

The inhibitory effect of a recent distracter

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Abstract

A series of experiments were conducted to examine the inhibitory effect of a visual distracter on saccadic eye movements. Participants were presented with a sequence of two critical displays. In one display a red target was presented together with a green distracter. This was followed by a display with a new red target presented in isolation at one of three locations with respect to the previous display. The lone target was presented either at the location of the recent target, the location of the recent distracter, or a new location. Participants were instructed to fixate the target in both displays and to ignore the green distracter. Experiment 1 revealed a significant increase in saccadic reaction times (SRTs) when the target was presented at the location of the recent distracter. Experiment 2 revealed that SRTs increased only in the conditions where the new target was presented at the location of the recent distracter, irrespective of its colour. Experiment 3 found that the inhibitory effect lasted for at least 2 s. In Experiment 4 the inhibitory effect was abolished when a lone distracter (i.e., anti-target) was presented without a target. Experiments 5 and 6 revealed that inhibition at the location of the *recent target* ('inhibition-of-return') also emerged with a shorter inter-display interval and when the distracter was removed from the recent display. These results distinguished between inhibition of a recent distracter and 'inhibition-of-return' and are consistent with models of competitive interactions which generate inhibitory effects on the spatial representation of a distracter.

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1. Introduction

A target for a saccadic eye movement is usually selected from an array of other potential targets and distracters. Yet, within a fraction of a second, the eye takes off in a precise trajectory towards the correct target. How is this selection achieved? This is a non-trivial task for the visual system because many cells have large receptive fields that are highly sensitive to an ambiguous signal. The normal activity of many cells in visual cortex to a stimulus in their receptive field may be completely silenced when a similar stimulus is presented in the sur-

rounding region (Desimone, Albright, Gross, & Bruce, 1984; Kniermin & Van Essen, 1992).

Increasing evidence from cognitive research has suggested that a distracter is actively inhibited in tasks of selective attention (Bahcall & Kowler, 1999; Cepeda, Cave, Bichot, & Min-Shik, 1998; Mounts, 2000). One pointer also emerged from oculomotor research on the trajectories of saccadic eye movements. When a target was presented with a distracter, the saccade curved away from the distracter (Doyle & Walker, 2001; Godijn & Theeuwes, 2002; Sheliga, Riggio, & Rizzolatti, 1994; Sheliga, Riggio, & Rizzolatti, 1995; Tipper, Howard, & Houghton, 2000; Tipper, Howard, & Paul, 2001). It was reported that on 30–40% of occasions the eye was driven to the location of the distracter rather than the target (Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999) and saccadic reaction times (SRTs) increased

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when the eye went directly to the target. The evidence of saccadic curvature has provided supporting evidence for distracter inhibition when a target is selected for a saccadic eye movement. A system of inhibitory interactions between competing channels of information may be an important part of the potential solution to the problem of signal ambiguity (Desimone & Duncan, 1995).

In ‘race-models’ (Hallet, 1978; Theeuwes et al., 1999) visual attention is presumably distributed simultaneously to a target and a distracter and eye movements are programmed independently, and in parallel. On the basis of the ‘winner-takes-all’ principle, the direction of the eye is determined by the outcome of the race to complete the saccadic programme (Hallet, 1978). When the saccadic programme to the target is completed before the saccadic programme to the distracter, the eye moves to the target and the response to the distracter is aborted. Conversely, the eye will move to the distracter when the saccadic programme to the distracter is completed first. The increased SRTs of the correctly directed saccades can be explained in terms of the faster time course of exogenous saccades compared to endogenous saccades (Müller & Rabbitt, 1985). The early deviation in the saccadic trajectory to the target appeared to expose the parallel programming of two saccades; a dominant saccade towards the target, and a partially suppressed saccade to the distracter. However, a problem for the concept of ‘winner-takes-all’ is how to reconcile the reports of eye movement sequences, where an ‘erroneous’ movement to the distracter was invariably followed by a rapid corrective movement to the target (Fischer, Gezeck, & Hartnegg, 2000; McPeck & Keller, 2001; Mochler & Fischer, 1999; Theeuwes et al., 1999). Also, it is unlikely that multidirectional saccades would have been executed simultaneously, even though saccades may be programmed in parallel (Doyle & Walker, 2001).

A number of researchers have proposed alternative models of target selection that feature a common principle of inhibitory interactions between the competing signals for a saccade (Findlay & Walker, 1999; Godijn & Theeuwes, 2002; Tipper et al., 2000; Tipper et al., 2001, Trappenberg, Dorris, Munoz, & Klein, 2001). For example, in the ‘competitive integration’ model (Godijn & Theeuwes, 2002) the control signals for a saccade converge onto a single retinotopic spatial map. Distinct signals within this map are integrated to determine a region of peak activity. The activation from closely spaced locations is integrated to produce an activation peak. In contrast, distant signals within the map are subject to reciprocal inhibition. A critical feature of the model was the proposal of a process where inhibition acts directly at a specific location in the map. The function of this inhibition is to resolve any ambiguity between stimulation at different locations by biasing visual processing in favour of an attended target and against a distracter. This was deemed necessary because

of the automatic capture of attention by a new visual stimulus and the risk of an inappropriate motor programme (Hommel, Pratt, Colzato, & Godijn, 2001).

Given the findings of distracter inhibition that have been reported in studies of visual attention (Bahcall & Kowler, 1999; Cepeda et al., 1998; Mounts, 2000) and the related phenomenon of negative priming (Tipper, 1985b) it is surprising that there is little evidence from saccadic eye movement research. Little is known of the inhibition source of a saccadic distracter. Is the inhibition of a saccadic distracter general or feature specific? If so, which features of a saccadic distracter are inhibited? How long does the inhibition of saccadic distracter last? The approach we have taken in this study was based on the view that inhibitory effects might be revealed when a new stimulus was presented at the location of a previous distracter. We therefore examined the processing of a saccadic distracter by probing responses when the distracter had been removed from the display. A quantitative measure of the inhibitory effect of a recent distracter (IRD) was obtained by contrasting SRTs at the location of the previous distracter in relation to the old and new target locations. We report the results of six experiments. Experiment 1 revealed that saccadic eye movements were delayed to a location that was recently occupied by a saccadic distracter. Experiment 2, demonstrated that the inhibitory effect was derived from the location, not the identity (i.e., colour), of the distracter. Experiment 3, revealed that the effect had a duration of at least 2 s. In Experiment 4 the inhibitory effect was removed when a single distracter was displayed without a target. Two further experiments revealed that inhibition at the location of the recent target (‘inhibition-of-return’) also emerged with a shorter inter-display interval (Experiment 5) and when the distracter was removed from the recent display (Experiment 6).

2. Experiment 1

2.1. Methods

2.1.1. Participants

All participants (4 males, 9 females, mean age = 26.8 years, range = 19–46, $SD = 7.4$) had normal or corrected visual acuity (assessed with the Snellen chart), and intact colour vision according to the Ishihara test (Ishihara, 1983). No participant had consumed any alcohol in the 12-h preceding the experiment or taken nicotine in the hour prior to testing. None of the participants had a history of mental health problems and none were currently taking any form of medication. Participants were screened in this manner for all subsequent experiments. The study was approved by the Lancaster University departmental ethical research committee.

