

Programming of Endogenous and Exogenous Saccades: Evidence for a Competitive Integration Model

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Participants were required to make a saccade to a uniquely colored target while ignoring the presentation of an onset distractor. The results provide evidence for a competitive integration model of saccade programming that assumes endogenous and exogenous saccades are programmed in a common saccade map. The model incorporates a lateral interaction structure in which saccade-related activation at a specific location spreads to neighboring locations but inhibits distant locations. In addition, there is top-down, location-specific inhibition of locations to which the saccade should not go. The time course of exogenous and endogenous activation in the saccade map can explain a variety of eye movement data, including endpoints, latencies, and trajectories of saccades and the well-known global effect.

A key issue in oculomotor research is the degree to which saccades are controlled by the properties of the visual environment or by the goals and intentions of the observer. Saccades made on the basis of goals of the observer are called *endogenous* (top-down control or goal directed), and saccades made on the basis of stimulus properties, irrespective of the goals of the observer, are called *exogenous* (bottom-up control or stimulus driven).

Previous studies have shown that when participants have to execute an endogenous saccade toward a specific target object, the eyes are often captured exogenously by the abrupt onset of a new object even though participants know that the onset is always task irrelevant. For example, Theeuwes, Kramer, Hahn, Irwin, and Zelinsky (1999; also see Theeuwes, Kramer, Hahn, & Irwin, 1998; Irwin, Colcombe, Kramer, & Hahn, 2000) presented participants with displays containing six gray circles spaced equally around an imaginary circle. Centered within each circle was a small figure-eight premask. After 1 s, all of the circles except one changed into red, and the premasks changed into small letters by removing some of their line segments. On half the trials, an additional irrelevant red circle (an abrupt onset) was added to the display simultaneously with the color change of the distractors. Participants were required to move their eyes to the uniquely colored gray circle and to determine whether the letter inside it was a *C* or a reversed *C*. A saccade to the target letter was required because its size was so small that it needed to be foveated to be identified. The results showed that, even though the onset distractor was never relevant for the task, the eyes initially went toward the onset distractor in about one third of the trials. Furthermore, the fixation duration on the onset distractor prior to the subsequent saccade to the target

was less than 150 ms on 90% of those trials. Theeuwes et al. (1998, 1999) concluded that these fixation durations were too brief to allow the programming of a new saccade. According to Theeuwes et al., the results suggested the parallel programming of two saccades: an exogenous saccade toward the onset distractor and an endogenous saccade to the target. They further suggested that the two saccade programs ran to completion in an undisturbed fashion. In other words, the programming of one saccade was not affected by the programming of another. The program that was completed first was executed first. We call this model the *independent horse-race model* to emphasize its two distinguishing features: The two saccade programs are independent of one another, and the destination of the first saccade depends on which program is completed first. According to the independent horse-race model, there are separate systems responsible for the programming of endogenous and exogenous saccades (e.g., Kramer, Irwin, Theeuwes, & Hahn, 1999). The suggestion of separate systems for endogenous and exogenous saccades was motivated by evidence of separate pathways in the brain for the programming of saccades (e.g., Schiller, 1985; Schiller & Sandell, 1983), a posterior pathway projecting to the superior colliculus (SC) and an anterior pathway involving the frontal eye fields (FEF). Theeuwes et al. (1998, 1999) suggested that exogenous saccades might be programmed in the posterior pathway and endogenous saccades in the anterior pathway.

As an alternative to the independent horse-race model, we propose a *competitive integration model*, which assumes that the control signals for exogenous and endogenous saccades converge on a common saccade map. Similar to a number of previous models (e.g., Findlay & Walker, 1999; Kopecz, 1995; Trappenberg, Dorris, Munoz, & Klein, 2001), according to the competitive integration model, saccade programming occurs on a common saccade map with a retinotopic representation, in which information from different sources (e.g., endogenous and exogenous) is integrated. Figure 1 illustrates the basic idea of the competitive integration model. Saccade-related activation at one location spreads to neighboring locations but inhibits distant locations (Figure 1A). Thus, saccade programming is a competition between activation at locations represented in the saccade map. When two relatively distant locations are activated, this activation is mutually

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We thank Robin Walker and two anonymous reviewers for their excellent comments on a draft of this article.

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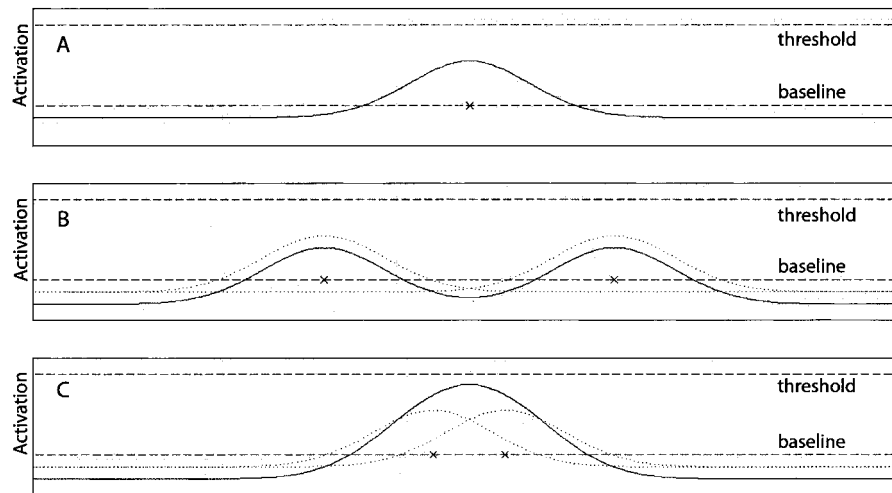


Figure 1. Activation patterns in the saccade map. A: When a saccade is programmed to a certain location x in the saccade map, representing a location in the visual field, the activation spreads out to neighboring locations but inhibits distant locations. B: When two saccades are programmed in parallel, activation related to both locations (dotted lines) is combined (continuous line), and when the two locations are relatively far apart, activation is mutually inhibitory. C: On the other hand, when two locations are relatively close together, the combined activation may result in a high activation peak somewhere between the two locations. Note that although the visual field is represented unidimensionally in this illustration (as a simplification), it is assumed that the saccade map holds a two-dimensional representation of the visual field.

inhibitory (Figure 1B), but when two nearby locations are activated, the combined activation results in a relatively high peak somewhere between the two locations (Figure 1C). In accordance with Trappenberg et al. (2001), the execution of a saccade is triggered when the activation at a specific location in the saccade map reaches threshold. Trappenberg et al. (2001) developed a neural-field model based on the principle of competitive integration of exogenous and endogenous signals in the SC. Their model produced activity patterns very similar to activity patterns of cells in the SC. Furthermore, the saccade latencies of the model fit well with a range of oculomotor effects, such as the remote distractor effect. The remote distractor effect (e.g., Walker, Deubel, Schneider, & Findlay, 1997) refers to the finding that saccade latencies are longer when a target is presented simultaneously with a distractor but only when the distance between target and onset is relatively large. Furthermore, when the distractor is presented near the target, the eyes often land in between target and distractor (global effect or center-of-gravity effect; e.g., Coren & Hoenig, 1972; Findlay, 1982). These findings are consistent with the lateral inhibition structure of the competitive integration model. However, it is important to note that the global effect and the remote distractor effect found in these studies (e.g., Walker et al., 1997) cannot be taken as evidence against the independent horse-race model because the target, which was presented with an abrupt onset, presumably generated both endogenous and exogenous activation. Therefore, in these studies, saccades to the onset target cannot be considered completely endogenous.

The model of Trappenberg et al. (2001) assumes that exogenous saccade-related input in the saccade map has a relatively brief duration. Once the exogenous activation no longer increases, it can be suppressed by lateral inhibition within the saccade map. In addition to this lateral inhibition, an additional inhibition mecha-

nism, which acts directly on the exogenous activation evoked by a distractor, has been proposed on the basis of analyses of saccade trajectories (e.g., Tipper, Howard, & Houghton, 2000; Tipper, Howard, & Paul, 2001). A number of studies have shown that when a saccade is executed to a target and a distractor stimulus is successfully ignored, the trajectory of the saccade to the target is curved away from the distractor (e.g., Doyle & Walker, 2001; Sheliga, Riggio, & Rizzolatti, 1994; Sheliga, Riggio, & Rizzolatti, 1995; Tipper et al., 2000, 2001). According to Tipper et al. (e.g., 2000, 2001), the initial direction of the saccade is based on the mean vector of activity in the saccade map (e.g., Sparks, Lee, & Rohrer, 1990) and the location-specific inhibition of the distractor location causes a sub-baseline level of activation at this location. This results in a mean vector of activity which is shifted away from the distractor location, and therefore, the saccade trajectory is curved away from the distractor. This location-specific inhibition would facilitate the programming of a saccade to the target and thereby avoid oculomotor capture by objects that evoke exogenous, saccade-related activity.

In the present study, we tested the predictions from the independent horse-race model and the competitive integration model using a modified version of the oculomotor capture paradigm (e.g., Irwin et al., 2000; Theeuwes et al., 1998, 1999). Six equidistant red circles were presented on an imaginary circle around a central fixation point. After 600 ms, one of the circles turned gray, and participants were required to saccade to this uniquely colored target circle. On some trials, an irrelevant new circle (the onset distractor) appeared simultaneously with the target color change. In contrast to Theeuwes et al. (1998, 1999), no letters were presented in the circles, and no manual response was required. Another modification to the original oculomotor capture paradigm was that the target was defined by a (equiluminant) color change,

whereas in Theeuwes et al. (1998, 1999) the no-onset distractors changed color and the target did not.¹ This paradigm was used because it allowed a detailed examination of endogenous and exogenous saccade programming. Irwin et al. (2000) showed that color singletons, which resulted from an isoluminant color change, did not elicit saccades when they were used as distractors, but abrupt onsets did. Therefore saccades to the color singleton target can be considered endogenous, and saccades to the onset distractor, which is completely task irrelevant, can be considered exogenous. It is important to note that one can only speak of genuine exogenous saccades when participants are instructed to execute a saccade to a specific location while the eyes move to the onset despite this instruction (see Godijn & Theeuwes, 2001).

