

Inhibition-of-return and oculomotor interference

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Abstract

The present study shows that inhibition-of-return reduces competition for selection within the oculomotor system. We examined the effect of a distractor when it was presented at an inhibited location (IOR). The results show that due to IOR distractors cause less interference. This was evident in all three measures. First, there was less oculomotor capture when a distractor was presented at an inhibited location. Second, the saccade latency to the target was shorter when a distractor appeared at an inhibited location than when it appeared at a non-inhibited location. Third, there was less curvature towards the distractor when it was presented at inhibited location relative to a non-inhibited location. The observation that there is less interference for a distractor presented at an inhibited location suggests that IOR reduces the exogenous activation of the distractor within the saccade map.

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1. Introduction

Everyday environments are relatively cluttered and may contain many objects that could serve as potential targets for saccadic eye movements. In order to make an accurate eye movement to an object located in such a cluttered environment it is crucial to select the location of the target object and suppress other (competing) locations that may contain distracting stimuli. In everyday life when making saccadic eye movements we tend to look at stimuli relevant for the task at hand. For example, when searching for one of our lost kids at the daycare center, we try to remember what the child was wearing that day so that the color of the sweater may guide our saccadic search process. We try to fixate those objects in the visual environment that match our internal top-down goal, e.g., the color of the sweater. We try to avoid fixating objects that are irrelevant for our task.

Typically, saccadic selection is quite accurate. We are able to direct our eyes at will to those objects in the environment that are relevant for our everyday life. However, in some conditions saccadic selection becomes very inaccurate and our eyes move against our intentions to a location that is opposite to where we tried to

move them in the first place. In the recently developed oculomotor capture paradigm (Theeuwes, Kramer, Hahn, & Irwin, 1998; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999) these striking conditions were demonstrated for the first time. In this task, observers are required to make a voluntary, goal-directed saccade to a uniquely colored element in the display. In half of the trials, simultaneously with the presentation of the target, a new object presented with an abrupt onset appears somewhere in the display. Observers know that the visual onset is never relevant for the task. The results demonstrate that the intended goal-directed eye movement towards the uniquely colored element was disrupted by the appearance of the visual onset. In about 30–40% of the trials the eyes went to the irrelevant onset before they went to the uniquely colored target. This phenomenon is referred to as *oculomotor capture* (Theeuwes et al., 1998, 1999), articulating conditions in which the eyes move exogenously to an event or an object. The oculomotor capture paradigm demonstrated that a goal-directed saccade towards a uniquely colored target could be disrupted by the appearance of the onset distractor. In trials in which the eyes moved to the onset, the eye often landed for a very short period of time (25–100 ms) near the onset before the eyes moved on the target. The observation that a distractor may capture our eyes and forces our eyes to move to a particular location is a dramatic demonstration of a distractor interference effect.

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Note that in those 60–70% of the trials in which the eyes were not captured by the distractor (but moved directly to the target) another distractor interference effect was found. Relative to a condition in which no distractor was present, saccade latencies were increased indicating that it took longer to initiate a saccade to the target when a distractor was present (see e.g. Godijn & Theeuwes, 2002a). Also, in those trials, the presence of a distractor had an effect on the saccade trajectory. When making a saccade to the target in some conditions, the eyes curved towards to location of the distractor (Godijn & Theeuwes, 2002a, 2002b; McPeck & Keller, 2001; McPeck, Skavenski, & Nakayama, 2000), while in other conditions the eyes curved away from the distractor location (Doyle & Walker, 2001; Godijn & Theeuwes, 2002a, 2002b; Rizzolatti, Riggio, Dascola, & Umiltà, 1987).

In sum, a distractor may cause three related interference effects: the distractor may capture the eyes, the distractor may increase saccade latencies to the target and the distractor may cause curved saccade trajectories either towards or away from the distractor location.

The described interference effects caused by the onset distractor can be explained by the recently developed competitive integration model of saccade programming of Godijn and Theeuwes (2002a; see also Findlay & Walker, 1999; Kopeck, 1995; Trappenberg, Dorris, Munoz, & Klein, 2001 for similar models). This model assumes that saccade programming occurs on a common saccade map with a retinotopic representation. Thus, saccade programming to a location in space implies saccade-related activation at the corresponding location within the saccade map. A lateral inhibition structure exists within the saccade map, so that when activation rises at a particular location within the saccade map, there is inhibition at distant locations. According to the competitive integration model, a saccade is executed when a certain activation threshold is reached at a location in the saccade map. Furthermore, it is assumed that the eyes move in the direction of the mean vector of activity.

