, which will vary systematically with the relative processing speeds of the competing visual signals. In agreement with this, we found that, when varying the contrast of distractor stimuli, the presentation delay between target and distractor that maximizes interference varies systematically for different target–distractor pairs, correlated with the difference in saccadic latency for the pair. Second, our data illustrate a crucial methodological point: when comparing the effect of different distractors, measuring at only one time-point (e.g. simultaneity, as most studies have done) can produce misleading and contradictory results. Thus, it is essential to take the temporal dynamics of the system into account. Lastly, the framework predicts that the optimal delay for the latency distractor effect is different from that maximizing error rate, and our data confirms this.

Keywords: eye movements, contrast, remote distractor effect, motor planning, competition, race model

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Introduction

Exploration of the visual world involves frequent eye movements (saccades), alternating with brief periods of fixation. Before each saccade, the saccadic system has to resolve two questions: where to look next and when to go. The solution to these questions is thought to involve a competition between fixating and moving, and between all the potential saccade targets. This competition is influenced both by high level goals on the one hand and by automatic stimulus-driven mechanisms on the other. Quantitative models have been quite successful in predicting the latency distributions of saccades to single target onsets (e.g. Carpenter, 1981) and how saccade latency is affected by both low level features, such as contrast or rate of provision of information (Carpenter, 2004; Reddi, Asress, & Carpenter, 2003), and high level influence such as probability (expectancy) and urgency (Carpenter & Williams, 1995; Reddi & Carpenter, 2000). In everyday life, of course, multiple stimuli are the rule, with some stimuli being more relevant for saccades than others. These models can make predictions about choice in multiple target situations, with different motor plans racing to reach threshold and trigger a saccade (Leach & Carpenter, 2001; see also Theeuwes, Kramer, Hahn, & Irwin, 1998), and have been used to explain how stimulus-driven and goal directed signals compete with each other (Godijn & Theeuwes, 2002; Kopecz, 1995; Trappenberg, Dorris, Munoz, & Klein, 2001). However, an important

factor that has been largely neglected in the study of saccade planning and competition is that different kinds of visual stimuli have different processing speeds (see below). Therefore, we aim here to extend these kinds of model into a framework for how different stimuli compete and interfere with each other. Our purpose here is to provide a conceptual framework that makes new predictions, rather than a fully specified quantitative model.

The distractor effect

One well established phenomenon illustrating saccadic competition is the remote distractor effect (RDE), in which saccades to simple visual targets are delayed when an irrelevant stimulus appears elsewhere in the visual field (e.g. Born & Kerzel, 2008; Griffiths, Whittle, & Buckley, 2006; Honda, 2005; Lévy-Schoen, 1969; Ludwig, Gilchrist, & McSorley, 2005; Walker, Deubel, Schneider, & Findlay, 1997; Walker, Kentridge, & Findlay, 1995; White, Gegenfurtner, & Kerzel, 2005). This latency effect is usually accompanied by some directional errors, when the irrelevant stimulus triggers a saccade. The RDE is thought to be essentially automatic since it occurs even when the direction of the saccade target is known in advance and distractors, appearing always in the opposite hemifield, are voluntarily ignored (Benson, 2008; Walker et al., 1995; Walker, Mannan, Maurer, Pambakian, & Kennard, 2000). The RDE has been hypothesized to involve long-range lateral inhibition between cell populations coding for the

saccades to target and distractor, either at the level of the superior colliculus (Olivier, Dorris, & Munoz, 1999) or within the cortical eye fields (see discussion in Dorris, Olivier, & Munoz, 2007). Competition between ‘fixate’ and ‘move’ sub-systems in the superior colliculus has also been suggested as a source (Findlay & Walker, 1999; Walker et al., 1997).

Importantly, in all cases, the presence of a visual distractor is thought to automatically produce a signal in some visual, decision or execution map, which reduces the activity related to making the saccade to the target. Most current models of saccade generation envisage an accumulation of motor-decision activity in some sensorimotor area, until some threshold is reached and a saccade can be triggered (e.g. Carpenter, 1981; Carpenter & Williams, 1995; Godijn & Theeuwes, 2002; Kopecz, 1995; Trappenberg et al., 2001) (see Figure 1). When more than one potential target is present at a time, it has been proposed that the corresponding decision signals compete in a race to threshold while mutually inhibiting each other, which causes their accumulation rates to decrease, resulting in longer latencies (Godijn & Theeuwes, 2002; Kopecz, 1995; Leach & Carpenter, 2001; Trappenberg et al., 2001). This idea of mutual inhibition in the context of a competitive race has become widely accepted, but, as we shall see below, this framework actually makes predictions that run counter to beliefs that also appear to have become accepted in the field.

Main components of the competition framework

To account for the basic RDE phenomenon and associated directional errors in a race framework, three main ingredients are needed (Godijn & Theeuwes, 2002; Trappenberg et al., 2001). First, distractor-related activity must enter the motor competition, even though the distractor is known to be irrelevant for the task (i.e. there is some degree of automatic activation of potential motor plans even by irrelevant stimuli). Second, distractor-related activity has to be able to inhibit target-related activity, in order to delay its reaching the saccade initiation threshold. As said above, this can be achieved by assuming that signals inhibit each other when they overlap in the sensorimotor area(s) where saccadic motor competition is played out (note that early visual transients may also be subject to mutual inhibition, but for simplicity most models do not consider this separately from motor competition). Third, there must be some component of goal-directed inhibition or filtering of the sensorimotor signal, or an extra “endogenous signal,” otherwise the distractor could often inhibit the target to the point of winning the race, which would result in many more errors than are typically measured. Note that a baseline shift for neurons favoring one location (e.g. Carpenter & Williams, 1995) will not suffice when targets are defined by their