2.1.2. Stimuli

The stimuli consisted of an array of white, green, and red LEDs (5 mm diameter), embedded in a black screen at a distance of 3 m from the participant. LED targets were presented at one of four positions, 0°, ±5° (horizontal plane), and +5° (vertical plane, see Figs. 1A and B). Saccadic eye movements were measured using an infra-red reflection method (Skalar Medical Iris System) with a spatial resolution of 0.5° and a linear range of ±15°. To restrict head movements participants were seated in a dentist’s chair fitted with a head restraint. Analogue signals were digitized at 500 Hz with a 12-bit analogue-to-digital converter. The data was recorded online with the Eyemove V2.0 (Amtech GmbH) software where it was stored for subsequent offline analysis. The experiments were conducted in the dark, neither the display board or the unlit LEDs were visible to the participant.

2.1.3. Procedure

The experiment was conducted in the eye movement laboratory at Lancaster University. Each participant began with a practice session of 24 trials to familiarise themselves with the conditions of the experiment. A trial began with the onset of a white (LED) fixation point at the centre of the display (fixation *display*₁) for a period of 750–1000 ms; this time was randomised to prevent anticipatory responses. The fixation point was then switched off and immediately followed by a red target and a green distracter (Fig. 1) (target *display*₁) presented simultaneously for 1500 ms. Participants were instructed to a look at

the red ‘light’ as quickly and as accurately as possible and to ignore the green ‘light.’ Once the target *display*₁ was removed the fixation point re-appeared for a randomised interval of 750–1000 ms (fixation *display*₂). Finally, participants were instructed to fixate a single red LED (target *display*₂) that was presented for 1500 ms. The stimulus onset asynchrony (SOA) between the target *display*₁ and target *display*₂ was 2250–2500 ms. A blank interval of 3500 ms elapsed before the next trial commenced.

The spatial configuration and mapping of the target *display*₁ (recent) and target *display*₂ (new) was the key manipulation of this study (see Figs. 1A and 1B). The target *display*₁ configurations was randomly selected from one of the 18 displays illustrated in Fig. 1B. The pairings of target *display*₁ and target *display*₂ generated three types of trials; (1) on the *Target* → *Target* (T₁ → T₂) trials the *display*₂ target was presented at the location that was previously occupied by the recent target in *display*₁. (2) On the *Target* → *Distracter* (T₁ → D₂) trials the *display*₂ target was presented at the location previously occupied by the recent distracter in *display*₁. (3) On the *Target* → *New* (T₁ → N₂) trials the *display*₂ target appeared at a new location, not previously occupied by either the target or the distracter in *display*₁. The experiment consisted of 120 mixed, randomly interleaved trials. On 50% of the trials the target location was repeated in *display*₂ (i.e., T₁ → T₂ trials) and on 50% of trials the target location was different to the *display*₂ target (25% T₁ → N₂ +25% T₁ → D₂), to ensure that the target location in *display*₁ was non-informative. Therefore, within a complete

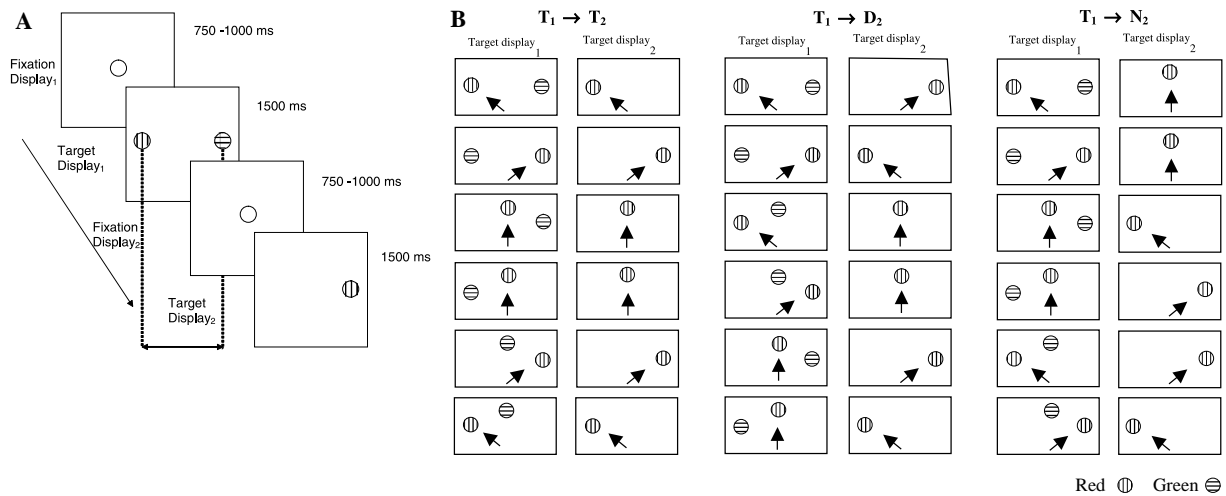


Fig. 1. (A) The sequence and the timings of the eye movement displays in Experiment 1. Fixation *display*₁ shows the fixation target at the start of a trial. Participants were instructed to fixate on the red target and to ignore the green distracter in target *display*₁. This was followed by fixation *display*₂. Participants fixated a lone target in target *display*₂. (B) The target–distracter conditions of Experiment 1. On the T₁ → T₂ trials, the target (red) was presented at the same location in target *display*₁ (T₁) and target *display*₂ (T₂). On the T₁ → N₂ trials the target in the target *display*₂ was presented at a new location, that was not previously occupied by the target or distracter. On the T₁ → D₂ trials, the target in target *display*₂ was presented at the location of the distracter in the target *display*₁. The vertical striped pattern represents a red target; horizontal striped pattern represents a green distracter. The black arrows indicate the target for a saccadic eye movement.

block of trials each $T_1 \rightarrow T_2$ was repeated 10 times, while a given $T_1 \rightarrow D_2$ and $T_1 \rightarrow N_2$ was repeated five times.

2.1.4. Data analysis

The analyses were conducted on the primary saccadic eye movement to the $display_2$ target. Trial 1 of the experiment was discounted to reduce any effects of alertness or lack of readiness. The analyses of this experiment were based on a total of 1560 trials and the mean SRTs were submitted to SPSS for statistical analyses.

2.2. Results

Table 1 shows the mean SRTs and standard deviation to the $display_2$ target. There was a significant main effect of trial type ($F(2,24) = 19.2$, $p < 0.001$) on SRT. Post hoc pair wise comparisons revealed that SRT was significantly longer on the $T_1 \rightarrow D_2$ trials (281 ms) than both the $T_1 \rightarrow N_2$ (256 ms) and $T_1 \rightarrow T_2$ trials (228 ms), (p 's < 0.01). There was no evidence of IoR, since the mean SRTs was reduced on $T_1 \rightarrow T_2$ trials in comparison to $T_1 \rightarrow N_2$ trials.