The model can explain the above mentioned interference effects. First, a distractor may capture the eyes when the activation at the location of the onset distractor reaches threshold. Second, the distractor causes an increase in saccade latency because of the lateral inhibition structure. There is activation at the target location and at the distractor location and the lateral inhibition between the locations slows the speed at which the threshold can be reached. Third, the effect of the distractor on the saccade trajectory is due to inhibition that acts directly on the activation at a specific location (e.g. Tipper, Howard, & Paul, 2001). This additional location-specific inhibition resolves the conflict when two distant locations are strongly activated and biases saccade programming toward desired locations.

The reasons for finding either curvature towards or away from the distractor lies in the amount of inhibition that is or can be applied to the location of the distractor. When inhibition is not complete and the distractor location is still more active than other areas in the visual field the eyes will curve toward the location of the distractor; when inhibition is complete and the distractor location is less active than other areas in the visual field, saccades curve away from the distractor location. When a saccade is required to a specific target the degree to which a distractor interferes presumably depends on the strength of activation at the distractor location (e.g. Godijn & Theeuwes, submitted for publication; Tipper et al., 2001). Thus, if the activation level at the distractor location is inhibited less interference is expected on saccade programming to the target.

One well-documented effect in the literature that has been associated with inhibitory control is inhibition-of-return (IOR; Posner & Cohen, 1984). In a typical IOR study a cue, such as a task-irrelevant luminance increment is presented in the periphery and after a varying stimulus-onset-asynchrony (SOA) a target is presented at the cued location or at an uncued location. IOR is observed when response times (manual or oculomotor) are longer when the target is presented at the cued location than when it is presented at an uncued location.

A number of studies have shown that saccades are inhibited from moving toward previously fixated locations (e.g. Abrams & Dobkin, 1994; Klein & MacInnes, 1999). It is generally agreed that the function of IOR is to bias orienting away from already inspected locations, so that visual search becomes much more efficient (see Klein, 2000). IOR places inhibitory tags on objects that recently have been inspected (either by overt or covert orienting) so that these locations no longer compete for selection and subsequent search is directed to novel objects only. Note that it takes time for this inhibitory tagging to build up and IOR is typically observed when a target is presented at least 300 ms after presentation of the irrelevant cue (see e.g. Klein, 2000). According to Klein and colleagues (e.g. Klein, 2000; Taylor & Klein, 1998; see also Rafal, Calabresi, Brennan, & Sciolto, 1989) IOR occurs at locations that have been activated within the oculomotor system.

The goal of the present study is to examine how inhibition (IOR) affects the interference from distractors on saccade programming. Typically IOR is examined by comparing responses to targets presented at inhibited locations with responses to targets presented at uninhibited locations. Presumably, the inhibition should also affect the way in which distractors compete within the oculomotor system. In line with the function of IOR as a foraging mechanism we assume that inhibition at a specific location affects the oculomotor system in such a way that distractors presented at inhibited locations compete less for selection within the oculomotor system

than distractors presented at novel-non-inhibited locations. As described above oculomotor interference from distractors is related to three measures (1) oculomotor capture, (2) saccade trajectory deviations, (3) saccadic latencies. If presenting a distractor at a previously inhibited location causes less interference within the oculomotor system than a distractor at a non-inhibited location one expects (1) less oculomotor capture from the distractor presented at the inhibited location, (2) a reduction in saccadic trajectory deviations toward the distractor, and (3) a reduced saccadic latency.

2. Method

2.1. Participants

Ten students were paid for their participation and reported having normal or corrected-to-normal vision. They were not familiar with the purpose of the experiment.