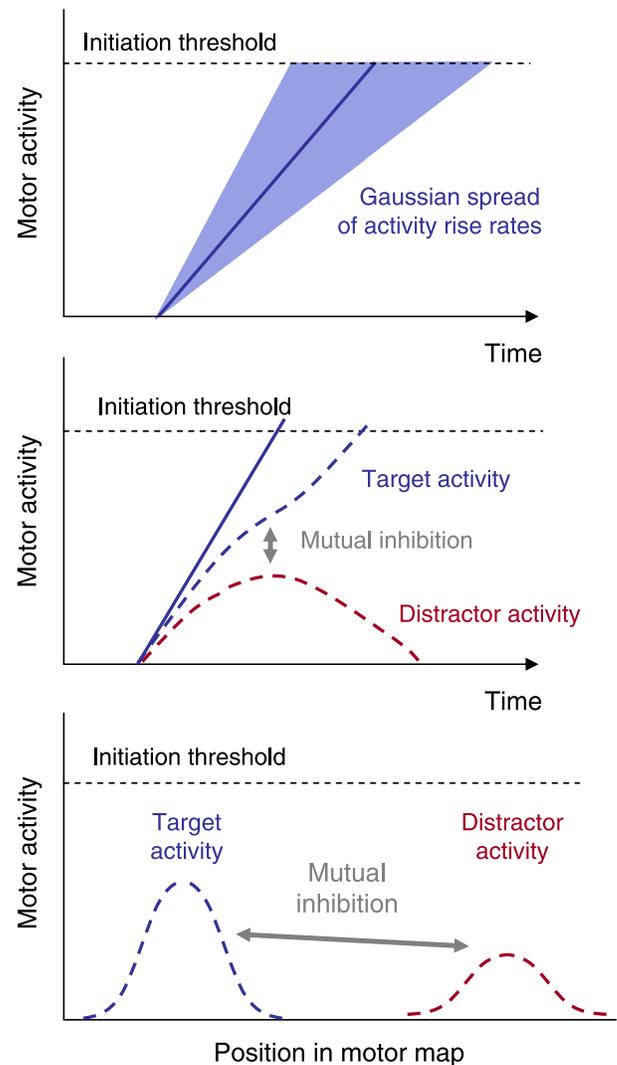


Figure 1. Main components of our saccadic competition framework for the distractor effect inspired by current models of saccade generation. Top: According to the popular models (e.g. Carpenter, 1981; Godijn & Theeuwes, 2002; Kopecz, 1995; Trappenberg et al., 2001), saccade latency to a visual target is determined by a rise to threshold of accumulating motor-related activity in some sensorimotor decision area. If the rise rate has a Gaussian distribution, this can account for the basic shape of the saccadic latency distribution (e.g. Carpenter, 1981). Middle and lower panels: Signals corresponding to different potential saccade endpoints, for instance a target and a distractor (blue and red dashed lines), compete in a race while mutually inhibiting each other (Godijn & Theeuwes, 2002; Trappenberg et al., 2001). The solid blue line represents target activity without a distractor present. By delaying the time when the target activity can reach the threshold, the presence of a distractor delays the saccade to the target. Note that although the original model assumes linear rates for single stimuli (but see Brown & Heathcote, 2005), in the competition framework non-linear rises will occur due to the dynamically changing degree of mutual inhibition.

visual features rather than by their location, as is the case in our study for example. Thus there must be a feature-based influence that affects the accumulation of motor activity.

Temporal dynamics of the distractor effect

Distractor-related motor activity is expected to be transient, either because it does not receive goal directed support (e.g. Trappenberg et al., 2001), or because goal-directed inhibition acts to send non-relevant activity back to baseline (e.g. Godijn & Theeuwes, 2002). Thus its ability to interfere with saccade planning will be limited to a certain time-window. Therefore, the main prediction of this framework is that the crucial factor for interference is the temporal window during which signals from target and distractors can overlap in the critical region(s) of the brain where competition occurs. Thus, the amplitude of the RDE is expected to be reduced for distractors presented either too early, at a time when the target signal has not yet arrived, or too late, when target activity is already reaching the initiation threshold.

This prediction is consistent with the results from studies that have varied the time delay between distractor and target presentation. In particular, Walker et al. (1995) instructed their participants to make a saccade always to a right target, in the presence or absence of the same stimulus on the left side. They obtained a bell-shape pattern for RDE amplitude against SOA (stimulus onset asynchrony), such that distractors produced significant latency increases at delays ranging from 20 ms before target to 80 ms after target and little effect before or after this interval. Their main conclusion was that optimal interference was obtained with simultaneous presentation of targets and distractors. Trappenberg et al. (2001) provided modeling results that also showed peak effect at simultaneous presentation (their Figure 3B). Accordingly, it appears to have become accepted across the literature that simultaneous presentation maximizes the RDE, and this condition has been the default choice in almost all subsequent investigations of the RDE. However, some studies have obtained maximal interference with various delays up to 100 ms after the target (Reingold & Stampe, 2002; Ross & Ross, 1980; White et al., 2005).

These variations across studies are not surprising to our view since the critical parameter is not the *presentation* delay between target and distractor but the *overlap window in the motor competition*. The arrival time of signals at the motor competition will depend not only on stimulus presentation time, but also on visual factors such as eccentricity, contrast, color and on top-down factors such as spatial or feature-based attentional biases or inhibitory strategy. Thus there is no reason to expect different experimental designs to reveal the same optimal stimulus timing.

This being said, the delay maximizing the RDE should not be arbitrary. We propose that this optimal SOA should correspond systematically with the difference in processing speed for target and distractor sensory signals. Although there is no way to access directly such difference in neuronal transmission times with behavioral measures, we propose that there is a straightforward way to predict how the optimal SOA should vary when varying target and distractor stimuli. We make the assumption that arrival times of signals into the competition process are correlated with the latencies of saccades to those corresponding visual stimuli (Bell, Meredith, Van Opstal, & Munoz, 2006). Consequently, the latency difference between two stimuli when these are used as saccade targets should be correlated with the delay maximizing the RDE when one is used as a distractor and the other one as target.

An illustrative default prediction would be that, for example, if mean latency to stimulus A is 40 ms longer than to stimulus B, then in order to maximize interference, stimulus A should be given a 40 ms head-start when used as a distractor and B is the target. Thus for any two stimuli, this default hypothesis would predict a perfect correlation between their latency difference and their SOA of maximum RDE, with a slope of 1 and an offset of zero (i.e. an equality). Actually, such equality would only happen if saccade latencies depended exclusively on arrival times of signals in the competition and we know that this is not the case. Saccade latencies depend on many other factors, including top-down influences such as attention, strategy and expectation, and these will differ between observers and between different experimental conditions. These factors may also influence the SOA of maximum RDE by modulating both sensory processing speed and the competition process. Nevertheless, as long as top-down factors do not destroy all influence of sensory arrival time, it is a fundamental prediction of the competition framework that there should be a correlation between the latency difference and the optimal SOA.

Effect of stimulus properties and the methodology of comparing RDE amplitudes

All distractors do not appear to be equally efficient in delaying saccades to a target. For instance, it is expected that a distractor with a high contrast should interfere more strongly than a low-contrast distractor. However, Born and Kerzel (2008) recently found that manipulating luminance contrast of the distractor produced surprisingly small variations in the amplitude of the RDE.

A related prediction is that the efficiency of a visual distractor will depend on the sensitivity of the saccadic system for the particular features possessed by the distractor. Accordingly, several studies have used the RDE as a probe to test the sensitivity of the saccadic

system to particular features. For instance, larger RDEs have been observed for low versus high spatial frequencies distractors (Ludwig, Gilchrist, & McSorley, 2005), for large versus small distractors (White et al., 2005), and for luminance versus colored distractors (Irwin, Colcombe, Kramer, & Hahn, 2000; Sumner, Adamjee, & Mollon, 2002; but see Bompas & Sumner, *in press*), leading to specific conclusions about the relevance for the saccadic system of these features.

Other studies have tested the importance of feature overlap between distractor and target. For instance, Born and Kerzel (2008) manipulated both target and distractor contrast to investigate whether higher interference would arise from distractors that were similar to targets. Their results show no evidence in favor of this hypothesis. On the other hand, Ludwig, Gilchrist, and McSorley (2005) varied the spatial frequency of distractors and targets and reported that while low and medium frequency distractors produced robust effects on all targets, high frequency distractors affected only high frequency targets.