2.3. Discussion

These results demonstrated that the movement of the eye was delayed to a target that appeared at the location of a recent distracter, showing that a previous distracter inhibited a saccadic eye movement to a prospective target. Visuomotor centres appeared to have access to the memory trace of recent distracter. However, the source of the effect was unclear from this study. This uncertainty stemmed from the characteristics of the $T_1 \rightarrow D_2$ trials. Although the target shared only the location of the distracter, the inhibition of location might in principle extend to any feature of the object at the distracter location. It was unclear whether the inhibitory effect of the recent distracter (IRD) was attributable to the distracter location, colour or a combination of both features. A

further issue concerned the possibility that the IRD may have resulted from a masking effect, generated by the green distracter masking the new red target. Although a colour masking explanation seemed unlikely, considering the long intervals and intervening events between the two critical displays, in principle a masking might have contributed to the longer saccade SRTs to the new target. In Experiment 2 we introduced two additional experimental conditions designed to address both of these issues.

3. Experiment 2

The principle aim of Experiment 2 was to determine whether the IRD was driven primarily by location or colour information. The experiment also included a specific condition to test for the possibility of colour masking. The key features of the experiment are briefly outlined before the experiment is described in detail. The critical feature of this experiment was the independent control of the display properties of colour and location. The experiment contained five types of trials, two additional sets of trials supplemented the three previous conditions of Experiment 1 (see Fig. 2); one set of the trials probed for a selective effect of *distracter colour*, independent of location. The relevant display controlled the spatial positions of the target and the distracter of $display_1$ by changing their positions with respect to the new target in $display_2$ (e.g., target $display_1$ (right target (+5°) + left distracter (-5°)), target $display_2$ (upper target (+5°))). However, the same *colour* was assigned to the recent distracter ($display_1$) and the new target ($display_2$). Therefore, the *colour* of the recent distracter in $display_1$, but not the location, was used for the new target in $display_2$. If the IRD was determined primarily by a colour signal (e.g., the colour in relation to the distracter or the generic colour per se) then SRTs should increase in this condition. In the second set of additional trials, the new target ($display_2$) was assigned both the colour and the location of the recent distracter ($display_1$). We predicted that performance on these trials should determine whether there were any additive effects of location and colour. Furthermore, if the IRD was simply due to colour masking then saccadic eye movements to the new target should not be inhibited in this condition, since there was essentially no change in the colour of the distracter and target.

3.1. Method

All participants (4 males, 9 females, mean age = 26.8 years, range = 19–46, $SD = 7.4$) had normal or corrected visual acuity (assessed with the Snellen chart), and intact colour vision according to the

Table 1
Mean saccade reaction times (SRT) and standard deviations (SD) (Experiment 1)

	Target $display_1$ /target $display_2$			Sig.
	$T_1 \rightarrow T_2$	$T_1 \rightarrow N_2$	$T_1 \rightarrow D_2$	
SRT (ms)	228	256	281*	*
SD	25.2	36.9	45.5	

$T_1 \rightarrow T_2$, target in $display_2$ was presented at the target location in $display_1$; $T_1 \rightarrow N_2$, target in $display_2$ was presented at a new location that differed from the target or distracter in $display_1$; $T_1 \rightarrow D_2$, target in $display_2$ was presented at the location of the recent distracter in $display_1$.

* ($p < 0.01$).

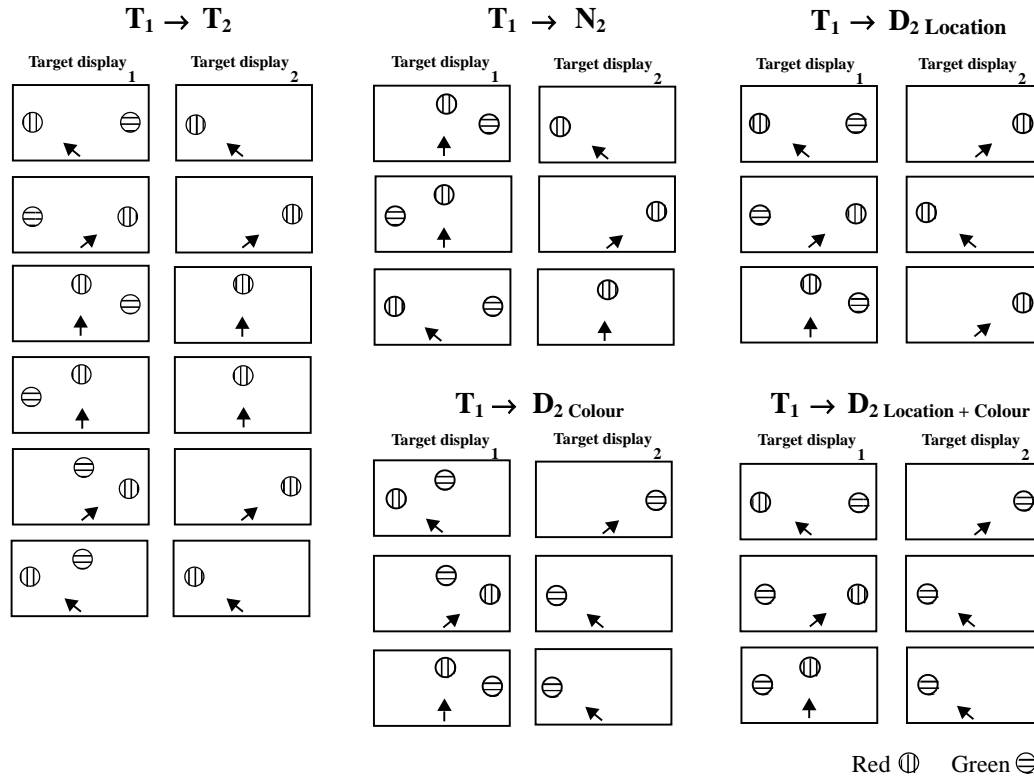


Fig. 2. The target–distracter conditions in Experiment 2. On $T_1 \rightarrow T_2$ trials the target was presented at the same target location in target $display_1$ and target $display_2$. On $T_1 \rightarrow N_2$ trials the target in target $display_2$ was presented at a new location. On $T_1 \rightarrow D_2 Location$ trials the target in target $display_2$ was presented at the location of the target $display_1$ distracter. On $T_1 \rightarrow D_2 Colour$ trials the target in target $display_2$ was presented with colour of the previous distracter. On $T_1 \rightarrow D_2 Location + colour$ trials the target in target $display_2$ was presented at the location and with the colour of the target $display_1$ distracter. Arrows show the target for the eye. The vertical striped pattern indicates the red target, the horizontal striped pattern represents the green distracter.

Ishihara test (Ishihara, 1983). The recording equipment, the experimental format and timings of the displays were identical to Experiment 1, with the exception that two additional sets of trials were included to identify the source of the effect. As in Experiment 1, each trial presented a sequence of four displays, the critical displays (target $display_1$ and target $display_2$) were separated by a central fixation point to cue the eyes back to the centre of the screen (fixation $display_1$ and $display_2$). In target $display_1$, the red target and the green distracter were presented simultaneously. In target $display_2$ a single red or green target was presented (see Fig. 2).