In the present study, we also examined the extent to which a spatial representation of the target was developed on the basis of visual information obtained prior to the execution of a saccade to the onset distractor. If a spatial representation of the target was based on visual information obtained prior to the execution of the saccade to the onset distractor, the target representation could have been used to program the subsequent saccade without requiring a new target search during fixation on the onset distractor. If a spatiotopic representation of the target was created, the appropriate location in the saccade map would be activated, despite the intervening execution of a saccade to the onset distractor. To examine this issue, we used a target-switch method in which, on some trials, the location of the target was switched with the location of a no-onset distractor during the saccade to the onset distractor. If a spatial representation of the target was used to program the second saccade without requiring a new search during fixation on the onset distractor, it was expected that the eyes would move on to the old target location. Otherwise, it was expected that the eyes would move on to the new target location.

Experiment 1

The main goal of Experiment 1 was to test the predictions of the independent horse-race model and the competitive integration model. First, the independent horse-race model predicted that the latency of the first saccade would be independent of the separation between target and onset distractor because the programming of the exogenous saccade to the onset distractor and the endogenous saccade to the color singleton target are assumed to be independent. On the other hand, the competitive integration model predicted that because of the lateral inhibition structure of the saccade map (see Figure 1), saccade latency would be shorter when target and onset distractor were close together (i.e., angular separation of 30°) than when they were far apart (i.e., angular separation of 90° or 150°). Second, according to the independent horse-race model, the time to program an endogenous saccade to the target should not be affected by the simultaneous programming of an exogenous saccade to the onset distractor (and vice versa). Furthermore, programming of both saccades should proceed until one of the programs is completed and subsequently executed. Therefore, long latency, initial saccades to the target were expected to be less frequent on onset trials (trials on which an onset distractor was presented) than on no-onset trials (trials on which no onset distractor was presented) because in cases in which it took relatively long to complete the programming of a saccade to the target, one would expect the saccade program to the onset distractor to be

completed first. On average, the latency of initial saccades to the target should therefore be longer on no-onset trials than on onset trials because of a relatively low frequency of long latency, initial saccades to the target on onset trials. On the other hand, according to the competitive integration model, the programming of an endogenous saccade is affected by the simultaneous programming of an exogenous saccade. That is, saccade programs are mutually inhibitory, resulting in a longer latency of the initial saccade. Therefore, it was expected that the latency of initial saccades to the target would be longer on onset trials, in which two saccades were programmed simultaneously, than on no-onset trials, in which there was no mutual inhibition between saccade programs.

A further goal of Experiment 1 was to examine in detail eye-movement measures such as the trajectory, amplitude, and end-point of saccades as well as the fixation duration between saccades to develop a better understanding of the interaction between endogenous and exogenous control of saccades.

Method

Participants. A total of 8 students of the Vrije Universiteit served as paid volunteers. All reported having normal or corrected-to-normal vision.

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 infrared, video-based tracking technology to compute the pupil center of both eyes. An eye movement was considered a saccade when the velocity exceeded 35 degrees/s or the acceleration exceeded 9,500 degrees/s². When participants were fixating the central fixation point at the start of each trial, they pressed a key, which caused a recalibration of the participant's gaze point on the central fixation point. After this, the trial started. Each participant was tested in a dimly lit room. Participants held their head on a chin rest that was located 75 cm away from the monitor.

Stimuli. At the start of each trial, participants viewed displays containing six equidistant red circles (1.3° of visual angle in diameter), positioned on an imaginary circle with a radius of 9.6° around a central fixation point (0.4°). After 600 ms, one of the circles turned gray, signaling the location to which a saccade had to be made (the target). The target was presented at a clock position of 1, 5, 7, or 11. On half the trials, simultaneously with the target color change, an additional red distractor appeared with an abrupt onset on the imaginary circle at a clock position of 2, 4, 8, or 10. This resulted in an angular separation between target and onset distractor of 30°, 90°, or 150°. All objects were removed after 1,200 ms, after which the central fixation point reappeared for the next trial. The colors of the circles—red and gray—were made equiluminant (14.2 cd/m²), and the circles appeared on a black background. See Figure 2 for an example of the stimulus display.

Procedure and design. There were two types of trials: onset trials, on which an additional distractor was added to the display simultaneously with the color change of the target, and no-onset trials, on which no additional distractor was presented. Participants performed a single session

¹ Changing the color of the target instead of the no-onset distractors may appear to make the endogenous–exogenous distinction between target and onset distractor less strong compared with the original oculomotor paradigm. However, Irwin et al. (2000) provided evidence that transient color changes do not elicit exogenous saccades. Furthermore, in a previous study (Godijn & Theeuwes, in press), we also changed the color of the target instead of the no-onset distractors and found remarkably similar results as Theeuwes et al. (1998, 1999).

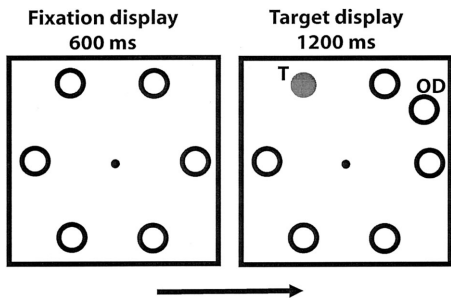


Figure 2. Example of the display sequence in Experiment 1. Participants viewed displays containing six equidistant red circles (represented by open circles) on an imaginary circle around a central fixation point. After 600 ms, one of the circles turned gray, signaling the location to which a saccade had to be made (the target). Simultaneous with the transient target color change, an additional red onset distractor, presented with an abrupt onset, appeared somewhere along the imaginary circle on half the trials. Participants were instructed to make an eye movement toward the uniquely colored gray circle as quickly as possible. T = target; OD = onset distractor.

consisting of four blocks of 300 trials, half of which were onset trials and half of which were no-onset trials.

Results

Discarded data. Trials on which the initial saccade latency was below 80 ms (1.7% of trials) or above 600 ms (0.1% of trials) were discarded from further analyses.

Initial saccade destination and latency. The initial saccade was assigned to a particular object if the endpoint of the initial

saccade had an angular deviation of less than 30° (i.e., half the distance between objects) from the center of the object on the imaginary circle around the central fixation point. However, when the angular separation between target and onset was 30°, this criterion made it impossible to discriminate saccades to the target from saccades to the onset distractor. These trials were therefore analyzed separately. On the no-onset trials, 97.2% of the initial saccades were directed to the target, and 2.8% went elsewhere. On the onset trials (90° or 150° of angular separation), 65.5% of the initial saccades were directed to the target, 28.5% were directed to the onset, and 6.0% went elsewhere. On the onset trials, initial saccades had shorter latencies when they were directed to the onset distractor ($M = 161$ ms) than when they were directed to the target ($M = 223$ ms), $t(7) = 11.67, p < .01$. Furthermore, initial saccades to the target had shorter latencies on no-onset trials ($M = 206$ ms) than on onset trials ($M = 223$ ms), $t(7) = 2.94, p < .02$.

Saccade latency distributions. To examine the effect of the onset distractor on saccade latencies, we calculated individual cumulative distribution functions of the initial saccade latency, irrespective of saccade destination for each separation between target and onset distractor as well as for no-onset trials for each observer. These were averaged using the vincentizing procedure (Ratcliff, 1979; see Figure 3). A within-subjects analysis of variance (ANOVA) with separation condition (30°, 90°, and 150°) and bin as factors revealed a main effect of separation condition, $F(2, 14) = 20.96, p < .01$. As can be seen in Figure 3, saccade latency was shorter in the 30° separation condition ($M = 194$ ms) than in the 90° ($M = 211$ ms) and 150° ($M = 212$ ms) separation conditions. Furthermore, an interaction between separation condition and bin was found, $F(18, 126) = 1.77, p < .04$. In the first bin, no difference in saccade latency was found between the separation

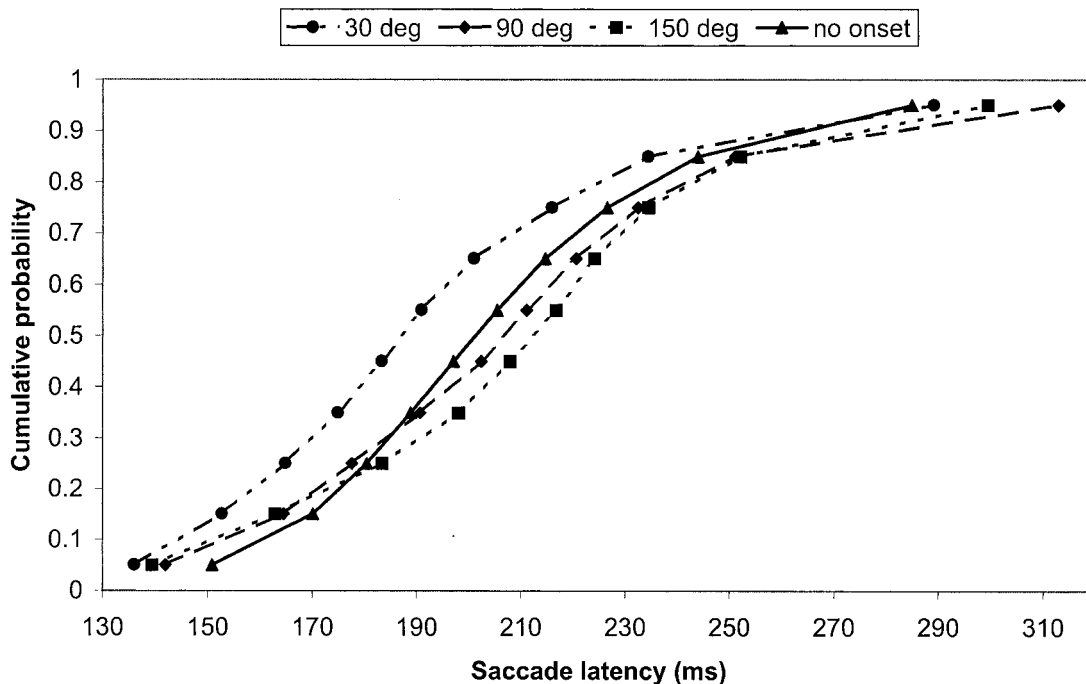


Figure 3. Cumulative distribution functions of the latency of the first saccade irrespective of saccade destination. deg = degrees.

conditions, $F(2, 14) = 2.71, p > .10$, but at the second bin, there was an effect of separation condition on saccade latency, $F(2, 14) = 10.03, p < .01$. This difference increased up to latencies of around 200 ms and then remained more or less constant.