However, the problem with comparing RDE amplitude between different stimuli is that changing the size, contrast, spatial frequency or color of the stimuli will modify the speed of the corresponding signals in the visual pathways, and therefore the temporal overlap window of signals in the crucial area where competition occurs. This point has sometimes been acknowledged by the authors themselves; for example, Born and Kerzel (2008) note in their study that high contrast targets elicit faster saccades than low contrast. Saccade latency has also been shown to increase with spatial frequency (Ludwig, Gilchrist, & McSorley, 2004, 2005), to be affected by size (Perron & Hallet, 1995; Ploner, Ostendorf, & Dick, 2004) and to be prolonged for color stimuli compared to luminance (see Bompas & Sumner, 2008, for a review).

Thus changing the visual properties of distractors and targets can have similar consequences to introducing a delay between them, which, as discussed above will also influence the RDE. Comparisons of distractor types are therefore confounded with changes in temporal dynamics. We suggest that this problem must be solved by measuring the amplitude of the RDE at its optimal delay, rather than at some fixed delay, such as simultaneity. The second aim of our study was to test whether such a method offers a material improvement over the previous studies that have simply employed simultaneous presentation—whether a different pattern of results might have been found if the SOA were manipulated.

Temporal dynamics of directional errors

Although latency effects and directional errors (“oculo-motor captures”) are both markers of saccadic competition, it is not simply the case that the conditions that maximize one will maximize the other. The framework outlined above predicts that errors and latency effects

should differ in their temporal dynamics. If we envisage that errors reflect the cases when the distractor signal actually reaches motor threshold and elicits a saccade (e.g. Godijn & Pratt, 2002), then there is a crucial difference between errors and latency effects: the latter require interference between two signals while errors do not. Thus while the latency effect will be maximal when the two signals maximally overlap in the competition process and thus maximally interfere with each other, error rates will be maximal simply when the distractor signal has the best chance of reaching motor threshold. This will occur when it *minimally* overlaps with the target signal, so that it receives little inhibition from the target-related activity.

Study outline: Distractor contrast and timing

We manipulated the processing speed of the distractors by varying their contrasts. Each distractor contrast was presented with 9 different delays relative to target onset, ranging from 80 ms before to 80 ms after the target, in order to evaluate for each contrast the delay maximizing the amplitude of the RDE. A preliminary block assessed saccade latencies to each contrast, and in the main experiment the target contrast was held constant. Thus we could evaluate the correlation between the optimal delay for each distractor in the main experiment and the latency differences between the target and that distractor. Note that although there may be many factors that affect the absolute saccade latencies measured for the targets and the distractors, and these may differ between participants and between blocks, as long as within a block the relative differences in latencies for the distractors are stimulus-driven, there should remain a correlation between latency and optimal distractor delay.

By manipulating both the temporal delay and one feature of interest (the contrast), our study also illustrates a decisive method for determining the effect of this feature that avoids the timing confound. This additionally enabled us to assess what the consequences would have been of only taking a snapshot of the effect of contrast at one SOA.

Last, the framework predicts that distractors should be presented earlier in order to elicit maximum errors. We analyzed the temporal dynamics of directional errors to verify this prediction.

Methods

Participants

Three observers participated in this experiment, two females and one male. Two were naïve to the purpose of the experiment. All were students at the Cardiff School of

Psychology, had normal vision and received payment for their time.

Material

Stimuli were displayed on a Sony Trinitron 19 inch GDM-F400T9 monitor, driven by a Cambridge Research Systems (CRS) ViSaGe graphics board at 100 Hz, calibrated with a CRS ColorCal and associated software. Stimuli were presented binocularly with 72 cm viewing distance. Eye movements were recorded using the CRS high speed video eye-tracker sampling at 250 Hz. The subject's head was stabilized by a chin rest and a headrest.

Stimuli

The target stimulus was a small black square (10 cd/m^2 , occupying 0.25 deg^2), presented at 8 deg eccentricity either on the left or on the right of fixation, on a gray background (MacLeod-Boynton coordinates, MLB, 0.643, 0.021) with 25 cd/m^2 luminance. Distractor stimuli consisted of larger gray squares (1 deg^2) also centered at 8 deg eccentricity. Luminance levels of distractor stimuli were chosen so that the luminance difference from the background started at 2 cd/m^2 (L_1) and increased according to $L_n = 1.5 * L_{n-1}$, resulting in logarithmically equidistant contrast levels ($C_{1..7} = (L_{1..7} - L_{\text{Background}}) / L_{\text{Background}} = 8, 12, 18, 27, 40.5, 61$ and 91%). The fixation point was a small light gray square (32 cd/m^2 occupying 0.1 deg^2).

Procedure

Main experiment

Each trial started with the reappearance of the central fixation point. After a fixed 700 ms delay, the target appeared randomly on the left or right of fixation, for 300 ms. The fixation point disappeared together with the target offset and reappeared some 500 ms later at the start of the next trial. Participants were instructed move their eyes as fast as they could to the target, ignoring any other stimuli.

On some trials, the target appeared alone while on others a distractor appeared opposite to the target (Figure 2). The proportion of no-distractor trials was 10%. Distractors were presented for 50 ms with 9 different stimulus onset asynchronies (SOA), ranging from 80 ms before to 80 ms after the target by steps of 20 ms. These distractor-present conditions were mixed with no-distractor trials, resulting in 64 conditions ($9 * 7 + 1$) for each target direction, 128 conditions in total. Each distractor-present condition was repeated 45 times (315 times for the no-distractor baseline) for each target direction, resulting in 90 saccades per condition after averaging directions. A total of 6300 saccades per observer were collected for the main experiment, split into 15 blocks of 15 minutes each.

Measuring saccade latency to the distractors

We also determined the saccadic latency to the stimuli used as distractors in the main experiment. Each trial consisted of the presentation of one of the 7 contrast levels on the left or right of fixation and for the same duration as