The five types of trials were as follows:

1. On the Target \rightarrow Target trials ($T_1 \rightarrow T_2$) the location and colour of the target in $display_2$ matched the $display_1$ target.
2. On the Target \rightarrow New trials ($T_1 \rightarrow N_2$) there was no match in the colour or location of the target in $display_2$ and the distracter in $display_1$.
3. On the Target \rightarrow Distracter-location trials ($T_1 \rightarrow D_2 Location$), the location of the target in $display_2$, but not the colour, matched the distracter in $display_1$.

4. On the Target \rightarrow Distracter-Colour trials ($T_1 \rightarrow D_2 Colour$), the colour of the target in $display_2$, but not the location, matched the distracter in $display_1$.
5. On the Target \rightarrow Distracter-Location + colour trials ($T_1 \rightarrow D_2 Location + colour$), the location and the colour of the target of $display_2$ matched the distracter in $display_1$.

3.1.1. Procedure

The testing and data analysis procedures were identical to those previously outlined in Experiment 1. Participants were informed that a red target and an irrelevant green distracter would be presented simultaneously in target $display_1$. They were instructed to fixate the target quickly and accurately and to ignore the distracter, before returning to the central fixation point. This was followed by a single target in $display_2$. Participants were instructed to fixate this target as quickly and as accurately as possible (see Fig. 2). One hundred and twenty trials were presented randomly with an equal proportion (12.5%) of $T_1 \rightarrow N_2$, $T_1 \rightarrow D_2 Location$, $T_1 \rightarrow D_2 Colour$, $T_1 \rightarrow D_2 Location + colour$, $T_1 \rightarrow T_2$ trials constituted 50% of the trials.

Experiment 2 generated the following hypotheses:

- (i) If the inhibition source was derived from the *location* of the distracter, SRTs should be increased on the $T_1 \rightarrow D_{2\text{Location}}$ AND $T_1 \rightarrow D_{2\text{Location} + \text{colour}}$ trials.
- (ii) If the inhibition source was derived from a *colour* source SRTs should be increased on the $T_1 \rightarrow D_{2\text{Colour}}$ AND $T_1 \rightarrow D_{2\text{Location} + \text{colour}}$ trials.
- (iii) If the locus of inhibition was derived from a location source that could affect a coincidental feature (e.g., colour) presented at the distracter location, SRTs should increase on the $T_1 \rightarrow D_{2\text{Colour}}$, $T_1 \rightarrow D_{2\text{Location}}$, AND $T_1 \rightarrow D_{2\text{Location} + \text{colour}}$ trials.
- (iv) If the inhibition source was derived from the combination of location AND colour then SRTs should increase only on the $T_1 \rightarrow D_{2\text{Location} + \text{colour}}$ trials.

3.2. Results and discussion

The means and standard deviations of the SRTs to the new target ($display_2$) are shown in Table 2. A one-way within-subjects analysis of variance (ANOVA) revealed a significant main effect of distracter condition ($F(4, 48) = 19.73, p < 0.001$). Planned comparisons revealed a significant increase in the mean SRTs from 212 ms on $T_1 \rightarrow T_2$ trials, 211 ms on $T_1 \rightarrow N_2$ trials and 213 ms on $T_1 \rightarrow D_{2\text{Colour}}$ trials to 229 ms on the $T_1 \rightarrow D_{2\text{Location}}$ trials (all p 's < 0.008). This result replicated the findings of Experiment 1. SRTs were also significantly increased on the $T_1 \rightarrow D_{2\text{Location} + \text{colour}}$ trials (mean = 244 ms) in comparison to the $T_1 \rightarrow T_2$, $T_1 \rightarrow N_2$, and $T_1 \rightarrow D_{2\text{Colour}}$ trials (all p 's < 0.001). SRTs on $T_1 \rightarrow D_{2\text{Location} + \text{colour}}$ trials were also significantly longer than the $T_1 \rightarrow D_{2\text{Location}}$ trials. No other post hoc SRT analyses reached statistical significance.

The data provided support for hypothesis (i) above. An increase in SRTs was detected when a new target shared both the location and colour or just the location, of a recent distracter. When the new target shared only the colour of the recent distracter there was no detectable effect on SRTs. There was an additional delay on

the $T_1 \rightarrow D_{2\text{Location} + \text{colour}}$ trials, beyond the level of the $T_1 \rightarrow D_{2\text{Location}}$ trials. This suggests that there was increased inhibition when the new target shared both the location and colour of the previous distracter. In $T_1 \rightarrow D_{2\text{Location} + \text{colour}}$ trials the same colour was used for the target $display_1$ distracter and the $display_2$ target. Therefore, it is unlikely that the prolonged SRTs to the $display_2$ target can be explained by colour masking. These converging data revealed that the overlap in the encoding of the 'location' of the distracter and new target was necessary and sufficient for the observed increase in SRTs.

4. Experiment 3

Experiments 1 and 2 demonstrated that a visual target elicited slower SRTs when the target was presented at the location of a recent distracter. This implies that an internal representation of the distracter was maintained for a period and signalled its influence on a later eye movement. This representation appears to be in the form of a spatial signal, since it yielded a directionally selective effect on a saccadic eye movement.

Experiments 1 and 2 employed a single, fixed interval between target $display_1$ and target $display_2$ and so these experiments were unable to explore the temporal dimension of the IRD. The aim of Experiment 3 was to explore this temporal dimension. The IRD was traced across time by contrasting $T_1 \rightarrow T_2$ and $T_1 \rightarrow D_2$ trials. The experimental stimuli and eye movement recording were as described for Experiment 1.

4.1. Methods

All participants (5 males, 8 females, mean age = 24.4 years, range = 19–32, $SD = 4.4$) had normal or corrected visual acuity (assessed with the Snellen chart), and intact colour vision according to the Ishihara test (Ishihara, 1983).

Table 2
Mean saccade reaction times (SRT) and standard deviations (SD) (Experiment 2)

	Distracter condition				
	$T_1 \rightarrow T_2$	$T_1 \rightarrow N_2$	$T_1 \rightarrow D_{2\text{Location}}$	$T_1 \rightarrow D_{2\text{Colour}}$	$T_1 \rightarrow D_{2\text{Location} + \text{colour}}$
SRT (ms)	212	211	229*	213	244*
SD	22.86	21.55	23.19	28.59	27.01

$T_1 \rightarrow T_2$, target in $display_2$ was presented at the previous target location with identical colour; $T_1 \rightarrow N_2$, target in $display_2$ was presented at a new location that differed from the previous target and distracter location and colour; $T_1 \rightarrow D_{2\text{Location}}$, target in $display_2$ was presented at the location of the previous distracter; $T_1 \rightarrow D_{2\text{Colour}}$, target in $display_2$ presented at with the colour of the previous distracter; $T_1 \rightarrow D_{2\text{Location} + \text{colour}}$, target in $display_2$ was presented at with the colour and location of the previous distracter.