2.2. Apparatus

A Pentium II computer with a 21 in. color monitor controlled the timing of the events and generated stimuli. Eye movements were recorded by means of an Eyelink tracker with a 250 Hz temporal resolution and a 0.2° spatial resolution. The Eyelink tracker uses an infra-red video-based tracking technology to compute the pupil center of both eyes. An eye movement was considered a saccade when the velocity exceeded 35°/s or the acceleration exceeded 9500°/s². When participants were fixating the central fixation point at the start of each trial they pressed a key, which caused a recalibration of participants' gaze point on the central fixation point. After this the trial started. Each participant was tested in a dimly lit room. They held their head on a chinrest, located 75 cm away from the monitor.

2.3. Stimuli, procedure and design

At the start of each trial participants viewed displays containing six gray squares (1.0° of visual angle; luminance 2.2 cd/m²) around a central fixation cross at an eccentricity of 8°. Two squares were located directly above and below the central fixation cross and the four other squares were located at the corner positions of an imaginary square around the fixation cross. After one second the first saccade target and distractor appeared at two of the four corner positions. The saccade target was a green luminance increment (11.3 cd/m²) and the distractor was a white luminance increment (55.5 cd/m²). After 600 ms the colors at the first target and distractor locations were reset to gray. Another 700 ms later the second target (green luminance increment) and

distractor (white luminance increment) were presented. The second distractor appeared at one of the four corner positions and the second target appeared at one of the six positions. Only the second target could be presented at either of the vertical locations, since these locations were exclusively used to examine the effect of distractors on trajectory deviations of saccades to the target. After 600 ms the colors at the second target and distractor locations were reset to gray. Participants were instructed to execute a saccade to the first and second target as quickly and accurately as possible and after each saccade to return the eyes from the target back to central fixation. See Fig. 1 for an illustration of the display sequence. After a practice block of 20 trials participants performed four blocks of 240 trials. The locations of the first and second target and distractor were randomized within blocks.

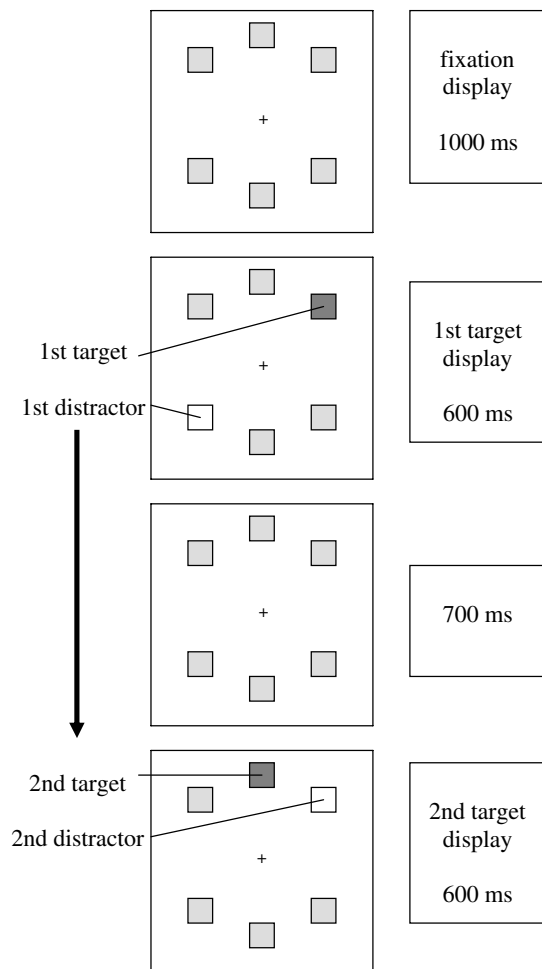


Fig. 1. Example of the display sequence. After the fixation display a target and a distractor are presented for 700 ms. Observers have to make a saccade to the target and return back to the middle fixation point. Another 1300 ms later a new target and distractor is presented. Again observers have to make a saccade to the target location.

3. Results

3.1. Discarded data

A total of 19.6% of trials was discarded because of eye movement errors (trials on which one of the targets was not fixated and trials with saccade latencies shorter than 120 ms or longer than 600 ms). Since cues were always presented at corner locations, latencies of saccades to cued locations were always compared to saccades directed to uncued corner locations. In other words, for the calculation of latencies vertical saccades were discarded.