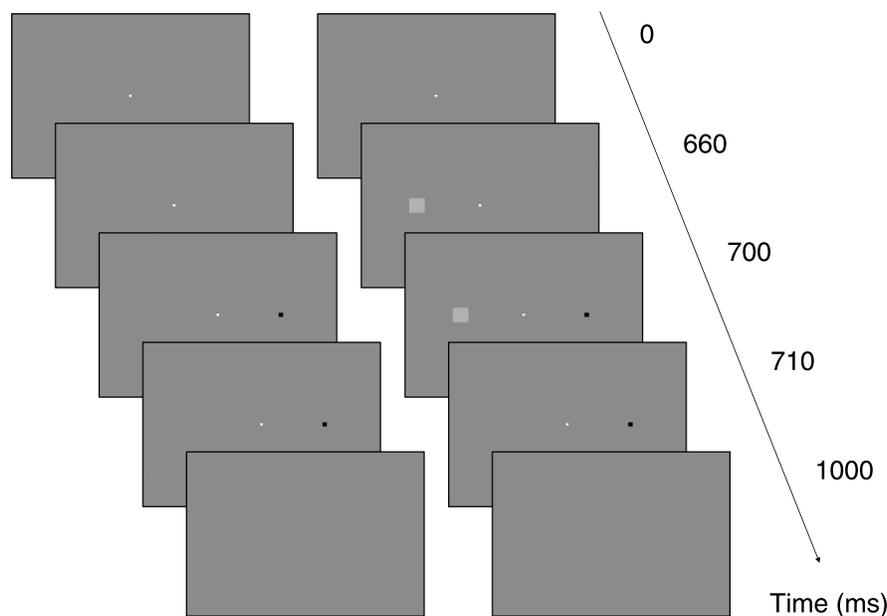


Figure 2. Time sequence within a trial. A fixation point was present throughout the trial and disappeared together with the target. Left panel: on some trials, the target (small black square) appeared alone. Right panel: on most trials, a distractor (larger square) appeared opposite to the target for 50 ms, illustrated here in the condition $\text{SOA} = -40 \text{ ms}$. The target always appeared at 700 ms and stayed on for 300 ms. Sizes of stimuli are enlarged for illustration purposes.

in the main experiment (50 ms), 700 ms after the beginning of the trial. Participants were instructed to make a saccade as fast as they could to the stimulus. Contrast levels and direction were presented in a randomized order. Each contrast level was presented 90 times for each direction, resulting in 180 saccades per condition after averaging directions. This involved collecting another 1260 saccades per observer, split into 3 sessions of 15 minutes.

Because this block was performed before the main experiment, it is possible that differences between these latencies and those in the main experiment were exaggerated by the effect of practice, as saccades tended to get a bit faster during this preliminary block. To take this into account, we also performed our analysis by considering only the last third of the preliminary block. This had only a minor impact on our results and affected in no way our conclusions.

Complementary experiment

Because latencies to all distractor contrasts happened to be longer than the latencies to the targets (in the no-distractor baseline), all our latency differences (target-distractor) were on the negative side. We designed a complementary experiment to see whether the pattern observed in the main experiment generalized to positive latency differences. Setup and design were similar to that described above, but participants were instructed to ignore the small black square and saccade to the larger white square (28 cd/m², corresponding to the second lowest contrast level in Experiment 1). This time, the larger white square (target) appeared for 300 ms and the black square (distractor) only 50 ms. Saccade latency to the 50 ms small black square was assessed in a separate block.

Eye movement analysis

Saccades were detected automatically off-line and then checked visually and corrected if necessary. Saccades were detected using a velocity criteria of 100 deg/s and saccade onsets were defined at velocity 24 deg/s. Saccadic latencies were defined as the duration between the appearance of the target and the onset of the eye saccade. We calculated the mean of each saccadic distribution separately for each participant and distractor condition (contrast \times SOA \times target side). Considering medians instead of means did not alter any of the conclusions in the present article. We removed saccade latencies shorter than 75 ms, which were considered to be anticipations, and latencies longer than 350 ms, which were not considered to be true speeded responses to the target. This excluded less than 5% of saccades for each sub-condition and each participant, with one exception for Participant 1 when saccading to the lowest contrast

distractor. In this condition, Participant 1 failed to see the stimulus on one third of the trials, as estimated from the sum of his omissions and directional errors, while these were extremely rare for the other conditions and participants. Excluding this contrast level for participant 1 did not alter the conclusion from Experiment in any way.

In all subsequent analyses, mean reaction times were extracted for each sub-condition and then averaged across directions. RDE for each distractor condition was calculated by subtracting the mean latency in the no-distractor condition from the mean latency in the distractor condition.

Results and discussion

Manipulation of processing speed

First, manipulating the contrast of the distractor succeeded in varying the saccadic latency to the distractor when it was used as a target ($F(1,6) = 10.3, p < 0.001$), as illustrated [Figure 3](#). These latencies showed the expected dependency on contrast, with a sharp decrease in latency at the lowest contrast levels, stabilizing at higher contrast levels. For comparison, mean latencies in the no-distractor condition in the main experiment were 151, 156 and 136 ms for our 3 participants, all shorter than the latencies to the various distractor stimuli.

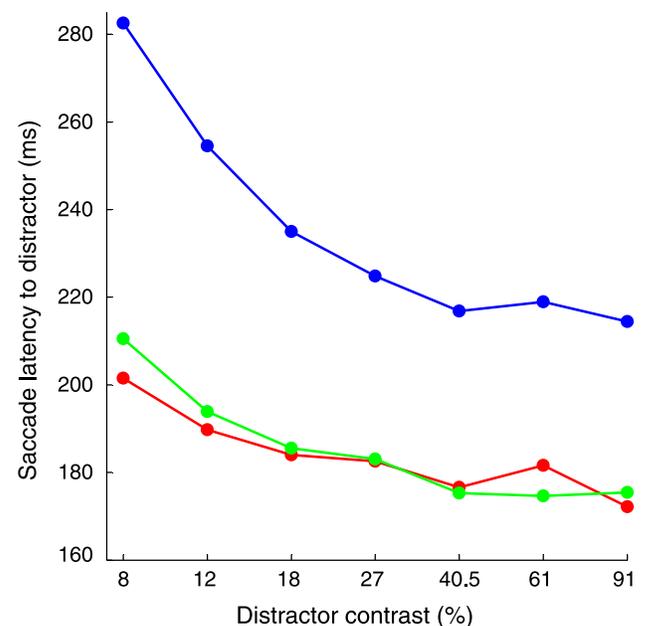


Figure 3. Mean saccadic latencies to the stimuli used as distractors for the 7 contrast levels for participants 1 (blue), 2 (red) and 3 (green).

Effect of timing on distractor effect

Figure 4 represents the RDE as a function of SOA and growing contrast level (rows) for each participant (columns). Negative SOAs mean that the distractor was presented before the target. Robust RDEs were observed for a range of SOAs for every contrast and participant. The RDE was significantly affected by SOA ($F(1,8) = 7.6$, $p < 0.001$), with an overall dependency pattern best described as a symmetric bell-shape (dominated by quadratic component ($p = 0.017$) with no linear or cubic

trend ($p = 0.92$ and 0.87). This confirms that distraction occurs only during some limited time window.