* $p < 0.05$, increased saccadic reaction times in comparison to the $T_1 \rightarrow T_2$, $T_1 \rightarrow N_2$ and $T_1 \rightarrow D_{2\text{Colour}}$ trials. Saccade reaction times on the $T_1 \rightarrow D_{2\text{Location}}$ and $T_1 \rightarrow D_{2\text{Location} + \text{colour}}$ trials did not differ significantly from each other.

A trial began with the onset of a white fixation LED at the centre of the display for a random period of 750–1000 ms (fixation *display*₁). The fixation LED was then switched off and immediately followed by a red target and a green distracter (target *display*₁), presented for 1500 ms. The target *Display*₁ was immediately removed and the fixation point was presented (fixation *display*₂) for 750–1000 ms. The fixation point was removed and a red target was presented for 1500 ms (target *display*₂). An interval of 1, 2, 5 or 10 s (equivalent to average SOAs of 2375, 3375, 6376, and 11375 ms) separated the offset of target *display*₁ and the onset of target *display*₂. When target *display*₂ was removed a blank interval of 3500 ms elapsed, before the next trial commenced. Forty-eight trials at each delay were presented in a block of trials, yielding a total of 192 trials per participant. Each block of trials consisted of equal proportion of T₁ → T₂ and T₁ → D₂ trials. The order of blocks was run in a fixed pseudo-random sequence of 24 trials. The T₁ → T₂ and T₁ → D₂ trials were identical to those of Experiment 1. Trials were presented in blocks for each display interval.

4.2. Results and discussion

Table 3 shows the mean SRT latencies. Across the participants there was a significant increase in SRTs with increasing delay ($F(3, 36) = 22.849$, $p < 0.001$); T₁ → D₂ trials generated longer SRTs than T₁ → T₂ trial ($F(1, 12) = 41.87$, $p < 0.001$). There was also a significant interaction of trial type and delay ($F(3, 36) = 7.64$, $p < 0.001$). There was a significant increase in mean SRTs of 20–25 ms on the T₁ → D₂ trials at the 1 s ($t(12) = -8.814$, $p < 0.001$) and the 2 s interval ($t(12) = -8.544$, $p < 0.001$). The IRD declined steeply and was not significant at the 5 s ($t(12) = -1.38$, ns) or the 10 s ($t(12) = 1.507$, ns) intervals.

Consistent with the pattern of Experiments 1 and 2 the IRD here showed a reliable effect for the inter-display delays of 1 and 2 s.

Table 3
Duration of the inhibitory effect of a recent distracter (IRD) (Experiment 3)

Delay (secs)	T ₁ → T ₂ (ms)	SD	T ₁ → D ₂ (ms)	SD	Diff
1	205	18.9	230	18.3	25*
2	210	20.5	231	24.7	21*
5	243	22.5	251	25.7	8
10	259	28.4	265	31.3	6

T₁ → T₂, target in *display*₂ was presented at the previous target location in *display*₁; T₁ → D₂, target in *display*₂ was presented at the location of the previous distracter in *display*₁.

* $p < 0.001$.

5. Experiment 4

These data demonstrated that a saccadic distracter yielded a signal that persisted for several seconds after the display was removed which slowed the generation of a saccadic eye movement to a new target. This response slowing was reminiscent of the negative priming effect that has been reported in studies of somatomotor reaction times (Tipper, 1985a, 2001). It has been suggested that distracter inhibition emerges in the context of selection between competing inputs (Houghton & Tipper, 1994). The competition generated in a selective attention environment provided the initial conditions for inhibition of an irrelevant stimulus feature. This idea that a competitive interaction was responsible for the distracter inhibition provides a clear and testable hypothesis. If the target and the distracter are both necessary, distracter inhibition should not be generated when the distracter is presented in isolation. The following experiment examined this hypothesis by removing the target from target *display*₁ and presenting only the distracter. The primary task was to initiate a saccadic eye movement in the opposite direction to the target *display*₁ stimulus (i.e., antisaccade), followed by a target-directed saccade to the target *display*₂. As in the previous experiments, *display*₂ presented a solitary target, but in this experiment a lone distracter (or anti-target) was presented in target *display*₁. According to a competitive interaction hypothesis, the IRD should be eliminated under these conditions¹.

5.1. Methods

All participants (8 males, 5 females, mean age = 24.3 years, $SD = 6.8$) had normal or corrected visual acuity (assessed with the Snellen chart), and intact colour vision according to the Ishihara test (Ishihara, 1983). The experiment began with 24 practice trials. The sequence of displays followed the format of Experiments 1–3. In fixation *display*₁ a white fixation point was presented at the centre of the display for a randomised time of 750–1000 ms. The fixation point was then switched off and immediately followed by a green distracter (i.e., anti target), that was presented for 1500 ms (target *display*₁). This ‘distracter’ was presented at one of four positions, $\pm 5^\circ$ in the horizontal or vertical planes (see Fig. 3). Participants were instructed to fixate quickly and accurately at the mirror-image projection of the target in the opposite hemifield. At this stage individuals would be expected to attend initially to the target, to estimate a saccadic eye movement in the required direction, and then inhibit

¹ Given that a saccade to the ‘target’ must be avoided the target can be regarded as ‘saccadic’ distracter in a limited sense, but in contrast to the previous experiments the ‘anti-target’ here is task relevant in that it is required to compute the direction and amplitude of the antisaccade.

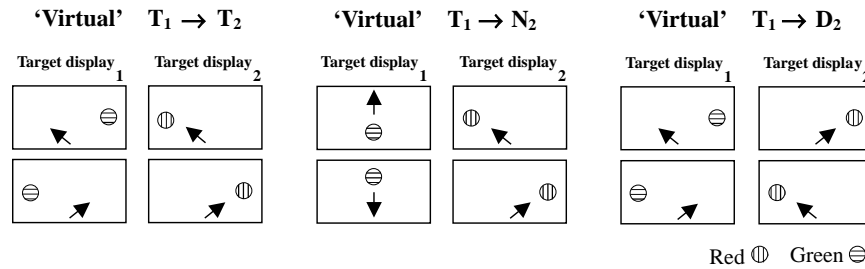


Fig. 3. The target–distracter conditions in Experiment 3. In each display a single stimulus was presented. Individuals were instructed to fixate the mirror-image location ('virtual' target), in the opposite direction to the green distracter. This was followed by a target-directed saccade to target $display_2$. The vertical striped pattern indicates a red target, the horizontal striped pattern indicates a green distracter.

the natural tendency to generate a prosaccade to the target². Target $display_1$ was removed and the fixation LED was illuminated for a randomised interval of 750–1000 ms (fixation $display_2$). Finally, a red (prosaccade) target (target $display_2$), was presented for 1500 ms. A block of trials consisted of 50% 'virtual' $T_1 \rightarrow D_2$ (this is equivalent to the target location of $T_1 \rightarrow T_2$ in Experiments 1–3), 25% 'virtual' $T_1 \rightarrow T_2$ and 25% 'virtual' $T_1 \rightarrow N_2$. The sequence of blocks was run in a fixed pseudo-random sequence of 24 trials. Five blocks of 24 trials at each delay were presented, yielding a total of 120 trials for each participant.