Separate ANOVAs were performed to compare the saccade latency distribution of the no-onset condition with each of the three separation conditions. Saccade latencies were shorter in the 30° condition than in the no-onset condition, $F(1, 7) = 8.52, p < .02$, but there was no interaction between the distributions of these two conditions, $F(9, 63) = 1.03, p > .40$. There was no difference in saccade latency between the no-onset condition and the 90° separation condition, $F(1, 7) < 1$, but there was an interaction between the distributions of these conditions, $F(9, 63) = 3.28, p < .01$. Figure 3 shows that at the first bin, saccade latencies were shorter in the 90° separation condition than in the no-onset condition, but this difference reverses for longer saccade latencies. There is no difference in mean saccade latency between the no-onset condition and the 150° condition, $F(1, 7) = 1.19, p > .30$, and the interaction between the distributions of the no-onset condition and the 150° separation condition did not reach significance, $F(9, 63) = 1.59, p > .10$. However, the absence of a significant interaction between the no-onset condition and the 150° condition was probably due to a large standard error at the final bin. Without this bin, the interference did reach significance, $F(8, 56) = 3.63, p < .01$.

Saccade endpoints in the 30° separation condition. To examine whether a global effect (e.g., Findlay, 1982) was present, we examined the distribution of saccade endpoints in the 30° separation condition. The proportion of saccades to five adjacent areas with a width of 15° on the imaginary circle around the fixation point was examined. The five areas represented (a) the area adjacent to the target, (b) the target area, (c) the area intermediate between the target and the onset distractor, (d) the onset distractor area, and (e) the area adjacent to the onset distractor. Furthermore, to examine the time course, we split the trials into four quartiles based on saccade latency. Figure 4 shows the proportion of initial saccades landing in the five respective areas for the four quartiles. A within-subjects ANOVA was conducted with quartile and landing area as main factors. A main effect of landing area was found, $F(4, 28) = 12.25, p < .01$. As can be seen in Figure 4, the target area was the most frequent saccade destination, and a large number of saccades also landed in the intermediate area. An interaction between landing area and quartile, $F(12, 84) = 12.21, p < .01$, indicated that the distribution of saccade endpoints changed as a function of saccade latency. In the first quartile (i.e., the fastest saccades), a large number of saccades were directed to the onset distractor area, but the intermediate area was the most frequent saccade destination. This global effect was still present at the second quartile but disappeared in the third and fourth quartiles, in which the distribution of saccade endpoints was centered around the target area.

Trajectories of saccades to the target. To examine the trajectories of saccades to the target, we calculated the angular deviation of the saccade path relative to the required saccade path from fixation to the target for each 4-ms sample point of the saccade.² Positive and negative angular deviations were assigned in such a manner that an onset distractor located 90° away from the target within the same hemifield was always at -90°, an onset distractor located 90° away from the target within the opposite hemifield was

always at 90°, and an onset located 150° away from the target was always at 150° (see Figure 5 for examples). Two types of saccades that ultimately ended near the target were identified: (a) redirected saccades (e.g., Corneil, Hing, Bautista, & Munoz, 1999; McPeck & Keller, 2001; Minken, Van Opstal, & Van Gisbergen, 1993), which were initially directed toward a distractor object but turned around in midflight toward the target and (b) regular saccades, which were not redirected (see Figure 5). To distinguish between these two types of saccades, we calculated the angular deviation relative to the saccade path from fixation to the target for the fourth sample of the saccade (i.e., 16 ms after saccade initiation).³ Saccades that had an initial angular deviation of more than half the distance between objects (i.e., more than 30° of angular deviation) were considered redirected saccades. On onset trials, around 5%–13% of the saccades that ended near the target had an initial angular deviation of more than 30° in the direction of the onset distractor (see Table 1). Note that on approximately 1%–3% of the trials, the initial angular deviation was more than 30° in the opposite direction of the onset. Although these saccades were classified as redirected saccades, the possibility could not be excluded that some of these saccades were regular saccades with an extreme curvature. In fact, previous research has shown that oblique saccades can be strongly curved (e.g., Smit, Van Opstal, & Van Gisbergen 1990), and, therefore, some overlap in curvature between regular saccades and redirected saccades may be expected. To examine the saccade trajectories of regular saccades to the target (saccades that were not redirected in midflight), we averaged the angular deviation across all sample points of each saccade with an initial angular deviation of less than 30°. Table 1 shows the median of the averaged angular deviation for each condition.⁴ A within-subjects ANOVA revealed a significant effect of onset distractor location on the median angular deviation, $F(2, 14) = 25.99, p < .01$. There was a significant angular deviation in the direction opposite the location of the onset distractor for each of the three onset distractor locations (see Table 1 and Figure 5).

Saccade amplitude and fixation duration. On no-onset trials, saccades to the target had a mean amplitude of 9.5° (an undershoot relative to the target location of just 0.1°). On onset trials, the amplitude of saccades to the target was larger (mean amplitude = 9.1°; mean undershoot = 0.5°) than saccades to the onset distractor (mean amplitude = 7.9°; mean undershoot = 1.7°), $t(7) = 11.67, p < .01$. On these trials, approximately 40% of the initial saccades to the onset distractor and 18% of the initial saccades to the target had an undershoot of more than 2°. Furthermore, short amplitude

² An alternative way to examine saccade trajectories is to calculate the deviation of the saccade path relative to a straight line from fixation to the saccade endpoint (e.g., Doyle & Walker, 2001). However, this is not a measure of deviation but of saccade curvature.

³ To distinguish between redirected and regular saccades, we used the fourth sample instead of the first few samples because at the start of the eye movement, the angular deviation is typically relatively large, even for regular saccades and especially for oblique saccades (e.g., Smit, Van Opstal, & Van Gisbergen, 1990).

⁴ We analyzed the median instead of the mean because with the criterion of 30° angular deviation at the fourth sample, it was still possible that some redirected saccades were included, which would have had an extreme effect on the mean. The median suffers less from such extreme cases.

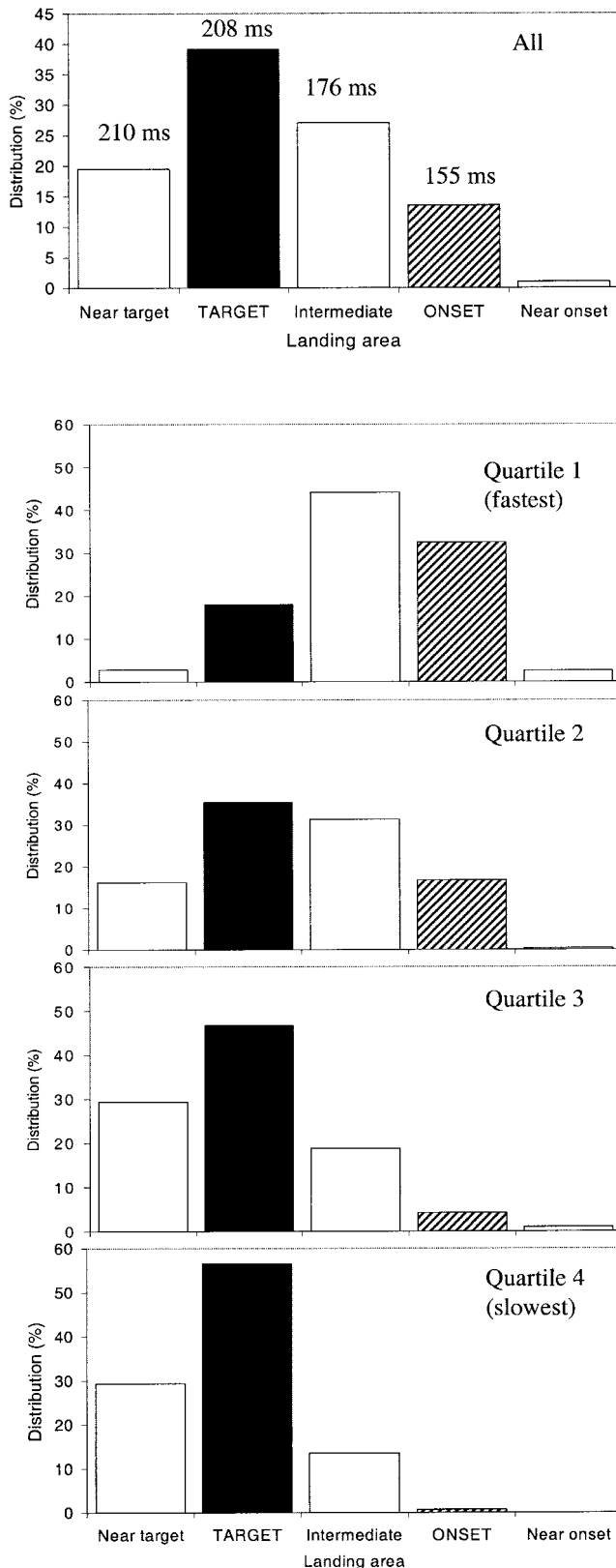


Figure 4. Distribution of saccade endpoints around the target and onset distractor in the 30° separation condition as a function of saccade latency quartile.

saccades to the onset distractor (i.e., undershoot of at least 2°) were followed by shorter fixation durations ($M = 84.2$ ms) prior to the saccade to the target than long amplitude saccades (i.e., undershoot of less than 2°) to the onset ($M = 100.7$ ms), $t(7) = 3.00$, $p < .02$.

Discussion

The results of Experiment 1 showed that latencies of saccades to the target were longer when an onset distractor was present than when it was absent and that saccade latencies were longer when the target and onset distractor were relatively far apart (90° or 150° separation) than when they were relatively close together (30° separation). Moreover, in the 30° separation condition, a high proportion of saccades, particularly short latency saccades, landed somewhere between the target and onset distractor (global effect). All these results provide support for the competitive integration model and are inconsistent with the independent horse-race model.

In addition to these results, we found an effect of the onset distractor on saccades to the target. That is, the trajectories of saccades to the target were deviated in the contralateral direction relative to the onset distractor. This deviation of saccade trajectory has been interpreted as a result of suppression of the to-be-ignored stimulus (i.e., the onset distractor). According to Tipper and colleagues (e.g., Tipper et al., 2000, 2001), suppression of the saccade-related activity of the onset distractor results in a sub-baseline level of activation at this location, causing the mean vector of activity to shift away from the distractor location. If the direction of the saccade is determined by the mean vector of activity, this explains the deviation of the saccade trajectories to the target.