We fitted the RDE as a function of SOA with a Gaussian curve to extract 1) the center, defining the optimal SOA (“SOA_{opt},” i.e. the SOA producing the maximum RDE) and 2) the amplitude of the RDE at this optimal SOA (“RDE_{max}”). This procedure gave very satisfying fits. However, we do not make any claim about using a Gaussian in particular, as we did not have any reason to choose one bell-shape curve over another. To account for the fact that for the very early distractors, the

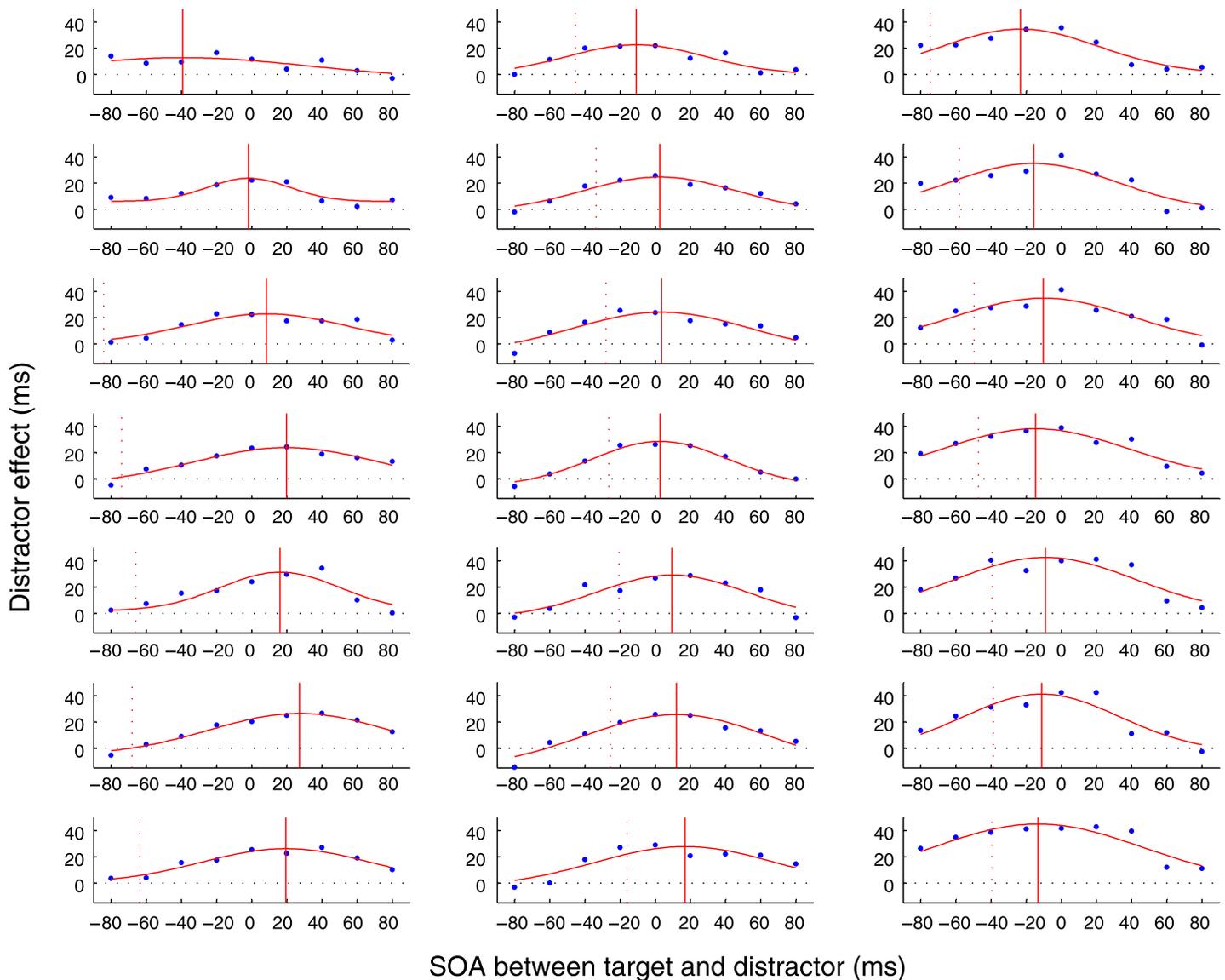


Figure 4. Distractor effect as a function of SOA for each contrast level (C1 to C7 from top to bottom) and participant (in columns, participant 1 to 3 from left to right). The distractor effect is defined as the latency increase in the presence of a distractor compared to the no-distractor baseline. Positive SOA means that the distractor appears after the target. Red curve: Gaussian fit of the distractor effect. Continuous red bar: center of the Gaussian, representing the SOA maximizing the distractor effect. Dashed red bar: difference in latency between saccades to the target (no-distractor case) and saccades to the each distractor stimulus (note that in some cases this dashed bar is not plotted because it falls outside the range of SOA).

RDE sometimes became negative (possibly showing the first signs of inhibition of return), we used a Gaussian function with four free parameters, including center, amplitude, standard deviation and some offset in the ordinate, which was allowed to be negative. The fitted curve appears as the red continuous curve on [Figure 4](#), with the red vertical continuous bar representing the SOA_{opt}. These varied between -39 and $+27$ ms across conditions and participants.

Correlation between optimal SOA and latency differences

Our main hypothesis in this study was that the optimal SOA should vary systematically with the latency difference between target and distractor. [Figure 5](#) shows that this is what we found. There is a significant correlation for each participant ($r^2 = [0.93\ 0.89\ 0.80]$; $F(1,6) = [64\ 41\ 19]$; $p = [0.0005\ 0.0014\ 0.0069]$). This means that, as stimulus contrast increases and elicits shorter saccades when acting as a target, the optimal onset time for distracting saccades is progressively later. This result supports the idea that the degree of interference between a target and a distractor depends on the relative arrival times of their sensory signals at saccadic competition, and these arrival times in turn depend on stimulus properties such as contrast.

Also plotted in [Figure 5](#) (star symbols) are the results for the complementary experiment, in which the target was similar to the distractors in the main experiment and the distractor was the target stimulus of the main experiment. The results appear fairly well aligned with the main results for all three participants, indicating that the

correlation between SOA_{opt} and target–distractor latency difference appears still to apply for more positive latency differences.

As outlined in the Introduction, an illustrative default prediction would be that SOA_{opt} should be exactly equal to the latency difference between target and distractor stimuli. This prediction is represented graphically on [Figure 4](#) by red vertical dashed lines on each SOA plot, and by the dashed gray line in [Figure 5](#). It is clearly not what happens (for the three participants, $y = a * x + b$, where $a = [0.86\ 0.88\ 0.32]$; $b = [80\ 30\ 2]$). The regression line is not of the form $y = x$ as proposed by the default prediction, but rather the slopes tend to be less than 1 (in particular for participant 3) and the line can be displaced (for participants 1 and 2). In the [General discussion](#) we will explain how this can be accounted for by factors including top-down influence and rise rate changes.

Effect of distractor contrast on RDE

The effect of contrast level on the amplitude of distractor effect at its optimal SOA ([Figure 6](#)) was significant ($F(1,6) = 3.95$, $p = 0.021$). Directional errors showed a similar pattern, with an overall increase with contrast ($F(1,6) = 3.61$, $p = 0.028$).