3.2. Inhibition-of-return

Latencies of saccades to the second target were longer when the second target was presented at the location of the first target (mean 220 ms) than when the second target was presented at a new location (mean 197 ms), $t(9) = 6.46$, $p < 0.001$. Latencies of saccades to the second target were also longer when the second target was presented at the location of the first distractor (mean 216 ms) than when it was presented at a new location, $t(9) = 10.00$, $p < 0.001$. Thus, IOR was found at the location of the first target and at the location of the first distractor. These locations can therefore be considered inhibited locations.

3.3. Distractors at inhibited locations

Now that we have established that the target and distractor locations (of the first display) are inhibited we examined the effect of distractors (in the second display) on oculomotor programming when the distractors were presented at inhibited locations.

To examine the effect of distractors at inhibited locations we analyzed those trials on which the target was presented at a location (one of the four corner locations) that did not contain a target or distractor in the first display, whereas the distractor in the second display was (old location) or was not (new location) presented at a location that contained a target or distractor in the first display.

3.4. Oculomotor capture

When distractors in the second display were presented at a new location (a location that did not contain a target or distractor in the first display) the eyes went to the distractor on 3.4% of the trials. The percentage of oculomotor captures was less when the distractor was presented at a location that had contained a target in the first display (1.0%), $t(9) = 3.42$, $p < 0.01$, or when the distractor was presented at a location than had con-

tained a distractor in the first display (0.5%), $t(9) = 5.63$, $p < 0.001$.

3.5. Latencies of saccades to the target

When distractors in the second display were presented at a new location, the mean saccade latency to the target was 200 ms. Saccade latencies to the target were shorter when the distractor in the second display was presented at a location that had contained a target in the first display (mean 196 ms), $t(9) = 2.37$, $p < 0.05$, or when the distractor was presented at a location that had contained a distractor in the first display (195 ms), $t(9) = 3.54$, $p < 0.01$.

3.6. Trajectories of saccades to the target

In order to examine the effect of distractors on the trajectories of saccades to the target we examined those trials on which the target was presented at the top or bottom location and the distractor was presented left or right (45° angular deviation) of the target location.¹ For each 4 ms sample point of the saccade the directional angle deviation (in degrees of arc) was calculated relative to a straight line from the start point of the saccade to the saccade target. The angular deviation was then averaged across the whole saccade. Since the effect of distractors on saccade trajectories depends on saccade latency (e.g. Godijn & Theeuwes, 2002a) trials of each condition were split into four quartiles based on saccade latency. Finally, to obtain a measure reflecting the effect of distractors on saccade trajectories for each condition the mean angular deviation of the left-distractor condition was subtracted from the mean angular deviation of the right-distractor condition. Positive values reflect saccade trajectory deviations toward the distractor, negative deviations reflect saccade trajectory deviations away from the distractor. The mean trajectory deviations (distractor on the right–distractor on the left) of each condition are shown as a function of saccade latency quartile in Fig. 2. An ANOVA on saccade trajectory deviations with distractor condition (distractor at old target location, distractor at old distractor location, distractor at new location) and saccade latency quartile revealed a main effect of distractor condition, $F(2, 18) = 9.81$, $p < 0.001$. As can be seen in Fig. 2 there was a stronger deviation toward the distractor when the distractor was presented at a new location than when it was presented at an old location. There was also a main effect of quartile, $F(3, 27) = 16.39$, $p < 0.001$. Generally, short latency saccades deviated toward the distractor

¹ We used these trials, because previous research has shown that the effect of distractors on saccade trajectories is best demonstrated when the distractor is relatively close to the target (e.g. Godijn & Theeuwes, 2002a; also see Sheliga, Riggio, & Rizzolatti, 1994, 1995).