5.2. Results and discussion

The mean SRTs of the saccadic eye movements are shown in Table 4. There was no reliable effect of the distracter trials on SRT ($F(2, 24) = 0.832$, $p = 0.447$ ns). The IRD that was observed in Experiments 1–3 was not detected for a lone distracter. The inhibitory and volitional operations that are responsible for the generation of an antisaccade do not appear to be responsible for the distracter effect here. Ironically, a single distracter, in the absence of a target, is not sufficient to generate distracter inhibition. These results provide support for the idea that inhibition of a previous distracter emerges from selective competition between the parallel operations on the target and the distracter.

6. Experiment 5

Experiments 1–3 demonstrated that saccadic eye movements were inhibited at the location of a previous distracter, in comparison to a target that was presented at a new location or the previous location of the target. Importantly, this inhibition was restricted to the location of the distracter. Attention research has demon-

Table 4

Mean saccadic reaction times (SRT) and standard deviations (SD) in Experiment 4

	'Virtual' $T_1 \rightarrow T_2$	'Virtual' $T_1 \rightarrow N_2$	'Virtual' $T_1 \rightarrow D_2$
SRT (ms)	224	229	226
SD	27.8	31.8	22.5

'Virtual' $T_1 \rightarrow T_2$, target in $display_2$ was presented at the virtual target location i.e., mirror-image of real target in $display_1$; 'Virtual' $T_1 \rightarrow N_2$, target in $display_2$ was presented at a new location that differed from the target or distracter in $display_1$; 'Virtual' $T_1 \rightarrow D_2$, target in $display_2$ was presented at the location of the previous distracter (i.e., the anti-target) in $display_2$.

strated that visual detection is more efficient, shortly after an attentional cue is presented at the cued location (Posner, 1980). However, at later cue intervals the speed of detection at the cued location is slower than a non-cued location (Posner & Cohen, 1985). This is known as 'inhibition-of-return' (IoR) (Posner, Rafal, Choate, & Vaughan, 1985). By inhibiting visual orienting to a location that has already received attention, the system develops a bias to favour a new, unexplored region of visual space (Klein, 2000; Maylor & Hockey, 1985a, 1985b). IoR has been shown to last up to 2.7 s (Klein, 2000), and generates inhibition at several locations simultaneously (Snyder & Kingstone, 2000). Rafal, Calabresi, Brennan, and Sciolto (1989) argued strongly in favour of an oculomotor source of IoR, but there is intense debate on the underlying mechanisms (Abrams & Dobkin, 1994; Hunt & Kingstone, 2003; Khatoun, Briand, & Sereno, 2002; Taylor & Klein, 2000).

The absence of IoR in the present experiments was intriguing and appeared to conflict with recent work (Theeuwes & Godijn, 2004). Theeuwes and Godijn (2004) used an oculomotor capture task to investigate saccadic eye movements towards a previous distracter or target. The initial display consisted of six grey squares and was presented for 1000 ms. One of the squares then changed to green (the target), and a second square changed to white (the distracter). When 600 ms had elapsed the distracter and target squares returned to their initial grey colour. After 700 ms a green target square and white distracter square were presented in a second display. The target

² A failure of this inhibitory system has been reported in many clinical and non-clinical studies (Broerse, Crawford, & den Boer, 2001).

could appear at the location of the previous target, previous distracter or a new location. Saccade latencies increased when the target was presented at the location of the previous distracter and at the location of the previous target. This suggested that inhibition was generated at both the target and the distracter. These results differ from the current findings in that we observed no inhibition on the $T \rightarrow T$ trials. However, there were important differences between the two studies that could account for this discrepancy. The Theeuwes and Godijn study presented a distracter together with a target in both displays. Christie and Klein (2001) demonstrated that a distracter in the second display can have a substantial effect on the pattern of inhibition. Perhaps more importantly the inter-display intervals of the two studies differed substantially. The Theeuwes and Godijn study used an SOA that was much shorter than that used in the current Experiments 1 and 2. It was possible that the IoR was undetectable in the current experiments given the longer SOAs. Therefore, in this experiment we re-visited the IRD using an SOA that was identical to that used by Theeuwes and Godijn (2004).

6.1. Methods

The 13 participants who volunteered for Experiments 1 and 2 were employed in Experiments 5 and 6. The experiment began with 24 practice trials. The sequence of displays followed the format of Experiment 1, with one critical change. In the current experiment the target $display_1$ was presented for 600 ms, the fixation $display_1$ for 700 ms, and the target $display_2$ for 600 ms. Thus, as in the Theeuwes and Godijn (2004) study, the SOA from the two critical displays was 1300 ms. All the target-displays were identical to Experiment 1.

6.2. Results and discussion

A one-way ANOVA revealed a significant main effect across trial type ($F(1, 12) = 21.2, p = 0.001$). Post hoc pair-wise comparisons revealed a significant increase in SRT in both the $T_1 \rightarrow T_2$ (mean = 232 ms, $SD = 34, p < 0.05$) and $T_1 \rightarrow D_2$ (243 ms, $SD = 31.2, p < 0.001$) trials, in comparison to $T_1 \rightarrow N_2$ trials (221 ms, $SD = 31.7$). The $T_1 \rightarrow T_2$ and $T_1 \rightarrow D_2$ did not differ significantly from each other ($p = 0.145$). It is worth noting that the same participants had failed to show IoR in Experiments 1 and 2. These results provide support for the idea the IoR and IRD emerge relatively early, but IRD persist for a longer duration following the termination of the display.

7. Experiment 6

Klein (Christie & Klein, 2001; Klein, 2000), demonstrated that IoR may operate differently in the presence

of a distracter, at least in the somatomotor system. Therefore, it was important to determine, whether the 'lifespan' of IoR could be extended by removing the distracter. In Experiment 6, we returned to the long SOAs of Experiments 1 and 2, and removed the distracters. The aim was to determine whether IoR would emerge when the distracter is absent from the recent display.

7.1. Methods

The 13 participants who participated in experiments 1, 2, and 5 took part in this study. The target $display_1$ configurations were randomly selected from one of the six $T_1 \rightarrow T_2$ and six $T_1 \rightarrow N_2$ displays in Fig. 1B, except the distracter was removed from the displays. Therefore, in contrast to previous experiments no distracter trials were presented. The pairings of target $display_1$ and target $display_2$ generated only two types of trials; (1) on the $T_1 \rightarrow T_2$ trials the $display_2$ target was presented at the location that was previously occupied by the target in $display_1$. (2) On the $T_1 \rightarrow N_2$ trials the $display_2$ target appeared at a new location, not previously occupied. The experiment consisted of 120 mixed, randomised trials, 50% consisted of $T_1 \rightarrow T_2$ and 50% were $T_1 \rightarrow N_2$ trials. The temporal sequence and duration of the target displays was identical to Experiments 1 and 2. Although Experiment 6 is reported here as the final experiment, it was conducted first to avoid carry-over effect from the distracter experiments.