Methodological point: How to compare RDE between conditions

To illustrate to what extent varying SOA offers a material improvement over previous studies that have

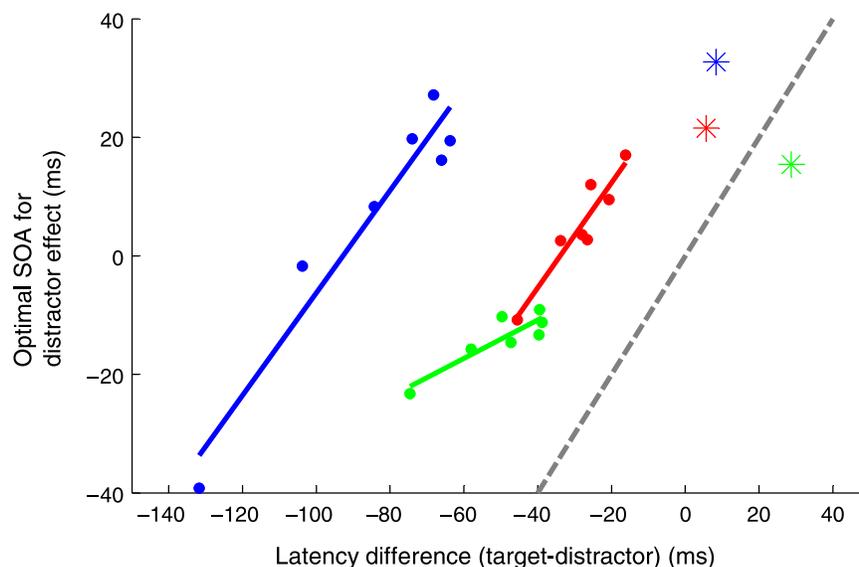


Figure 5. Results of Experiment 1 (circles) and 1b (stars). Data points represent the optimal SOA as a function of the latency difference between target and distractors for participants 1 (blue), 2 (red) and 3 (green) with regression lines. The gray dashed line illustrates the default prediction “SOA_{opt} = Latency difference”.

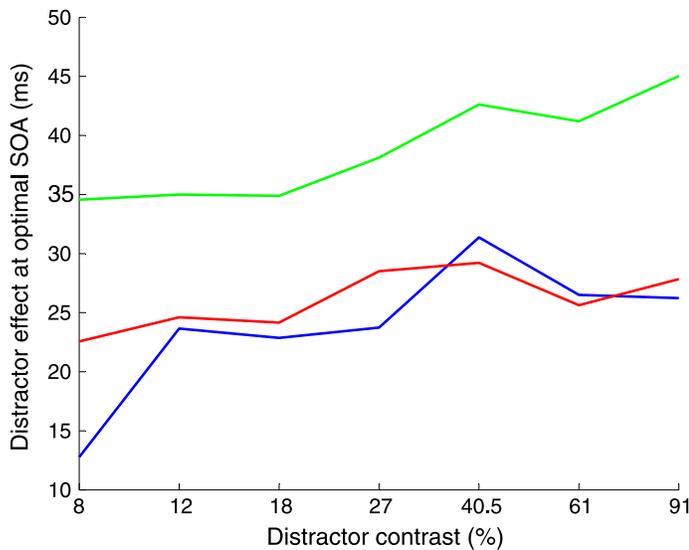


Figure 6. Effect of contrast level on distractor effect at its optimal SOA for participants 1 (blue), 2 (red) and 3 (green) in Experiment 1.

employed a single SOA (usually zero), we present now the effect of contrast on the RDE for each SOA independently (rather than the effect of contrast at SOA_{opt} , as presented above). To estimate the general tendency for this effect, we calculated the regression line

between RDE and growing contrast levels at each SOA separately and for each participant. The effect of contrast is given by the slope, with positive slope values indicating that the RDE increases with contrast. These slope values (effect of contrast) are then plotted against SOA in Figure 7, revealing an interesting, but clear pattern: depending on SOA, contrast can have opposite effects. For SOAs around or above SOA_{opt} , RDE increases with contrast, as indicated by the positive values. However, at negative SOA, much lower than SOA_{opt} , RDE decreases with contrast, as revealed by the negative values. This clear pattern was present whether the analyses were performed on the raw RDE data (data points on Figure 7) or the Gaussian-fitted RDE data (continuous lines). For a comparison, Figure 7 also shows the effect of contrast at the optimal SOA using the same analysis (stars represent the slope of the regression line on the data presented on Figure 6).

Although this pattern can appear surprising at first, it is perfectly consistent with the competition framework. It makes sense that early distractors ($SOA = -80$ ms) will suffer from increasing their contrast, as this shortens the transmission time between the eye and the crucial competition area, and will make the distractors arrive even earlier compared to the target. Note that the negative values are essentially observed for participants 1 and 2, for which SOA_{opt} were higher on average than those of participant 3. One additional factor could be that

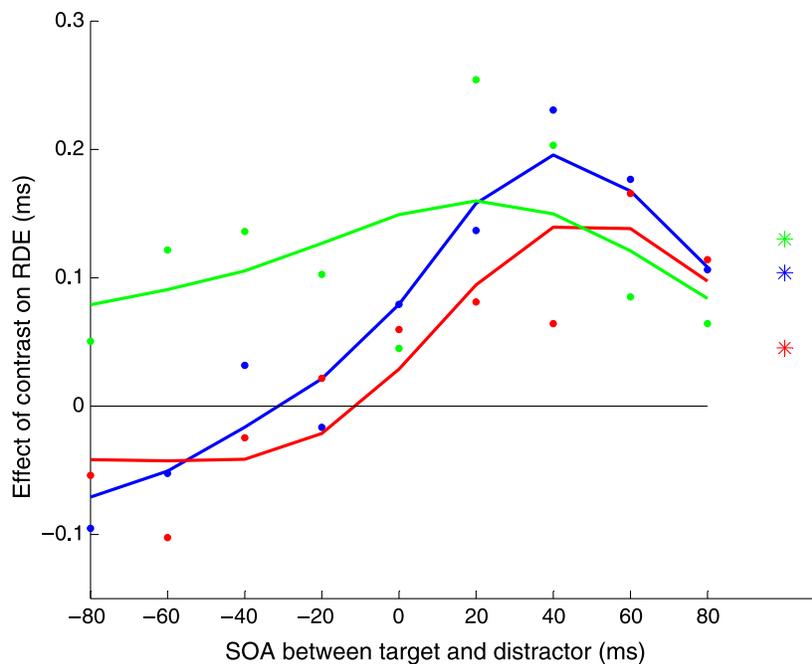


Figure 7. Effect of contrast on the distractor effect as a function of SOA for participants 1 (blue), 2 (red) and 3 (green). The effect of contrast is estimated from the slope of the regression line of distractor effect as a function of contrast level for each SOA, and is therefore expressed in ms. For illustration, a value of 0.1 on the y-axis therefore means that varying contrast level from 8% to 91% has produced an overall increase in RDE of 8.3 ms. The analyses were performed on the raw RDE values (data points) and on the Gaussian-fitted RDE (continuous lines, note that these are not the fit of the data points). The stars on the right represent the effect of contrast at the optimal SOA.

distractors that precede the target act as warning signals (Walker et al., 1995). A higher contrast distractor may be a more effective warning signal, reducing the latency of the target-directed saccade relatively more than a low contrast distractor. It also makes sense that, around SOA_{opt} and above, increasing contrast will make the distractor more efficient, by a combination effect of transmission time and intensity. The observed fluctuating pattern confirms that varying the SOA is essential if we are to reach firm conclusions about the effect of contrast, or indeed any factor that might affect transmission times and response latencies as well as RDE amplitude. In particular, the comparison with the effect of contrast at optimal SOA (stars on Figure 7) suggests that picking one single arbitrary SOA can have various spurious consequences: not only can the effect of the manipulated feature be underestimated or appear to go in a counter-intuitive direction (i.e. RDE decreasing with contrast at SOAs below the optimal SOA), but it can also be overestimated, since increases in RDE can be due to moving the optimal SOA closer to the chosen SOA.