It is presumable that when the eyes were captured by the onset distractor, the suppression of saccade-related activity at this location occurred too late to stop the saccade to the onset distractor. Saccades to the onset distractor often stopped well before reaching the onset distractor and fixated for a very short duration (around 100 ms) before moving on to the target. In fact, on a small proportion of trials, the eyes initially went toward the onset distractor and moved on to the target location without stopping. These results are further discussed in the General Discussion.

The short fixation durations between saccades to the onset distractor and subsequent saccades to the target suggest that a spatial representation of the target was acquired based on visual information obtained prior to the saccade to the onset distractor. It is presumable that this spatial representation of the target was used to program the saccade to the target without requiring a new search for the target after the saccade to the onset distractor. Furthermore, if the saccade from the onset distractor to the target was based on visual information obtained prior to the saccade to the onset distractor, the target representation must have been created in spatiotopic coordinates. This issue was further examined in Experiments 2 and 3.

Experiment 2

To examine whether a spatiotopic representation of the target was developed from visual information obtained prior to the saccade to the onset distractor, we used a saccade-contingent switch paradigm in which, on some trials, the location of the target was switched with the location of a no-onset distractor during the

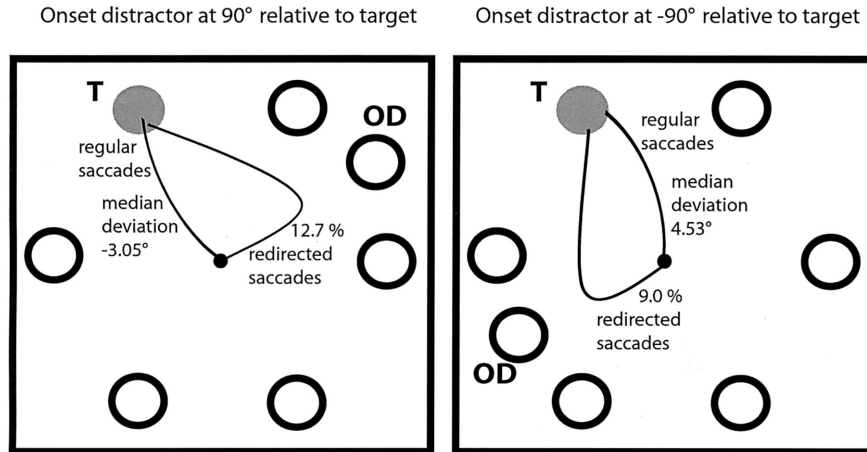


Figure 5. Two types of saccades—redirected saccades, which change their goal and turn around in midflight, and regular saccades, which do not change their goal in midflight—shown for two onset distractor positions. Note that although regular saccades do not change their goal during the saccade, they do show a significant deviation relative to the target location in the opposite direction of the onset distractor. T = target; OD = onset distractor.

saccade to the onset distractor. This procedure was similar to that of McPeck, Skavenski, and Nakayama (2000). If participants were able to create a spatiotopic representation of the target location based on visual information from the initial fixation, they might have been able to program the second saccade to the target based on this spatiotopic representation, without requiring a new search for the target after the saccade to the onset distractor. In this case, it was expected that after the saccade to the onset distractor, the eyes would move on to the old (but no longer valid) target location. If, on the other hand, a new search for the target was required after the saccade to the onset distractor, it was expected that the eyes would move on to the new target location.

Method

Participants. A total of 8 students of the Vrije Universiteit served as paid volunteers. All reported having normal or corrected-to-normal vision.

Stimuli. There were four differences relative to Experiment 1. First, an onset distractor was presented on all trials. Second, the angular separation between target and onset distractor was always 90° (in a clockwise or counterclockwise direction). Third, on 20% of the trials, the location of the

target and one of the no-onset distractors were switched during the execution of the first saccade. That is, the gray circle turned red, and one of the no-onset distractors turned gray. The new target location was located 120° from the old target location in a clockwise or counterclockwise direction. This resulted in a 30° or a 150° angular separation between the new target location and the onset distractor. Fourth, the target could appear at any of the object locations (clock positions of 1, 3, 5, 7, 9, and 11).

Procedure and design. There were two types of trials: switch trials (20%) and no-switch trials (80%). On switch trials, the target switched locations with a no-onset distractor during execution of the first saccade; on no-switch trials, it did not. To switch the location of the target during the initial saccade, we transferred the gaze-position data, which were recorded by the EyeLink system, to the subject computer through an etherlink with a delay of 10 ms. The gaze-position data were used in real time by the experimental program to initiate the target switch as soon as the eyes had moved at least 1° from the fixation point. After the target switch had been completed, a message was sent to the output file, which was used to check the timing of the target switch. It was determined that the target switch reliably occurred during the initial saccade by comparing the completion time of the target switch with the start and end times of the initial saccade. Participants performed a single session consisting of four blocks of 240 trials. The switch and no-switch trials were randomly ordered within

Table 1
Percentages of Redirected and Regular Saccades and Median Angular Deviations as a Function of the Location of the Onset Distractor Relative to the Target

Onset distractor location (deg)	Initial angular deviation (%)		Regular saccades > -30° and < 30°	Median angular deviation of regular saccades (deg)	Median angular deviation relative to target location
	Redirected saccades ≤ -30°	Redirected saccades ≥ 30°			
-90	9.0	2.7	88.3	4.53	$t(7) = 3.28, p < .01$
90	2.3	12.7	85.0	-3.05	$t(7) = 2.91, p < .02$
150	1.3	4.7	94.0	-2.63	$t(7) = 3.77, p < .01$
No onset distractor	1.0	0.9	98.1	-1.74	$t(7) = 1.92, p > .05$

Note. Redirected saccades are those that turn around in midflight; regular saccades are those that do not turn around in midflight. deg = degrees.

blocks. Prior to the start of the experiment, participants were instructed to make an eye movement toward the uniquely colored gray circle (the target) as quickly as possible. They were further instructed to make an eye movement as quickly as possible to the new target location when the target switched locations with a no-onset distractor.

Results

Discarded data. Trials on which the initial saccade latency was below 80 ms (anticipation errors; 3.1% of trials) or above 600 ms (0.3% of trials) were discarded from further analyses.

First saccade destination and latency. On 68% of the trials, the first saccade went to the target, on 29% it went to the onset, and on 3% it went elsewhere. The first saccade had a shorter latency when it was directed to the onset ($M = 155$ ms) than when it was directed to the target ($M = 214$ ms), $t(7) = 15.41, p < .01$.

Second saccade destination and fixation durations. The second saccade was assigned to a particular object if the endpoint of the second saccade was within 3° of visual angle from the center of the object. On 93% of the no-switch trials on which the first saccade went to the onset distractor, the second saccade went on to the target. The critical trials, however, were those on which the eyes initially went to the onset distractor, and the target location was switched during the first saccade (switch trials). Similar to Experiment 1, the 30° angular separation between the new target location and onset distractor did not enable a reliable distinction between saccades to the onset distractor and saccades to the new target location. Therefore, only the 150° angular separation between onset distractor and new target location was examined. On these trials, 82% of the second saccades was directed to the old target

location. Furthermore, the fixation duration on the onset distractor was shorter when the second saccade was directed to the old target location ($M = 92$ ms) than when it was directed to the new target location ($M = 213$ ms), $t(7) = 8.36, p < .01$ (see Figure 6).

We also examined fixation durations on the old target location on switch trials on which the eyes first went to the onset distractor and on trials on which the eyes went directly to the (old) target location. Note that when the eyes first moved to the onset distractor, the target switch occurred during this saccade, and it occurred prior to the saccade to the old target location. However, when the eyes went directly to the old target location, the switch occurred during this saccade. The results showed that fixation durations on the old target location were much shorter when the eyes first went to the onset distractor ($M = 233$ ms) than when the eyes went directly to the old target location ($M = 311$ ms), $t(7) = 5.97, p < .01$.

Discussion

The results of Experiment 2 showed that on the vast majority (82%) of target-switch trials on which the eyes first went to the onset distractor, the eyes moved on to the old (but invalid) target location. This indicates that on most trials, participants had created a spatial representation of the target location based on visual information obtained prior to the saccade to the onset distractor. After programming a saccade to the onset distractor, they programmed a saccade to the (old) target location on the vast majority of trials without requiring a new search for the target.

The question remains whether participants noticed the new target location after the saccade to the onset distractor. It is

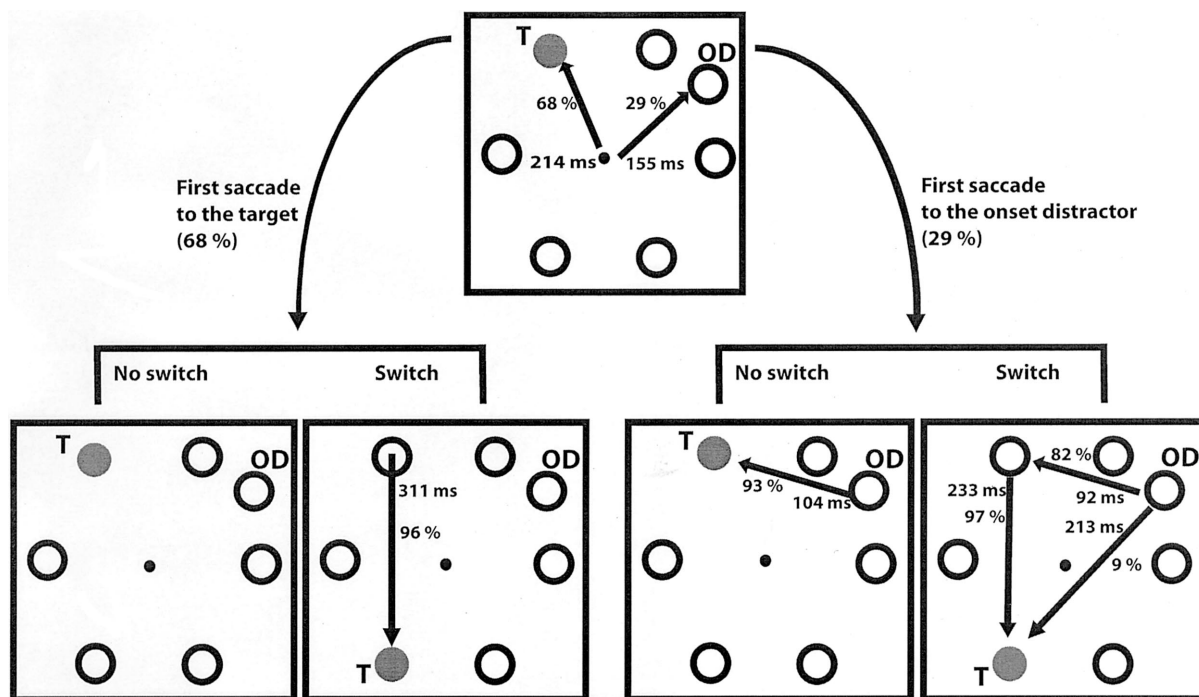


Figure 6. The destination and latency of saccades on trials on which the target location was switched with a no-onset distractor during the initial saccade (switch trials) and on trials on which the target location was not switched (no-switch trials). T = target; OD = onset distractor.

possible that visual information obtained during fixation of the onset distractor was sufficient to detect the new target location but that the saccade that was based on the spatial representation of the old target location could not be inhibited. A first indication that visual information concerning the new target location was obtained during fixation on the onset distractor is provided by the fixation durations on the old target location. When the eyes first went to the onset distractor prior to the saccade to the old target location, fixation durations on the old target location were shorter (233 ms) than when the eyes went directly to the old target location (311 ms). When the eyes went directly to the old target location, a search was required for the new target location during fixation on the old target location. However, when the eyes first went to the onset distractor, the new target location might have been found during fixation on the onset distractor. After the subsequent saccade to the old target location, a saccade to the new target location was then programmed on the basis of the already created spatial representation of the new target location. This issue was examined in Experiment 3.