7.2. Results and discussion

A one-way ANOVA revealed that there was a significant increase ($F(1, 12) = 21.25, p = 0.001$) in SRT on $T_1 \rightarrow T_2$ trials (233 ms, $SD = 25.2$), in comparison to $T_1 \rightarrow N_2$ trials (216 ms, $SD = 27.9$). The removal of the distracter increased the lifespan of IoR, to produce inhibition with the inter-display intervals of Experiments 1 and 2.

8. General discussion

A series of observations have emerged on the IRD: (1) a saccadic eye movement to a new target was inhibited when it was presented at the location of the previous distracter; (2) the effect was contingent on the location, rather than the colour of the distracter; (3) the effect declined over time (approximately 2–5 s); (4) saccadic eye movements were not inhibited on Target \rightarrow Distracter trials in the antisaccade task, when the distracter was presented in isolation. (5) Inhibition at the location of the recent target also emerged with a short inter-display interval and when the distracter was removed from the recent display. These findings suggest that a spatial

signal of the distracter was encoded and stored for 1–2 s, in a form that can restrain a saccadic eye movement.

It is interesting to note that participants were completely unaware of the inhibitory effects of the distracter, and greeted the disclosure of the phenomenon, during the debriefing sessions, with surprise. In view of the subtleness of the slowing (i.e., 20–25 ms) this may not be surprising. From the viewpoint of the participant the distracter was irrelevant to the task, so there was no incentive to evaluate its impact. The relatively long intervals between the target displays may also have disguised the relationship of the two key displays. These results are consistent with the idea that the sustained inhibition of a distracter contributed to the target selection process for a saccadic eye movement. We have demonstrated that this inhibition is more dependent on the location, than the colour of the distracter. Tipper et al. (2001) argued that the effect of the local inhibition was to distort the encoding of the neural population of the movement vector, resulting in a movement that deviated away from the distracter. It is our view is that the inhibition generated by a previous distracter may be explained by a similar inhibitory process.

8.1. Motor facilitation/inhibition?

In the current studies a centrifugal saccade to target $display_2$ was always preceded by a centripetal saccade to the fixation LED, therefore it is important to consider whether the inhibitory effect of a recent distracter could be explained in terms of motor facilitation or inhibition. Dorris, Taylor, Klein, and Munoz (1999) examined changes in SRT in the monkey. In one condition a sequence of saccades were triggered to a double target step, where the second target step was presented either in the same, the opposite or an orthogonal direction. Each target step was followed by a return saccade to a central fixation point. SRTs to the second target step were slowed when the saccade was preceded by a return movement to fixation. The authors proposed that the delay was generated by inhibition from the termination of activity of the first saccade. This puzzling phenomenon in the monkey appeared to contradict the gap effect reported in Carpenter (2001). Can the monkey data account for the effects of a recent distracter? If the monkey data is analogous to the recent distracter effect, we would expect the SRT of the second of two saccades in the same direction to be slowed, irrespective of the distracter trial. The $T_1 \rightarrow D_{2\text{Colour}}$ condition in Experiment 2 provided a critical test of this hypothesis. Saccadic eye movements in this condition followed the same sequence as the $T_1 \rightarrow D_{2\text{Location}}$ and the $T_1 \rightarrow D_{2\text{Location} + \text{colour}}$ trials, where a centrifugal saccade to the distracter was preceded by a centripetal saccade to the fixation point. Yet, SRTs were slowed on the $T_1 \rightarrow D_{2\text{Location}}$ and the $T_1 \rightarrow D_{2\text{Location} + \text{colour}}$

trials, but not on the $T_1 \rightarrow D_{2\text{Colour}}$ trials. This observation is consistent with the hypothesis that the IRD was derived from a location and not a colour signal. The pattern of data from Experiment 2 suggests the monkey phenomenon does not provide a parsimonious explanation of the IRD.

8.2. Relation to ‘inhibition-of-return’

Does the effect of a recent distracter reported in this study, conflict with the phenomenon of ‘inhibition-of-return’? The absence of ‘inhibition-of-return’ was at first glance, puzzling. However, there were important distinguishing features of the current experiments that may explain its absence. In contrast to ‘inhibition-of-return,’ which describes a response that is slowed at a previously attended location, in the current paradigm SRTs were slowed at the ‘unattended’ location of the distracter. Also, a target was presented simultaneously with a distracter in $display_1$, in contrast to the typical ‘inhibition-of-return’ paradigms where the inclusion of a distracter is unusual (but see Lupianez & Milliken, 1999; Milliken, Tipper, Houghton, & Lupianez, 2000). However, Milliken et al. (2000) obtained evidence of ‘inhibition-of-return’ in the context of a selective attention task, though they did not explore the temporal factors of effect to determine when it emerged. In addition the 1–10 s delay intervals used in the current experiments, was relatively long in comparison the majority of studies of visual attention. Finally, recent data (Lupianez & Milliken, 1999) highlighted some boundary conditions of ‘inhibition-of-return.’ They examined ‘inhibition-of-return’ effects on manual reaction times in a task where they varied the probability that a target would appear with a distracter. When the distracter was never presented ‘inhibition-of-return’ developed relatively late (700 ms stimulus onset asynchrony, SOA). Surprisingly, when a distracter was presented on every trial, ‘inhibition-of-return’ developed relatively early, but was short lived. ‘Inhibition-of-return’ was evident at 700 ms, but undetectable at the 1000 ms SOA. According to Klein (2000), the short duration of the inhibition may be explained by the effects of a distracter on attentional capture. In the absence of a distracter, the probability of attentional capture by the target was high, but the probability of removal of attention from the cue (i.e., the critical process for inhibition-of-return) was relatively low. Therefore, one would expect ‘inhibition-of-return’ to be delayed in this situation. Conversely, when the probability of a competing distracter was high, attention would be more easily removed from the cued location and ‘inhibition-of-return’ would be detected earlier.

Furthermore in an exhaustive analysis of target–distracter combinations Christie and Klein (2001) revealed critical conditions in which inhibition-of-return was absent. In particular inhibition-of-return was *not* obtained

on $T_1 \rightarrow T_2$ trials when a target was presented together with a distracter in the prime display (i.e., *display*₁), followed by a single target in the probe display (i.e., *display*₂). In this condition only inhibition of the distracter was observed. These were the precise conditions under which inhibition-of-return was undetected in the current experiments. Indeed, Taylor and Klein (2000) state... ‘a close examination reveals that IoR is revealed in cue-target paradigms that present a target without any distracter and/or that require participants to indicate whether the discrimination target appeared to the left or right... Although there are exceptions (e.g., (Kingstone & Pratt, 1999)) it appears that IoR is less robust when a target is presented together with a distracter.’ The general implication is that ‘inhibition-of-return’ had a shorter life span when a distracter was present. This early development and removal of ‘inhibition-of-return’ when there is a distracter competing for attention may explain its absence in Experiments 1 and 2. These ideas were supported by the emergence of inhibition-of-return when a shorter SOA was introduced (Experiment 5) and when the distracter was removed (Experiment 6). A relatively weak inhibition-of-return has also been reported using the anti-saccade task (Khatoon et al., 2002; Rafal, Egly, & Rhodes, 1994), however, these studies have used much shorter SOAs than used in Experiment 4.