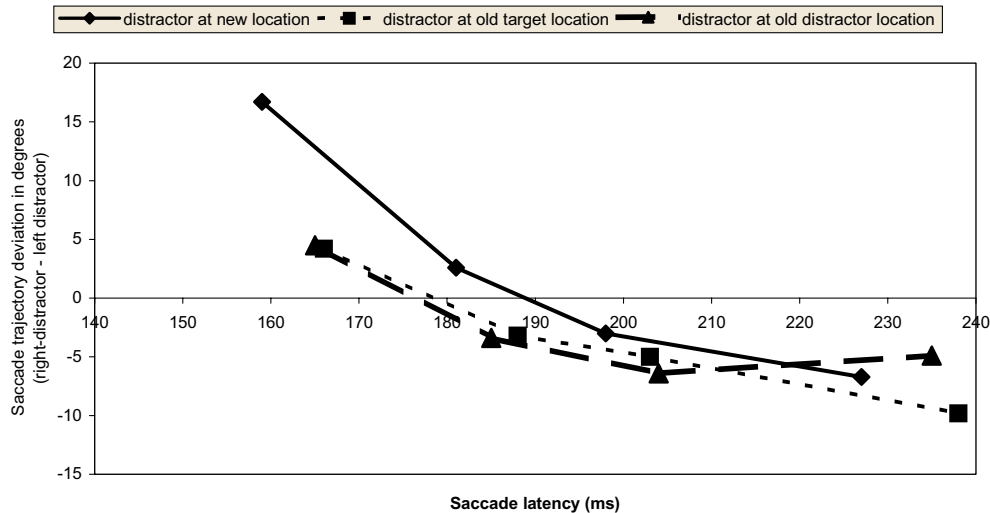


Fig. 2. Mean saccade directional angle deviations (distractor on the right–distractor on the left) in degrees of arc of saccades to the target (presented in the second display) as a function of distractor condition and saccade latency quartile. Positive values reflect deviations toward the distractor; negative values reflect deviation away from the distractor.

whereas long latency saccades deviated away from the distractor. Finally, an interaction was found between distractor condition and quartile, $F(6, 54) = 4.72$, $p < 0.001$. The difference in saccade trajectory deviation between the condition with a distractor at a new location and the conditions with a distractor at an old location (target or distractor) was greatest for short latency saccades and was reduced as saccade latency increased.

4. General discussion

We established IOR for locations that previously contained a target or a distractor. Specifically, distractors presented at these inhibited locations produced less interference than distractors at new locations. This was evident for all three measures. First, there was less oculomotor capture when a distractor was presented at an inhibited location. Second, the saccade latency to the target was slowed less when a distractor appeared at an inhibited location than when it appeared at a non-inhibited location. Third, there was less curvature towards the distractor when it was presented at inhibited location relative to a new location.

The function of IOR is to bias orienting away from already inspected locations. This inspection can occur either covertly by attention or overtly by eye movements (see Klein, 2000). The present experiment shows that the strength of IOR does not depend on whether orienting is overt or covert (see also Godijn & Theeuwes, 2002b). There was an IOR effect for the location to which a saccade was executed of 23 ms (first saccade location). There was a similar IOR effect of 19 ms for the location at which a distractor was presented.

It is generally agreed that IOR places inhibitory tags on locations or objects that recently have been inspected. The purpose of this inhibition is that these locations no longer compete for selection, so that orienting is biased towards new locations. The present study demonstrates that IOR indeed reduces competition for selection: irrelevant distractors compete less when presented at inhibited locations than when presented at non-inhibited locations.

Godijn and Theeuwes (2002a) recently developed a model to explain eye movement behavior in conditions in which there is a target that needs to be fixated and a distractor that needs to be ignored. In this competitive integration model, there is competition between the activity generated at the target and distractor location. It is assumed that saccade-related activity is integrated in a common saccade map. Activity at one location spreads to neighboring locations (see Fig. 3C), but inhibits distant locations (see Fig. 3B). This architecture is consistent with other models of saccade programming (e.g. Findlay & Walker, 1999; Kopecz, 1995; Trappenberg, Dorris, Munoz, & Klein, 2001). According to this model a saccade is executed when a certain activation threshold is reached at a location in the saccade map. Furthermore the model assumes that the mean vector of activity in the saccade map determines the displacement of the eyes. However, when other locations are activated when the threshold is reached saccade trajectory deviations from this threshold location may occur. When two nearby locations are strongly activated at the time a threshold is reached at either location (or at an intermediate location; see Fig. 3C) the saccade will typically land somewhere between the two locations (cf. so called ‘global effect’ or ‘center of gravity effect’). However, when two distant locations are active there is also lateral inhibition