Temporal dynamics of directional errors

We analyzed the effect of SOA on the number and latency of directional errors. First, we note that the number of errors in the no distractor condition was extremely small (<0.56% for all participants, 0.12% on average). The number of these errors was however deducted from the number of errors in the distractor conditions. Therefore, the number of errors presented thereafter truly represents the saccades directed to the distractor and not anticipations. As predicted, number of errors reduced with SOA for all participants ($F(1,8) = 4.0$, $p = 0.008$, see Figure 8), consistently at all contrast levels, showing maxima at SOA between -80 and -40 ms.

In the framework we outlined above, directional errors consist of the proportion of trials where the distractor signal is strong enough to reach the saccade initiation threshold before it gets inhibited, either by high level influences or by the target signal through mutual inhibition. Consistent with this, we observed that the latency of errors toward each distractor contrast was correlated with, and systematically shorter than, the latencies to the distractor stimuli when they were targets (by 68 ms on average, ranging from 12 to 148 ms across SOA, contrast and participants; note that here and in the following, error latencies are taken into account only for SOA -80 to -20 ms as the other conditions did not produce enough errors to provide a reliable estimate of the mean latency). Additionally, we observed that error latencies tended to decrease with SOA. This would be consistent with the idea that, as the number of errors decrease, only the strongest and fastest distractor signals manage to reach the threshold, leading to even shorter mean latencies.

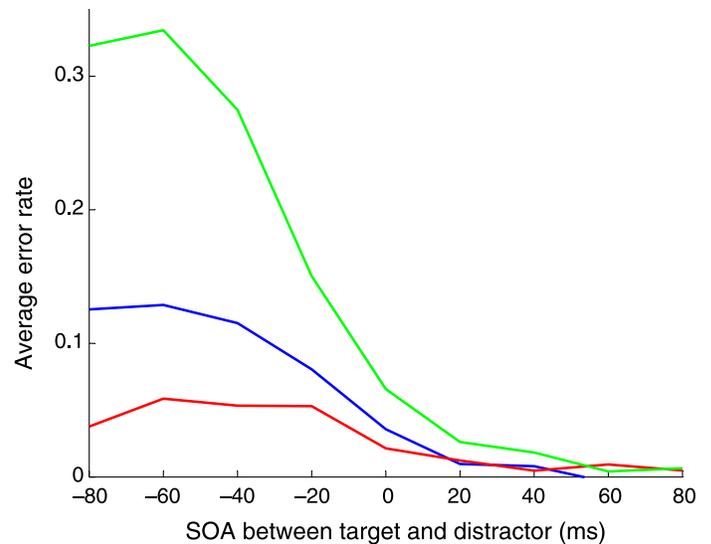


Figure 8. Error rate averaged across contrast levels as a function of SOA for the three participants.

It might seem surprising at first that the maximum number of errors does not occur more clearly at -80 ms, as the earlier the distractors come, the less inhibition they should suffer from the target and the more likely they should be to reach the initiation threshold. However, it should be noted that target onset in this experiment was fixed, so that some building readiness activity would be expected around the time the target is expected. Distractor signals would also benefit from this. Such a mechanism would favor signals arriving around target onset and would drag the maximum number of errors to some place between -80 ms and 0. This could also contribute to error latencies decreasing with SOA, as the effect of readiness activity would increase closer to target onset.

General discussion

Summary of the main results

We have reported three main results. First, we observe that the delay between target and distractor that maximizes the amplitude of the distractor effect varies between different distractors and is correlated with the latency difference between the two stimuli. This result verifies a fundamental prediction of the proposed framework: interference depends upon the temporal overlap of signals in the neural machinery where motor activity accumulates and competes.

Secondly, we showed that the pattern of dependency of the RDE on contrast changes depending on what SOA is employed. When a single SOA is picked, the RDE can either increase with contrast or decrease with contrast, or

stay the same, depending on how far the picked SOA is above or below the optimal SOA (Figure 7). Thus it is not safe to compare the RDE across different distractors at only one time-point. This arises because the amplitude of the RDE depends on both the delay between target and distractor, and the relative processing speeds of the two stimuli. This problem is therefore relevant for any study where the amplitude of the RDE is compared between two conditions that might have different optimal SOA. This is probably the case for most previous comparisons between distractor types, which manipulated features such as size, spatial frequency, contrast or color (e.g. Born & Kerzel, 2008; Irwin et al., 2000; Ludwig, Gilchrist, & McSorley, 2005; Sumner et al., 2002; White et al., 2005). Thus our results may be taken to cast new light on these previous studies, as already illustrated in the case of color (Bompas & Sumner, [in press](#)).

Third, we showed that the temporal conditions maximizing erroneous saccades to the distractor are not the same as those maximizing the distractor's influence on saccades to the target. This confirms that errors and latency effects are related but distinct consequences of the presence of distractor stimuli. The framework envisages that errors should be increased by minimizing the temporal overlap of target and distractor signals, while the effect on the latency of target saccades will be maximized by increasing the temporal overlap of target and distractor signals.

Effect of contrast on the RDE

Beyond the methodological point that the effect of contrast depends on SOA, our experiment confirmed that at the optimal SOA, distractor contrast does modulate the amplitude of the RDE. At optimal SOA, the effect of contrast should reflect changes in the rise rates of distractor signals, creating a general increase in the RDE with contrast. Note that there was no reason to expect a much bigger effect than the one we observed: since the effect of contrast on latency plateaus (Figure 3), rise rates are expected to plateau as well. There may also be an important top-down component in the effect of contrast, because different distractors may attract top-down inhibition to different degrees. If more salient distractors attract more inhibition, this would act to reduce the effect of contrast.

Top-down influence

It is important to consider what influence top-down factors such as attention, strategy and expectation would have on our results. First, such factors play an important role in determining saccade latency, and since latencies to the distractors were measured in a preliminary block, absolute latency differences between the two blocks could

reflect differences not only in sensory processing time but also in top-down influence, as well as possible effects of practice or fatigue. If top-down influences differed between when a stimulus is used as a target and a distractor, then this would produce an offset in the relationship between the latency differences and optimal SOA. Since top-down influences may vary between participants, this could account for the large individual differences in offsets.