8.3. Distracter inhibition

Early signs of competitive interactions came from the reported increase in SRTs when a target was displayed in one hemifield and the distracter in the opposite hemifield (Lévy-Schoen, 1969). More recent studies (Walker, Deubel, Schneider, & Findlay, 1997) revealed that the increased SRTs were obtained for a remote distracter that was displayed in either hemifield, with respect to the target. It was argued that a remote distracter activated a ‘fixate’ signal which competed with a ‘move’ signal in a retinotopic spatial map (Findlay & Walker, 1999). Closely spaced units shared overlapping receptive fields, leading to saccade averaging. More distant neuronal pools responded to non-overlapping stimuli and generated lateral inhibition leading to longer SRTs (Findlay & Walker, 1999; Godijn & Theeuwes, 2002; Schall & Hanes, 1993). These studies on the effects of a distracter provided support for the inference of competitive interactions in target selection. Recently, (Godijn & Theeuwes, 2002) obtained further support for the remote distracter effect (Walker et al., 1997) and averaging saccades (Findlay, 1982) a result which favoured a competitive interaction model and undermined the ‘race model.’ However, no account was taken of the differential effects on the spatial and temporal parameters of the saccadic eye movements. A number of other views of visual orienting also feature a competitive interaction between

the target and a distracter (e.g., Duncan, Humphreys, & Ward, 1997; Trappenberg et al., 2001). Evidence of mutually inhibitory connections in the superior colliculus was recognized at a relatively early stage in the history of oculomotor neurophysiology research (Rizzolatti, Carnada, Grupp, & Pisa, 1974; Wurtz, Richmond, & Judge, 1980). More recently, the principle of lateral inhibition within the superior colliculus and the inhibitory projections from cortical centres was also used to account for the remote distracter effect (Trappenberg et al., 2001). The model assumes that the distracter reduced the activation of build-up neurons within the superior colliculus causing inhibition of the saccadic eye movement. An impressive range of saccadic phenomena were accurately simulated by the model³.

Recent data from an fMRI study was consistent with the concept of distracter inhibition (Saenz, Buracas, & Boynton, 2002). In one experiment observers were presented with an overlapping field of red and green spots on one side of the central fixation point and asked to make a threshold judgement in a luminance detection task. Observers were required to attend to this array and to ignore a single field of red or green dots on the opposite side. The magnitude of the fMRI signal to the ignored stimulus was predicted by the congruence of the ‘ignored’ stimulus and the ‘attended’ stimulus. Importantly, the fMRI signal was *reduced, relative to baseline state*, when the stimulus for attention was incongruent with the ignored stimulus. The distracter appeared to be generating inhibition in accordance with distracter inhibition.

8.4. Neural mechanisms

The inhibition of a saccadic distracter provides an example of a wider principle of visual processing. Desimone and Duncan (1995) drew attention to the problem of feature selection in relation to the large size of the receptive fields in extrastriate cortex, where retinal information is coarsely coded. Similarly, saccadic activity is widely distributed across the superior colliculus (Munoz & Wurtz, 1995). Many of these cells have broadly tuned receptive fields that are active in response to stimulation across a large region of the visual field causing ambiguity in the processing of a saccade. Neural substrates of selective attention appear to improve actions directed towards a stimulus by generating a bias to attended targets and the inhibition of irrelevant distracters. Neurophysiological recordings have located single neurons that are active in response to an attended target property and suppressed to a distracter (Chelazzi, Miller, Duncan, & Desimone, 1993; Iba & Sawaguchi, 2002; Schall

³ Presumably, there is also a reciprocal inhibitory process that generates lateral inhibition of the distracter, to explain how the target is normally selected over the distracter.

& Hanes, 1993). Chelazzi et al. (1993), recorded activity in inferotemporal cortex during a match-to-sample task. A population of neurons showed the usual activation in response to a preferred target in the receptive field. Importantly, a population of neighbouring cells reduced their firing before a saccadic eye movement to a non-preferred stimulus. Remarkably, different populations of neurons displayed target-related or distracter-related activity for the duration of the delay period (up to 3000 ms), when the display was removed and the animal was required to maintain the image in working memory.

Converging neurophysiological data suggests that target selection may involve a network of cortical and subcortical areas. The prefrontal cortex is distinguished by a network of cell populations that may play an important role selective attention. One group of cells in dorsolateral prefrontal cortex (DLPFC) displayed spatially selective activity in the distinct phases of an eye movement memory task. A subset of prefrontal cells were also identified with a spatially selective *suppression* of neural activity during the memory period Glimcher and colleagues (Funahashi, 1991; Funahashi, Bruce, & Goldman-Rakic, 1989, 1990). Some neurons were characterised by an opponent memory field and displayed inhibition to a target of the opponent spatial polarity (Funahashi et al., 1989). Finally, topographically organized memory cells that are involved in the selection of a specific target from a background of distracters have been recently identified in prefrontal cortex (Iba & Sawaguchi, 2002).

Selection-related activity has been recorded in the frontal eye fields (FEF) (Glimcher, 2001; Schall, 1995; Schall & Hanes, 1993), inferior temporal cortex (Chelazzi et al., 1993) and the superior colliculus (SC) (Basso & Wurtz, 1997; Glimcher & Sparks, 1992). Glimcher and colleagues (Glimcher, 2001; Glimcher & Sparks, 1992) located a group of neurons in the superior colliculus which fired in relation to the selection of a target, up to 7 s before the movement. Several lines of evidence suggest that the interplay of excitation and inhibition in the SC may be regulated via descending projections from higher cortical centers. Schlag-Rey, Schlag, and Dassonville (1992) reported that the electrical stimulation of FEF that triggered a population of saccades, generated excitation in a region of the SC which coded the same population of saccades. Conversely, neurons in the SC which coded other saccadic vectors were inhibited by FEF. This network may help to insulate a saccadic programme from distracters in the environment.

9. Conclusions

The converging data from these experiments revealed evidence of inhibition of a saccadic eye movement at the location of a recent distracter. These data

are consistent with an inhibitory effect that was derived from the location of the distracter. The absence of inhibition when a distracter was presented in isolation supported the view that the inhibitory effect was contingent on the competitive interaction between the target and the distracter. Inhibition lasted for at least 1–2 s, but the detailed timing of the onset and duration requires further research. Visuomotor centres apparently have access to the spatial memory of a distracter which can inhibit an eye movement to that location. Our results are consistent with a process of competitive interaction in the selection of a target for a saccade. This mechanism would enhance the target-to-distracter noise ratio and may help to explain the high precision of saccadic eye movements.

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