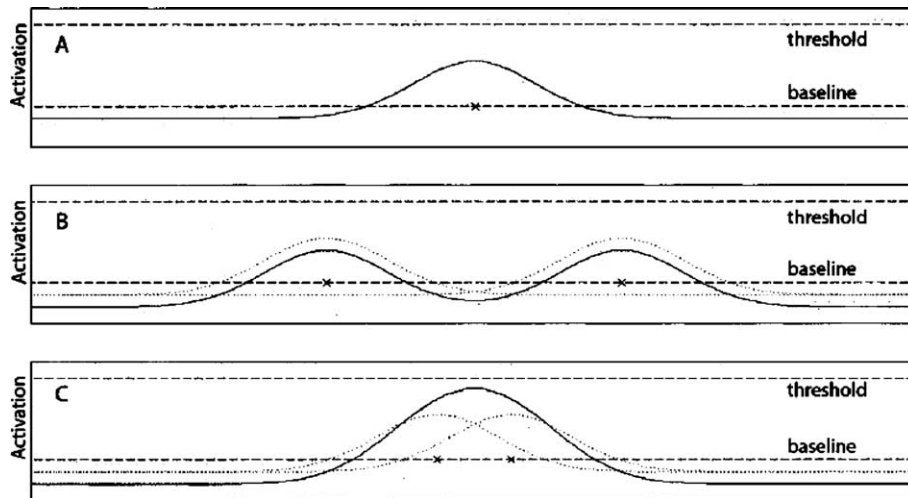


Fig. 3. Hypothetical activation pattern in the saccade map based on the competitive integration model of Godijn and Theeuwes (2002a). (A) When a saccade is programmed to a location in the visual field, there is activation in the saccade map. This activation spreads out to neighboring locations, but inhibits distant locations. (B) When two locations are simultaneously activated, activation related to both goals (the broken lines) is combined (continuous line) and when the two locations are relatively far apart activation is mutually inhibitory. (C) When two locations are close together, the combined activation may result in a high activation peak somewhere between the two locations (from Godijn & Theeuwes, 2002a).

between the locations, slowing the speed at which the threshold can be reached. This lateral inhibition causes saccade latencies to the target location to increase. Therefore, before the threshold can be reached at one of the locations more activation is required at one of the locations. Also, due to the lateral inhibition from the threshold location the activation at the other location will be diminished. In this case no global effect will occur. In addition to lateral inhibition within the saccade map an additional inhibitory mechanism is assumed that acts directly on the activation at a specific location (e.g. Tipper et al., 2001). This additional location-specific inhibition resolves the conflict when two distant locations are strongly activated and biases saccade programming toward the desired location. This inhibition of the distractor location explains that on trials in which the eyes directly go to the target, they never move on to the distractor. When inhibition is not complete the eyes will curve toward the location of the stimulus (see McPeck & Keller, 2001; McPeck et al., 2000). When inhibition is complete and the distractor location is less active than other areas in the visual field, saccades curve away from the distractor location (also see Doyle & Walker, 2001; Sheliga et al., 1994, 1995).

On the basis of this model, Godijn and Theeuwes (submitted for publication) developed a framework for understanding inhibitory control of saccades. The framework consists of three subsystems: a pre-oculomotor attentional map, a saccade map and an inhibitory control system (see Fig. 4). Within the saccade map (most likely in the superior colliculus) the final stage of saccade programming takes place (see Schall, 1991 for a

review). Activity within the saccade map will generate activity in the inhibitory control system (most likely dorsolateral pre-frontal cortex and/or frontal eye fields). Activity in the inhibitory control system generates an inhibitory tag within the pre-oculomotor attentional map (most likely the lateral intraparietal area). The