Experiment 3

In Experiment 3, we used a double-switch method to examine whether the new target location could be detected during the relatively short fixation on the onset distractor. A double-switch method was used in which, in addition to the trials on which a single target location switch occurred during the first saccade, there were also trials on which the target location switched twice. That is, during the second saccade, the target was switched back to its initial location. Because the target location switched twice on some trials, the terminology of *old or new target location* is replaced by the terminology of *initial or switched target location*. The initial target location is the location at which the target is initially presented and at which the target returns after the second switch. The switched target location is the location of the target after the first switch. Thus, on trials on which the eyes first went to the onset distractor, the first target location switch occurred. When the eyes subsequently went on to the initial target location, the target was switched back to its initial location. Therefore, when the eyes reached the initial target location, this location once again contained the target. If participants could not detect the first target location switch during the short fixation on the onset distractor, then on double-switch trials, it would have appeared as if no target location switch had occurred. The original intention was to ask participants after each trial whether they had noticed any target switch. However, in a pilot study, we found that the eye movement behavior already provided this information.

Method

Participants. A total of 8 students of the Vrije Universiteit served as paid volunteers. All reported having normal or corrected-to-normal vision.

Stimuli. The stimuli were similar to those in Experiment 2 with the following exceptions. The first target location switch occurred during the first saccade execution on 50% of the trials on which the first saccade was directed toward the onset. The switched target location was always directly opposite the initial target location (180° angular separation), and the angular separation between the switched target location and the onset distractor was always 90° in a clockwise or counterclockwise direction. Furthermore, a second target location switch occurred during the second

saccade on 50% of the trials on which a first target location switch occurred. That is, on these trials, the target location was switched back to its initial location during the execution of the second saccade (see Figure 7).

Procedure and design. There were three types of trials: single-switch trials, double-switch trials, and no-switch trials. On single-switch trials (25% of trials on which the eyes first went to the onset distractor), the target switched locations with a no-onset distractor during execution of the first saccade. On double-switch trials (25% of trials on which the eyes first went to the onset distractor), in addition to the first target location switch, a second target location switch occurred during execution of the second saccade, which caused the target to be located back at its original location. On all other trials, no target location switch occurred. The first target location switch was initiated when the eyes had moved at least 1° from the fixation point, and the angular deviation relative to the onset distractor was less than 45°. Because the endpoint of initial saccades to the onset distractor was rather variable, the second target location switch was initiated on the basis of a velocity criterion of 80 degrees/s. It was determined that the first and second target location switch reliably occurred during the appropriate saccade by comparing the completion time of the target location switch with the start and end times of the saccades. Participants performed a single session consisting of four blocks of 192 trials. Single-switch, double-switch, and no-switch trials were randomly ordered within blocks. Prior to the start of the experiment, participants were instructed to make an eye movement toward the uniquely colored gray circle as quickly as possible. They were further instructed to make an eye movement as quickly as possible to the switched target location when the target switched locations with a no-onset distractor but to refrain from making this eye movement if the target location had switched back to its initial location.

Results

Discarded data. Trials on which saccade latency was below 80 ms (anticipation errors; 7.5% of trials) or above 600 ms (0.2% of trials) were discarded from further analyses.

First saccade. On 75% of the trials, the first saccade went to the target, on 23% it went to the onset, and on 2% it went elsewhere. The first saccade had a shorter latency when it was directed to the onset distractor ($M = 159$ ms) than when it was directed to the target ($M = 215$ ms), $t(7) = 16.49$, $p < .01$ (see Figure 7).

Second saccade. On no-switch trials when the eyes first went to the onset distractor, the eyes subsequently moved on to the target location on 86% of the trials with a relatively short fixation on the onset distractor ($M = 93$ ms). On trials on which the target location was switched during the saccade to the onset distractor, the eyes still went on to the initial target location on 79% of the trials, and only on 9%, the eyes correctly moved on to the switched target location. Furthermore, when the eyes moved on from the onset distractor to the switched target location, fixation durations on the onset distractor were relatively long (202 ms).

Third saccade. The critical trials were the double-switch trials on which the target location was switched during the saccade to the onset distractor and switched back during the subsequent saccade to the initial target location. Despite the fact that the target was back at its initial location, which participants were fixating, a subsequent saccade was made to the switched target location on 42% of these trials. The fixation duration on the initial target location was shorter on these double-switch trials (mean fixation duration = 148 ms) than on single-switch trials on which a subsequent saccade to the switched target location was necessary (mean fixation duration = 179 ms), $t(7) = 3.37$, $p < .01$.

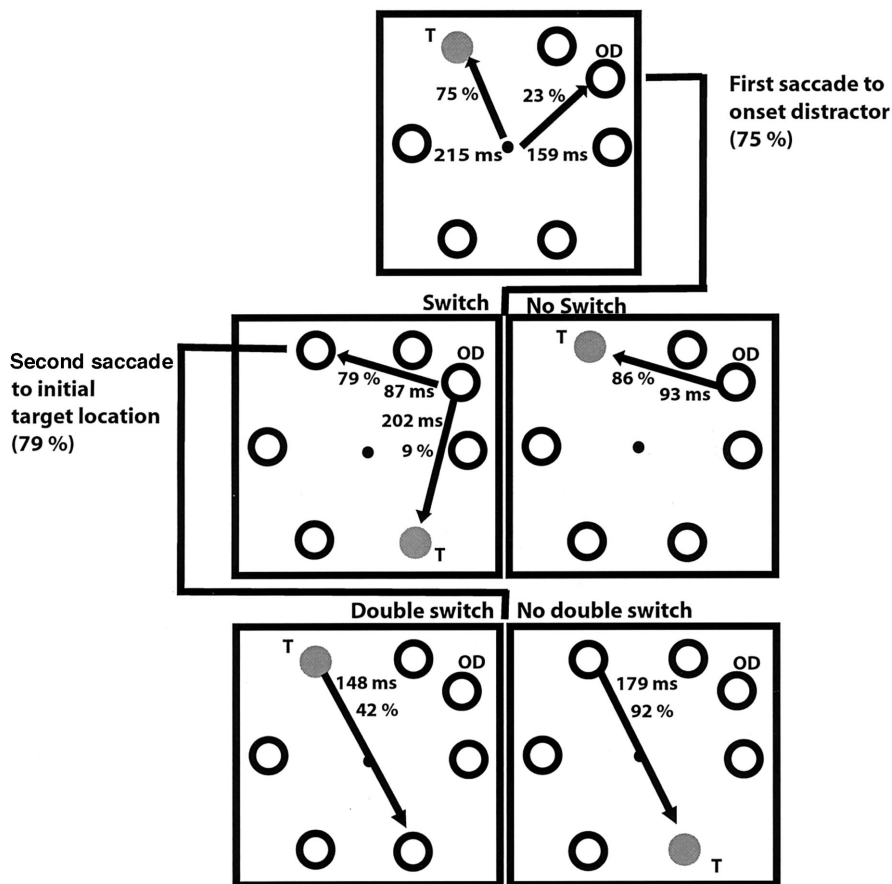


Figure 7. Displays and results of Experiment 3. On half the trials on which the eyes first went to the onset distractor, the target location was switched with one of the distractor locations during the first saccade to the onset distractor (switch trials). Furthermore, on half these trials, the target was switched back to its initial location during the execution of the second saccade (double-switch trials). Shown are the destination and latency of saccades for the first saccade, the second saccade for trials on which the first saccade went to the onset distractor, and the third saccade for trials on which the first saccade went to the onset distractor and the second saccade went to the initial target location. T = target; OD = onset distractor.

Discussion

The main result of Experiment 3 concerned the double-switch trials on which the eyes first went to the onset distractor and then on to the initial target location, which was invalid at the time of the saccade. During the saccade to the onset distractor, the target location was switched, but during the following saccade to the initial target location, the target was switched back to the initial location. Therefore, after the saccade to the initial target location, the target was fixated and no further saccades were needed. Nevertheless, on 42% of these trials, the eyes still moved on to the location to which the target had originally been switched. This indicates that on these trials, the switched target location was detected during fixation on the onset distractor, even though an erroneous saccade to the initial target location could not be inhibited. Therefore, after the saccade to the onset distractor, the next saccade was based on the spatial representation of the initial target location. It is presumable that the saccade program was already well underway before visual information obtained during fixation of the onset distractor allowed the detection of the switched target

location. The detection of the switched target location typically occurred too late to inhibit the saccade to the initial target location. Then, after the saccade to the initial target location, another saccade was programmed on the basis of the spatial representation of the switched target location obtained during fixation of the onset distractor. There are two possible reasons why this additional saccade to the switched target location was not executed on 58% of these trials. It could have been that on these trials, the switched target location was not detected during fixation of the onset distractor. A second possibility is that on these trials, visual information of the target which had been switched back to its initial location may have been obtained soon enough to inhibit an additional saccade to the switched target location.