It is also likely that top-down factors can modulate processing time and therefore affect the SOA of maximum distraction. When attempting to saccade toward a stimulus, the system is presumably biased to maximally allow stimuli with those properties to create motor activation. When this stimulus is an irrelevant distractor, the system is instead biased against these stimulus properties. Such attentional modulation may change the processing speed of a stimulus when it is a distractor compared to when it is a target (by changing the effective contrast for example, Carrasco, 2006). This would slow distractors down, meaning that to create maximal interference, they should need to be presented extra early, again creating an offset between measured latency differences and optimal distractor SOA. However, this is not the direction of our measured offset. Thus if anything, such goal directed biases may have lessened the measured offset, although differences in attentional modulation could contribute to the differences in offset between participants.

The essential point is that top-down influence would not create the correlation we measure between latency differences and optimal SOA. This arises from the relative differences in latency between distractor stimuli and relative differences in optimal SOA between distractor stimuli. These were each measured within a block with randomly intermixed stimuli, making it unlikely that top-down influences would differentially affect the different contrast levels within a block. Even if they did, it is hard to see how this would create the strong linear relationships we observe. Thus despite any top-down influences that may have affected the absolute values of our measured latencies and optimal SOAs, the relationship between the two is best attributed to sensory processing times.

Influence of rise rate

To achieve maximum interference, we proposed that the distractor signal should *arrive* at the competition in close temporal proximity with the target signal. However, saccadic latency is a measure of when the motor accumulation process reaches threshold. Differences in saccadic latency to different stimuli are assumed to derive both from different sensory transmission speeds and different motor accumulation rates, whereas it is the former that is most relevant for the arrival times of stimuli in the motor competition. Thus to achieve simultaneous arrival in the motor competition, it is the sensory differences that must be

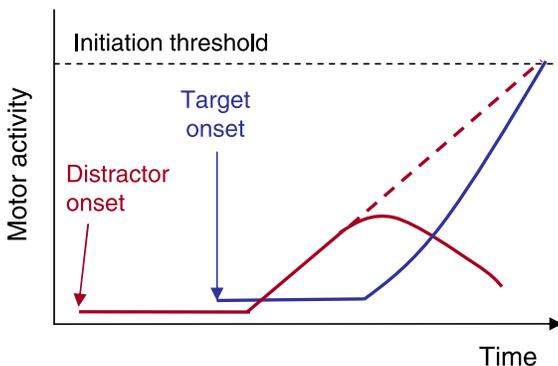
compensated for, not the differences in motor accumulation rate (see Figure 9).

If variations in rise rate are random, or due to factors unrelated to stimulus contrast, they would just add noise to the relationship between latency differences and optimal SOA. This would decrease the slope of the regression line correspondingly with the correlation coefficient by the statistical process of regression to the mean, which is sufficient to account for the slopes of participants 1 and 2 (which do not differ significantly from 1). However, if variation in rise rate is systematically related to contrast, which is likely because rise rate is assumed to be driven by sensory evidence, then this would act to reduce the slope without necessarily adding noise. This may account for the slope of participant 3, which does differ significantly from 1. Individual variations in slope might then suggest that participants' rise times are not equally affected by contrast.

Rise rates could also affect the measured offset. As discussed above, the accumulation rate has more influence on saccade latency than on the RDE, because RDE is

greater when signals coincide at the start of the competition (accumulation) stage, than if the SOA is such that they would coincide at the end (given no interference). If two stimuli, when presented together, arrived at the competition together (i.e. had the same sensory transmission time), but had different rise rates, this would cause a latency difference, but the optimal SOA would remain around zero. For our experiment, this scenario might happen due to stimulus duration. Sensory transmission time (and initial rise rate) might be mainly due to stimulus onset properties (contrast, spatial frequency etc), but overall rise rate may also depend on stimulus duration. In our design, targets and distractors were presented respectively for 300 and 50 ms, potentially causing slower rise rates for distractors—this would create the direction of offset that we have measured. In turn, this would indicate that the accumulation time window is larger than 50 ms, which is consistent with previous reports (Ludwig, Gilchrist, McSorley, & Baddeley, 2005). Comparison of saccade latencies between the main experiment and the complementary experiment is also consistent with this hypothesis: latencies to the small black square were shorter when it was presented for 300 ms than when it was presented for 50 ms (by 14 ms on average) while the opposite pattern was observed for the larger gray square used in both experiments (by 37 ms on average).

A. When SOA = latency difference, signals would coincide at end of competition



B. Interference greater when signals coincide near start of competition

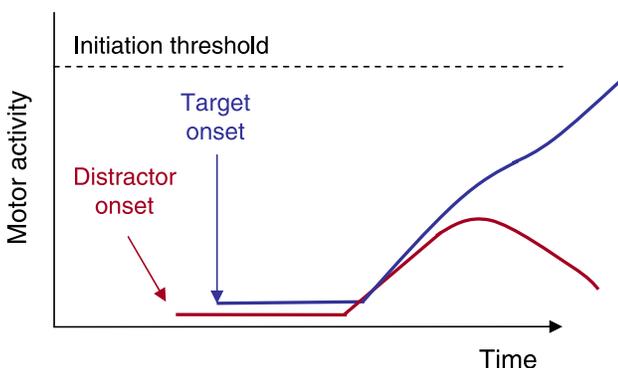


Figure 9. Effect of varying the delay between target and distractor onsets. A: Compensating fully for the latency difference between signals does not guaranty maximal interference, because rise rates might also differ. B: Distractor effect will be maximal when delays compensate only for arrival time of signals in the competition area.

Is it really necessary to measure multiple SOAs?

One conclusion of the present study is that it is not safe to compare distractor effects at only one timepoint. But couldn't it be argued that if target and distractor stimuli share the very same visual features, their visual processing times should be equal, so that simultaneous presentation will necessarily be the optimal SOA? It is important to note that even with similar stimuli, the participant must be instructed as to how to distinguish target from distractor, and however this is specified (by feature or location etc.), such instruction is expected to produce a bias in favor of the target. It is a common assumption that such endogenous (top-down) biases (i.e. "attention") can modulate the sensory signals at an early level (Carrasco, 2006) before they reach the locus of motor competition (the motor map), and therefore target signals would generally reach the motor map earlier than distractor signals. Thus employing similar stimuli would not necessarily suppress the difference in arrival times between target and distractor.

Conclusions

We have elaborated a conceptual framework for understanding interference between saccade targets and

distractors that differ in their perceptual properties and processing times. Our data measuring the temporal dynamics of the RDE (latency effects and directional errors) are entirely consistent with this framework. We have found that a widespread assumption about distractor interference—that simultaneous presentation maximizes the effect—is not always true. Rather, the optimal SOA depends on the particular target and distractor stimuli used in the study. Beyond supporting the competition framework, there is a methodological outcome: it is not safe to compare distractor effects at only one timepoint.

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