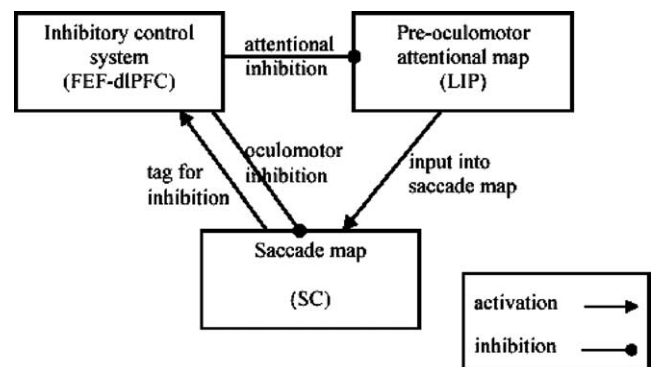


Fig. 4. A framework for understanding inhibitory control of saccades (from Godijn & Theeuwes, submitted for publication). The framework consists of a network of three subsystems that are involved in inhibitory control of saccades, a pre-oculomotor attentional map, a saccade map and an inhibitory control system. When a stimulus is presented activation flows through the pre-oculomotor map to the saccade map. Activation in the saccade map generates an inhibitory tag in the inhibitory control system. This tag is passed on to the pre-oculomotor attentional map. Inhibition in the pre-oculomotor attentional map reduces the input into the saccade map at the location at which the original stimulus was presented. This delays the execution of the saccade (IOR). It is speculated that the inhibitory control system is represented by the frontal eye fields (FEF) and/or the dorsolateral pre-frontal cortex (dIPFC), that the pre-oculomotor attentional map is represented by the lateral intraparietal area (LIP) and the saccade map is represented by the superior colliculus (SC).

current data fit well within this framework. When a distractor is presented in the periphery, it typically captures attention in an exogenous way (see e.g. Theeuwes, 1991; Yantis & Jonides, 1984). This so-called “capture of attention” implies that there is exogenous activation within the pre-oculomotor attentional map. This in turn generates oculomotor activation within the saccade map corresponding to the location in space where the stimulus is presented. However, as long as no eye movements have to be made and the observer remains fixated, this oculomotor activation within the saccade map has no consequences other than that it generates an inhibitory tag corresponding to the location of activation within the saccade map. We claim that any oculomotor activation will result in an inhibitory tag (see e.g. Klein, 2000; Rafal et al., 1989). This inhibitory tag is delivered to the inhibitory control system. By inhibiting the pre-oculomotor attentional map, the inhibitory control system inhibits (subsequent) activation at the location at which the distractor was presented. This mechanism of inhibitory control is what is typically referred to as IOR: after attention is reflexively shifted to the location of the initially presented stimulus, responding to stimuli subsequently displayed at the location is delayed.

In the current study at the moment a distractor is presented observers make a saccade to the target location. In order to make an endogenous saccade to the target location, within the saccade map, oculomotor activity has to be generated at the location of the target. As soon as there is oculomotor activation, an inhibitory tag is delivered to the inhibitory control system, which inhibits (subsequent) activation at the target location. Again, this will result in IOR but now at the target location. As noted by Rafal et al. (1989) not only exogenous capture of attention results in IOR (in the current study with our distractor) also the endogenous execution of a saccade or even the endogenous preparation of a saccade will result in activation within the saccade map and, as a consequence, in IOR.

In our study we examined the effect of a distractor on the second saccade when this distractor was presented at these inhibited locations i.e., the distractor location and the previous target location. Given the model described above, due to IOR less activation from the (second) distractor flows to the saccade map. Because IOR reduces the input in the saccade map, there is less distraction in all three measures, i.e., oculomotor capture, saccade latency and saccade curvature. The observation that there is less distraction for a distractor presented at an inhibited location suggests that IOR reduces the exogenous activation of the distractor within the saccade map. Indeed, due to a reduced activation in the saccade map, there are fewer trials in which the activation reached threshold to generate a saccade (less oculomotor capture), there is less lateral inhibition from the

distractor (therefore a smaller effect on saccade latencies) and the mean vector of activity is shifted less toward the distractor location, and therefore the saccade trajectory deviations toward the distractor are reduced.

The explanation in terms of reduced input into the saccade map fits well with some recent evidence by Dorris, Klein, Everling, and Munoz (2002). In this study neural activity of SC cells was recorded, while monkeys performed an IOR task, requiring a saccade to a peripheral target. During the interval between cue and target neural activity at the cued location was higher than at the uncued location. Thus, there was no evidence for active inhibition of neural activity during the cue-target interval within the SC (the saccade map). However, when the target appeared the target-related burst of activity of SC cells was greater when the target was presented at an uncued location than at a cued location. Therefore, the inhibition resulting in IOR was not caused by active inhibition of SC cells, but by reduced input into the SC.

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