General Discussion

The present study examined the programming of exogenous and endogenous saccades. In Experiment 1, two models were tested: the independent horse-race model and the competitive integration model. According to the independent horse-race model, there are

separate and independent systems for the programming of exogenous and endogenous saccades. Endogenous and exogenous saccades can be programmed simultaneously, and the program that is completed first is executed. In contrast, the competitive integration model assumes that endogenous and exogenous saccades are programmed within the same system. That is, saccade programming occurs on a common retinotopic saccade programming map in which information from different sources (e.g., endogenous and exogenous) is integrated. The competitive integration model assumes a lateral interaction structure in which saccade-related activation at a specific location spreads to neighboring locations but inhibits distant locations (see Figure 1). The two models were tested with a modified version of the oculomotor capture paradigm (e.g., Irwin et al., 2000; Theeuwes et al., 1998, 1999) in which endogenous saccades were directed toward a color singleton target and exogenous saccades were elicited by an abrupt onset distractor. The results of Experiment 1 provided substantial support for the competitive integration model. First, saccade latencies to the target were longer when an onset distractor was presented than when it was not so long as the onset distractor was not adjacent to the target. Second, saccade latencies were longer when the target and onset distractor were presented relatively far apart (angular separation of 90° or 150°) than when they were presented relatively close together (angular deviation of 30°). Third, in the 30° separation condition the eyes were often directed to a location somewhere between the target and the onset distractor (global effect; e.g., Findlay, 1982). These findings support the lateral interaction structure of the competitive integration model. Activation at a location in the saccade map spreads to neighboring locations but inhibits distant locations. Because the independent horse-race model assumes independence between saccade programs, these results are inconsistent with the independent horse-race model.

In Experiments 2 and 3, we used a saccade-contingent, target-switch paradigm (see McPeck et al., 2000) to examine whether a spatiotopic representation of the target location was created on the basis of visual information obtained prior to the exogenous saccade to the onset distractor. On some trials, the location of the target was switched during the initial saccade to the onset distractor. The results showed that even though the target was at a new location during fixation of the onset distractor, the eyes still went on to the old target location. This indicates that on the majority of trials, a spatiotopic representation of the (initial) target location was created prior to the exogenous saccade to the onset distractor and that the subsequent saccade was based on this representation. If we assume that the saccade map contains a retinotopic representation, then the oculomotor system must have a way in which to compensate for the intervening saccade to the onset distractor. If the representation of target location is created in spatiotopic coordinates, then this may enable the appropriate location in the saccade map to be activated to guide the eyes to the target location after the saccade to the onset distractor. In the section on the neurophysiology of the competitive integration model, we briefly speculate on how such a spatiotopic representation might be accomplished in the brain.

In Experiment 3, we found that on 42% of the trials on which the target was switched back to its initial location during the saccade from the onset distractor to the initial target location, the eyes nevertheless moved on to the location to which the target had

initially been switched despite the fact that the target was already being fixated at its initial location. It is presumable that when information concerning the switched target location was obtained during fixation on the onset distractor, the saccade program to the initial target location was already well underway and could no longer be inhibited.

Despite the differences between the three experiments of the present study, the results are very similar. The percentage of trials on which the eyes were captured by the onset distractor ranged from 23% to 29%. After the initial saccade to the onset distractor in all three experiments, the eyes stopped for a brief period of time (mean fixation durations were about 90–100 ms) and generally went on to the location at which the target was initially presented. The results are also quite similar to those of Theeuwes et al. (1998, 1999), although the percentage of trials on which the eyes were captured was slightly higher in Theeuwes et al. (1998, 1999; 30%–40%). It is possible that this difference was due to procedural differences concerning the presentation of the stimuli. That is, in Theeuwes et al. (1998, 1999), the no-onset distractors changed color, but the color of the target did not, whereas in the present study, the target changed color, but the no-onset distractors did not. In addition, there were other methodological differences between Theeuwes et al. (1998, 1999) and the present study. For example, in Theeuwes et al. (1998, 1999), there was also a manual response task. Maybe participants were more concerned with accurate manual responses than with accurate initial saccades. In the present study, there was no manual response task, and participants could fully concentrate on the saccade task.

In the following sections, we discuss the assumptions of the competitive integration model in more detail, and we discuss how the competitive integration model accounts for the results of the present study.

Architecture of Saccade Map

As discussed in previous sections, the main assumption of the competitive integration is that exogenous and endogenous saccades are programmed in the same system. That is, there is a single saccade map in which exogenous and endogenous saccade-related activity are integrated. Activity at one location spreads to neighboring locations (see Figure 1C) but inhibits distant locations (see Figure 1B). This architecture is consistent with other models of saccade programming (e.g., Findlay & Walker, 1999; Kopecz, 1995; Trappenberg et al., 2001).

Temporal Trigger

According to the competitive integration model, a saccade is executed when a certain activation threshold is reached at a location in the saccade map. Thus, the spatial and temporal aspects of the model are intimately related. This is similar to the models of Trappenberg et al. (2001) and Kopecz (1995), but it is in contrast with Findlay and Walker (1999). According to Findlay and Walker's model, there are separate "when" and "where" systems. There is competition between a fixate center, which is part of the when system, and a move center, which is part of the where system. When the activity in the fixate center falls below a certain threshold, a saccade is triggered. To explain the increased latency of saccades to a target when an onset distractor is presented, Findlay

and Walker need to assume in their model that onsets activate the fixate center causing a delay in saccade execution (Findlay & Walker, 1999). This counterintuitive assumption seems at odds with the fact that onsets typically elicit saccades with extremely short latencies (e.g., Fischer & Weber, 1993). Nevertheless, Findlay and Walker's model could account for a range of oculomotor phenomena, including the remote distractor effect and the global effect. The competitive integration model of the present study does not assume separate fixate and move centers; instead, the fixation location is part of the saccade map. That is, when observers are actively fixating a specific location, the central portion of the saccade map is strongly activated (also see Kopecz, 1995). There is lateral inhibition between the fixation location and peripheral locations precisely like the lateral inhibition between distant peripheral locations. This is consistent with evidence that fixation-related cells are similar to saccade-related cells (buildup neurons) but with a foveal receptive field (Krauzlis, Basso, & Wurtz, 1997; Munoz & Wurtz, 1992, 1993). The fact that fixation-related and saccade-related activation occurs in the same activation map does not mean that fixation-related activity plays a minor role. In fact, the activity at fixation is critical for the temporal trigger. If the fixation location in the saccade map is strongly activated, this prevents the threshold from being reached at peripheral locations because of the lateral inhibition from the fixation location. When a saccade is required, the fixation-related activation may be inhibited (typically referred to as oculomotor disengagement), releasing peripheral locations from the lateral inhibition from the fixation location. Klein and Shore (2000) have suggested that in the oculomotor capture paradigm (Theeuwes et al., 1998, 1999), the color change of the no-onset distractors, which indicates the presence of the color singleton target, may initiate oculomotor disengagement as the observer prepares to make a saccade. In the context of the competitive integration model, as soon as the no-onset distractors change color, activation at fixation is inhibited in a top-down manner, facilitating the programming of a saccade to a peripheral target. In the present study, there was no global color change of the no-onset distractors; nevertheless, the timing from the fixation display to the target display was constant so that fixation-related activity may have been inhibited as the target display was being anticipated.

Saccade Destination

In accordance with Tipper and colleagues (e.g., Tipper et al., 2000, 2001), we assume that the displacement of the eyes is determined by the mean vector of activity in the saccade map. The eyes will typically land nearby the location corresponding with the location in the saccade map at which the threshold was reached. However, because other locations may be somewhat activated when the threshold is reached, deviations from this threshold location may occur. When two nearby locations are strongly activated at the time that a threshold is reached at either location (or at an intermediate location; see Figure 1C), the saccade will typically land somewhere between the two locations (global effect). However, when two distant locations are active, there is lateral inhibition between the locations, slowing the speed at which the threshold can be reached. Therefore, before the threshold can be reached at one of two distant locations, more activation is required at one of the locations, and because of the lateral inhibi-

tion from the threshold location, the activation at the other location will be diminished. No global effect will occur in this case.

Location-Specific Inhibition

Apart from the lateral inhibition within the saccade map, we assume an additional inhibition mechanism 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 desired locations. According to Tipper and colleagues (e.g., Tipper et al., 2000, 2001), the inhibition of a location results in a sub-baseline activation at that location, causing the mean vector of activity in the saccade map to be deviated away from the inhibited location. This is consistent with the finding of the present study that saccades to the target were deviated away from the onset distractor (also see Doyle & Walker, 2001; Sheliga et al., 1994, 1995).

Time Course of Endogenous and Exogenous Activation

The present study has provided substantial evidence that exogenous activation arrives in the saccade map well before endogenous activation does. First, latencies of exogenous saccades to the onset distractor were much shorter than latencies of saccades to the target. Second, in the 30° separation condition, there was a shift over time in the distribution of landing points from the onset location toward the target location. In other words, the mean endpoint of short latency saccades was close to the onset distractor, and the mean endpoint of long latency saccades was close to the target location (see Figure 4). Third, for the 10% fastest saccades (see Figure 3), which typically went to the onset distractor, there was no effect of target location, suggesting that target-related activation had not yet arrived in the saccade map. Otherwise, because of the lateral interaction structure of the saccade map, saccade latencies of these saccades would have been shorter with a 30° separation than with a 90° or 150° separation between target and onset distractor. Fourth, when the eyes move to both the onset distractor and the target on a single trial, they always first move to the onset distractor before moving to the target and never vice versa.

The difference in time course between endogenous and exogenous activation is presumably due to additional processing required for endogenous saccades. That is, the properties of the stimuli must be related to the goals of the observer to determine the appropriate response.

Control Signals

Although the competitive integration model is particularly concerned with the processing that goes on in the saccade programming map, it is important to consider some aspects of processing preceding this final saccade programming stage. Before a saccade to a target can be programmed, a spatial representation of the target location must be created, and top-down control signals must be delivered to the saccade programming map. In Experiments 2 and 3, we have shown that when an exogenous saccade to the onset is made, a spatiotopic representation of the target can be used to program the subsequent saccade without requiring a new search

for the target. The top-down control signals not only refer to the activation of relevant locations but also the inhibition of irrelevant locations. This location-specific inhibition is applied to irrelevant peripheral locations that initially evoke saccade-related activity (e.g., onset distractors) as well as to the fixation location when the generation of an eye movement is desired. Thus, in the competitive integration model, fixation disengagement is achieved by top-down inhibition of the fixation location.

Neurophysiology of the Model

Although the competitive integration model is a functional model, it is in part motivated by the neurophysiology of saccade programming. The SC plays a critical role in saccade programming (for reviews, see Schall, 1991; Sparks & Mays, 1981; Wurtz, Basso, Paré, & Sommer, 2000). It receives input from a wide range of areas, such as the FEF, the supplementary eye fields (SEF), and the posterior parietal cortex (PPC). It has been suggested that the intermediate layers of the SC integrate endogenous and exogenous saccade-related activation (Trappenberg et al., 2001). The SC contains a retinotopic map of the visual field (e.g., Wurtz et al., 2000), and there is substantial evidence for short-distance excitation and long-distance inhibition within the map (e.g., Munoz & Istvan, 1998; Olivier, Porter, & May, 1998), consistent with the competitive integration model. It has been suggested that a frontoparietal circuit, involving the FEF and PPC, is responsible for developing spatial representations required for saccade programming and delivering the control signals to the SC (e.g., Chelazzi & Corbetta, 2000). The FEF and the dorsolateral prefrontal cortex (dlPFC) are prime candidates for inhibiting specific locations in the SC. The inhibitory role of these areas is based on lesion studies, which have shown that either FEF lesions (e.g., Guitton, Buchtel, & Douglas, 1985; Rafal, Machado, Ro, & Ingle, 2000) or

dlPFC lesions (e.g., Pierrot-Deseilligny, Rivaud, Gaymard, & Agid, 1991; Walker, Husain, Hodgson, Harrison, & Kennard, 1998) result in a deficit in inhibiting reflexive saccades. Furthermore, electrical microstimulation of the FEF results in suppression of saccades in a variety of tasks (Burman & Bruce, 1997).

Given the retinotopic representation of the SC, the oculomotor system must have a way to compensate for eye displacement when fast corrective saccades, such as redirected saccades, are to be accurately directed to a target location. One possibility points to a role for the lateral intraparietal area (LIP) in the PPC, because cells in this area shift their receptive field just before the execution of a saccade in anticipation of the upcoming saccade (Duhamel, Colby, & Goldberg, 1992). Thus, the LIP may play an important role in compensating for eye movements when control signals are delivered to the SC on the basis of visual information obtained during a preceding saccade. Despite the presumed retinotopic representation of the saccade map, we present the competitive integration model in the following section as if the saccade map contains a spatiotopic representation.

Competitive Integration in the Present Study

Figure 8 shows the time course of activation in the saccade map during a typical trial on which the eyes move to the target according to the competitive integration model. At the start of the trial, before target and onset distractor are presented, there is strong activation around the central fixation location (Figure 8A). After the presentation of the target display, the fixation location receives top-down inhibition as the observer prepares to make a saccade. Exogenous activation related to the onset distractor reaches the saccade map (Figure 8B). Before the activation at the onset location can reach threshold, target-related input reaches the saccade map, and top-down inhibition acts on the location of the onset

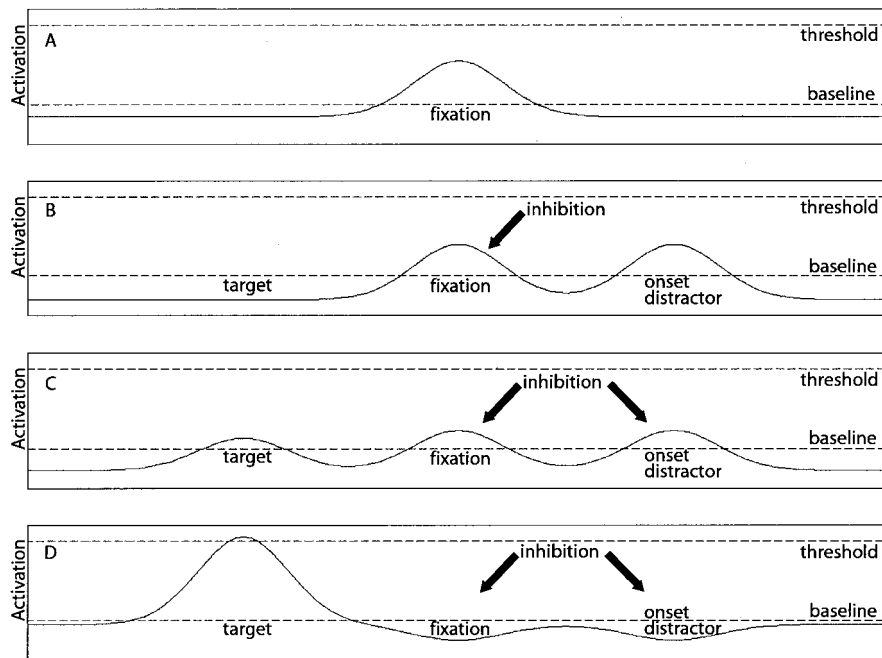


Figure 8. Time course of activation in the saccade map according to the competitive integration model.

distractor (Figure 8C). Activation at the target location eventually reaches threshold, and a saccade is directed to the mean vector of activity in the saccade map (Figure 8D). Because of the inhibition at the onset distractor location, the eyes move to the target location but with a slight deviation away from the onset distractor. If the activation at the onset distractor location reaches the threshold before it can be inhibited, the time course is basically the same, with the only difference being that the eyes first move to the onset distractor. Thus, the onset distractor location does receive top-down inhibition, but it sets in too late to prevent the exogenous saccade to the onset distractor. If the location of the onset distractor is inhibited shortly after the threshold is reached, the saccade falls short of the onset distractor, and the reduced activation at that location will allow the threshold to be reached at the target location relatively quickly. In other words, we propose that both the reduced amplitude of saccades to the onset distractor and the extremely short fixation durations on the onset distractor are the result of top-down inhibition at the onset distractor location.

Spatial Competition in Other Paradigms

A number of other paradigms have also provided evidence for spatial competition of saccade programming. However, it is important to note that these paradigms typically could not make a distinction between endogenous and exogenous saccades, and, therefore, they were not suitable to test the independent horse-race model. A number of studies have used a task in which an onset target is either presented alone or together with an onset distractor (e.g., Walker et al., 1997; Weber & Fischer, 1994). The findings are typically similar to the present paradigm: Saccade latencies are longer when a distractor is presented at a relatively large distance from the target than when no distractor is presented. Also, when the distractor is presented relatively close to the target, a global effect is found. However, in these distractor studies (e.g., Walker et al., 1997), there is no difference in mean saccade latency between trials on which a distractor is presented close to the target and trials on which no distractor is presented. This seems inconsistent with the suggestion of the competitive integration model that activation in the saccade map spreads to neighboring locations. As shown in Figure 1C, if activation spreads to neighboring locations, the threshold should be reached sooner than without spreading of activation. Therefore, this finding may be interpreted as evidence against spreading of activation in the saccade map. However, these distractor effects should be interpreted with caution. For example, it has been suggested (Ottes, Van Gisbergen, & Eggemont, 1985) that on some trials, participants may delay their response when target and distractor are presented close together to avoid an inaccurate saccade. Such a strategy may obscure any reduction in saccade latency because of the spreading of activation.

The results of Walker et al. (1997) suggested that a global effect only occurs when the angular distance between target and distractor is 20° or less. However, in the present study as well as in Ottes et al. (1985), a global effect was also found at an angular distance between target and distractor of 30°. The reason for this difference is unclear. One speculation is that the area within which a global effect occurs may depend on differences between studies in the use of (inhibition) strategies that may be adopted to avoid inaccurate global saccades.

The study of Walker et al. (1997) also demonstrated the critical importance of eccentricity in the programming of saccades. Latencies of saccades to the target were increased as the distractor was presented closer to fixation. Relative to a no-distractor control condition, the saccade latencies to the target were still increased when the distractor was presented at an eccentricity of 10°. Walker et al. interpreted this as evidence for a fixation zone extending to about 10° away from the fovea. These data can also be interpreted without reference to a fixation zone. It is possible that there is a continuum from the fovea to the periphery as proposed by the competitive integration model but with a reduced sensitivity of locations in the saccade map as a function of eccentricity (Findlay & Walker, 1999, authors' fourth response [R4]).

Further evidence for spatial competition of saccade programming has been provided by studies examining the effects of short-term priming on the oculomotor system (McPeck & Keller, 2001; McPeck et al., 2000). McPeck et al. (2000) presented participants with displays containing three diamond shapes positioned on an imaginary circle. The color of one of the diamond shapes was different from the other two, and participants were required to saccade toward this uniquely colored target. On each trial, the target color was randomly chosen to be red or green, and the distractors were of the opposite color. The results showed that the initial saccade was often directed to one of the distractors, especially when the target and distractor colors differed between trials. As in the present study, initial saccades to a distractor often landed somewhere between the fixation point and the distractor with a significant undershoot, and subsequent fixation durations were extremely short (around 100 ms). McPeck et al. also used a saccade-contingent target switch similar to Experiment 2 of the present study. The results showed that when the target location was switched with that of a distractor during the initial saccade to one of the distractors, the subsequent saccade was directed to the old and invalid target location on 90% of the trials. Thus, similar to the present study, the second saccade was based on a spatial representation of target location obtained prior to the initial saccade to the distractor.

One paradigm that can make a distinction between endogenous and exogenous saccades is the antisaccade task (e.g., Hallet, 1978; Hallet & Adams, 1980; Guitton et al., 1985; Mokler & Fischer, 1999). In this task, participants are required to make a saccade in the opposite direction of an abrupt onset. Erroneous saccades to the onset may be considered exogenous, and saccades correctly directed to the opposite location may be considered endogenous. The results are typically quite similar to the oculomotor capture paradigm. When the eyes are captured by the onset, a subsequent corrective saccade will follow after a relatively short fixation duration. Furthermore, these exogenous saccades sometimes undershoot the onset by a significant margin. Similar to the present study, Mokler and Fischer (1999) found that relatively short amplitude saccades to the onset were followed by shorter fixation durations compared with relatively long amplitude saccades to the onset. Despite the similar results, there are a number of significant differences between the antisaccade task and the oculomotor capture paradigm. First, in the antisaccade task, the location of the onset is not irrelevant to the task. In fact, the required saccade destination is defined in terms of the location of the onset. Furthermore, the effect of separation between onset and target can not be adequately examined, and there can be no condition in which no

onset is presented. Therefore, the oculomotor capture paradigm is more suitable to test the assumptions of the competitive integration model and the independent horse-race model. Nevertheless, the similarities between the results of the present study and these other paradigms suggest that the present results may be generalized to other tasks and that they are not specific to the oculomotor capture paradigm.

Conclusion

The present study provides strong evidence for competitive integration of endogenous and exogenous saccade-related activity. One of the strengths of the competitive integration model is that its assumptions are based on a variety of eye-movement parameters (latency, endpoint, amplitude, trajectory, fixation duration). However, its assumptions require further testing from different paradigms. In contrast to the independent horse-race model, it is not restricted to competition of saccade programming between an exogenous and an endogenous saccade, so that it can be tested in a variety of paradigms, which do not make a distinction between exogenous and endogenous saccades.

References

- Burman, D. D., & Bruce, C. J. (1997). Suppression of task-related saccades by electrical stimulation in the primate's frontal eye field. *Journal of Neurophysiology*, *77*, 2252–2267.
- Chelazzi, L., & Corbetta, M. (2000). Cortical mechanisms of visuospatial attention in the primate brain. In M. S. Gazzaniga (Ed.), *The new cognitive neurosciences* (pp. 667–686). Cambridge, MA: MIT Press.
- Coren, S., & Hoenig, P. (1972). Effect of non-target stimuli on the length of voluntary saccades. *Perceptual and Motor Skills*, *34*, 499–508.
- Corneil, B. D., Hing, C. A., Bautista, D. V., & Munoz, D. P. (1999). Human eye-head gaze shifts in a distractor task: I. Truncated gaze shifts. *Journal of Neurophysiology*, *82*, 1390–1405.
- Doyle, M., & Walker, R. (2001). Curved saccade trajectories: Voluntary and reflexive saccades curve away from irrelevant distractors. *Experimental Brain Research*, *139*, 333–344.
- Duhamel, J., Colby, C. L., & Goldberg, M. E. (1992, January 3). The updating of the representation of visual space in the parietal cortex by intended eye movements. *Science*, *255*, 90–92.
- Findlay, J. M. (1982). Global processing for saccadic eye movements. *Vision Research*, *22*, 1033–1045.
- Findlay, J. M., & Walker, R. (1999). A model of saccade generation based on parallel processing and competitive integration. *Behavioral & Brain Sciences*, *22*, 661–721.
- Fischer, B., & Weber, H. (1993). Express saccades and visual attention. *Behavioral & Brain Sciences*, *16*, 553–610.
- Godijn, R., & Theeuwes, J. (2001). *The relationship between exogenous and endogenous saccades and attention*. Manuscript submitted for publication.
- Godijn, R., & Theeuwes, J. (in press). Oculomotor capture and inhibition of return: Evidence for an oculomotor suppression account of IOR. *Psychological Research*.
- Guitton, D., Buchtel, H. A., & Douglas, R. M. (1985). Frontal lobe lesions in man cause difficulties in suppressing reflexive glances and in generating goal directed saccades. *Experimental Brain Research*, *58*, 455–472.
- Hallet, P. E. (1978). Primary and secondary saccades to goals defined by instructions. *Vision Research*, *18*, 1279–1296.
- Hallet, P. E., & Adams, W. D. (1980). The predictability of saccade latency in a novel oculomotor task. *Vision Research*, *20*, 329–339.
- Irwin, D. E., Colcombe, A. M., Kramer, A. F., & Hahn, S. (2000). Attentional and oculomotor capture by onset luminance and color singletons. *Vision Research*, *40*, 1443–1458.
- Klein, R. M., & Shore, D. I. (2000). Relations among modes of visual orienting. In S. Monsell & J. Driver (Eds.), *Attention and performance XVIII: Control of cognitive processes* (pp. 196–208). Cambridge, MA: MIT Press.
- Kopecz, K. (1995). Saccadic reaction times in gap/overlap paradigm: A model based on integration of intentional and visual information on neural dynamic fields. *Vision Research*, *35*, 2911–2925.
- Kramer, A. F., Irwin, D. E., Theeuwes, J., & Hahn, S. (1999). Oculomotor capture by abrupt onsets reveals concurrent programming of voluntary and involuntary saccades. *Behavioral & Brain Sciences*, *22*, 689–690.
- Krauzlis, R. J., Basso, M. A., & Wurtz, R. H. (1997, June 13). Shared motor error for multiple eye movements. *Science*, *276*, 1693–1695.
- McPeck, R. M., & Keller, E. L. (2001). Short-term priming, concurrent processing, and saccade curvature during a target selection task in the monkey. *Vision Research*, *41*, 785–800.
- McPeck, R. M., Skavenski, A. A., & Nakayama, K. (2000). Concurrent processing of saccades in visual search. *Vision Research*, *40*, 2499–2516.
- Minken, A. W. H., Van Opstal, A. J., & Van Gisbergen, J. A. M. (1993). Three-dimensional analysis of strongly curved saccades elicited by double-step stimuli. *Experimental Brain Research*, *93*, 521–533.
- Mokler, A., & Fischer, B. (1999). The recognition and correction of involuntary prosaccades in an antisaccade task. *Experimental Brain Research*, *125*, 511–516.
- Munoz, D. P., & Istvan, P. J. (1998). Lateral inhibitory interactions in the intermediate layers of the monkey superior colliculus. *Journal of Comparative Neurology*, *276*, 169–187.
- Munoz, D. P., & Wurtz, R. H. (1992). Role of the rostral superior colliculus in active visual fixation and execution of express saccades. *Journal of Neurophysiology*, *67*, 1000–1002.
- Munoz, D. P., & Wurtz, R. H. (1993). Fixation cells in monkey superior colliculus: II. Reversible activation and deactivation. *Journal of Neurophysiology*, *70*, 576–589.
- Olivier, E., Porter, J. D., & May, P. J. (1998). Comparison of the distribution and somatodendritic morphology of tectotectal neurons in the cat and monkey. *Visual Neuroscience*, *15*, 903–922.
- Ottes, F. P., Van Gisbergen, J. A. M., & Eggermont, J. J. (1985). Latency dependence of colour-based target vs. nontarget discrimination by the saccadic system. *Vision Research*, *25*, 849–862.
- Pierrot-Deseilligny, C., Rivaud, S., Gaymard, B., & Agid, Y. (1991). Cortical control of reflexive visually-guided saccades. *Brain*, *114*, 1473–1485.
- Rafal, R. D., Machado, L. J., Ro, T., & Ingle, H. W. (2000). Looking forward to looking: Saccade preparation and control of the visual grasp reflex. In S. Monsell & J. Driver (Eds.), *Attention and performance XVIII: Control of cognitive processes* (pp. 155–174). Cambridge, MA: MIT Press.
- Ratcliff, R. (1979). Group reaction time distributions and an analysis of distribution statistics. *Psychological Bulletin*, *86*, 446–461.
- Schall, J. D. (1991). Neural basis of saccadic eye movements in primates. In A. G. Leventhal (Ed.), *Vision and visual dysfunction: Vol. 4. The neural basis of visual function* (pp. 388–442). London: Macmillan.
- Schiller, P. H. (1985). A model for the generation of visually guided saccadic eye movements. In D. Rose & V. G. Dobson (Eds.), *Models of the visual cortex* (pp. 62–70). New York: Wiley.
- Schiller, P. H., & Sandell, J. H. (1983). Interactions between visually and electrically elicited saccades before and after superior colliculus and frontal eye field ablations in the rhesus monkey. *Experimental Brain Research*, *49*, 381–392.
- Sheliga, B. M., Riggio, L., & Rizzolatti, G. (1994). Orienting of attention and eye movements. *Experimental Brain Research*, *98*, 507–522.

- Sheliga, B. M., Riggio, L., & Rizzolatti, G. (1995). Spatial attention and eye movements. *Experimental Brain Research*, *105*, 261–275.
- Smit, A. C., Van Opstal, A. J., & Van Gisbergen, J. A. M. (1990). Component stretching in fast and slow oblique saccades in the human. *Experimental Brain Research*, *81*, 325–334.
- Sparks, D. L., Lee, C., & Rohrer, W. H. (1990). Population coding of the direction, amplitude, and velocity of saccadic eye movements by neurons in the superior colliculus. *Cold Spring Harbor Symposia on Quantitative Biology*, *55*, 805–811.
- Sparks, D. L., & Mays, L. E. (1981). The role of the superior colliculus in the control of saccadic eye movements: A current perspective. In A. F. Fuchs & W. Becker (Eds.), *Progress in oculomotor research* (pp. 137–144). Amsterdam: Elsevier.
- Theeuwes, J., Kramer, A. F., Hahn, S., & Irwin, D. E. (1998). Our eyes do not always go where we want them to go: Capture of the eyes by new objects. *Psychological Science*, *9*, 379–385.
- Theeuwes, J., Kramer, A. F., Hahn, S., Irwin, D. E., & Zelinsky, G. J. (1999). Influence of attentional capture on oculomotor control. *Journal of Experimental Psychology: Human Perception and Performance*, *25*, 1595–1608.
- Tipper, S. P., Howard, L. A., & Houghton, G. (2000). Behavioral consequences of selection from population codes. In S. Monsell & J. Driver (Eds.), *Attention and Performance XVIII: Control of cognitive processes* (pp. 223–245). Cambridge, MA: MIT Press.
- Tipper, S. P., Howard, L. A., & Paul, M. A. (2001). Reaching affects saccade trajectories. *Experimental Brain Research*, *136*, 241–249.
- Trappenberg, T. P., Dorris, M. D., Munoz, D. P., & Klein, R. M. (2001). A model of saccade initiation based on the competitive integration of exogenous and endogenous signals in the superior colliculus. *Journal of Cognitive Neuroscience*, *13*, 256–271.
- Walker, R., Deubel, H., Schneider, W. X., & Findlay, J. M. (1997). Effect of remote distractors on saccade programming: Evidence for an extended fixation zone. *Journal of Neurophysiology*, *78*, 1108–1119.
- Walker, R., Husain, M., Hodgson, T. L., Harrison, J., & Kennard, C. (1998). Saccadic eye movement and working memory deficits following damage to human prefrontal cortex. *Neuropsychologia*, *36*, 1141–1159.
- Weber, H., & Fischer, B. (1994). Differential effects of non-target stimuli on the occurrence of express saccades in man. *Vision Research*, *34*, 1883–1891.
- Wurtz, R. H., Basso, M. A., Paré, M., & Sommer, M. A. (2000). The superior colliculus and the cognitive control of movement. In M. S. Gazzaniga (Ed.), *The new cognitive neurosciences* (pp. 573–587). Cambridge, MA: MIT Press.

Received March 21, 2001

Revision received February 5, 2002

Accepted February 8, 2002 ■

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