

Less attention is more in the preparation of antisaccades, but not prosaccades

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To make a saccadic eye movement to a target we must first attend to it. It is therefore not surprising that diverting attention increases saccade latency, but is latency increased in all cases? We show that attending to a peripheral discrimination task has a paradoxical effect. If the stimulus to be attended appears shortly (100 to 300 ms) before an eye movement is made in a direction opposite to that of a presented stimulus (an antisaccade), its latency is reduced to well below baseline performance. In contrast, latencies for saccades toward the stimulus (prosaccades) are increased under similar conditions. This paradoxical effect may arise from competition between the processes mediating prosaccades and antisaccades. When the discrimination task is presented at the critical moment, it interferes with a reflexive prosaccade, allowing faster antisaccades. The results suggest that the suppression of sensorimotor reflexes can facilitate volitional motor acts.

When a fixated stimulus is displaced, there are large differences in saccadic latency depending on whether participants make saccades to the new stimulus location ('prosaccades') or saccades of equal size in the direction opposite from the stimulus ('antisaccades')^{1–3}. This cost of making a saccade away from rather than toward the stimulus has been thought to reflect the need for the suppression of a reflexive saccade toward the stimulus as well as the generation of the saccade away from it^{4–7}. Thus, antisaccades may require more attentional and oculomotor resources than prosaccades, because active inhibition of the prosaccade in addition to the programming of the antisaccade is required. However, prosaccades also place considerable demands on attentional resources, because when observers are instructed to perform a secondary task along with a prosaccade, saccadic latencies can increase^{8–10}. Indeed, eye movements and attentional shifts may be controlled by overlapping neural mechanisms¹¹.

What, then, are the likely effects of an attention-demanding secondary task on pro- and antisaccade performance? If antisaccades place greater demands on attentional and oculomotor resources than prosaccades, a sufficiently challenging secondary task might increase antisaccade latency even more than prosaccade latency. Another possibility is that if antisaccades require disengagement from reflexive saccade programming, different results might be expected for pro- and antisaccades depending on whether the secondary task interferes with the generation of this reflexive saccade, which is the correct response in the prosaccade task but not the antisaccade task. Thus, the effects of the secondary task on antisaccade latency might not be as great as on prosaccade latency. Indeed, if a large component of the increased latencies for antisaccades is a result of reflex suppression, the performance of a secondary task immediately before the onset of the target could itself suppress the prosaccade reflex,

thereby decreasing antisaccade latency. Here we report the results of four experiments designed to investigate the effects of an attention-demanding task on pro- and antisaccade latencies, and to determine whether the effects of a secondary task depend on its timing relative to the presentation of the saccade target.

RESULTS

Saccades with a concurrent discrimination task

In the first experiment, observers made prosaccades toward or antisaccades away from a cross on the screen as soon as it was displaced to the left or right of its central position, while also deciding which of two horizontal sinusoidal gratings that appeared above and below the fixation point was of higher spatial frequency (Fig. 1a). The stimuli for the discrimination task were presented randomly at one of six different times relative to the saccade target displacement. This allowed us to test the effects of the discrimination task as a function of the stimulus onset asynchrony (SOA), which is the time of the eye movement target displacement relative to the appearance of the visual stimulus. Observers were told to make the saccade as quickly as possible and to respond to the discrimination task only after completing the saccade.

Performance of the secondary task increased prosaccade latencies at all SOAs with the largest effect at 0 SOA (Fig. 1b). This is not surprising, given the demonstrated need for a shift of attention to the target location just before a saccade is made^{8–11}. Surprisingly, when the discrimination stimuli were presented 100 to 300 ms before the saccade target displacement, antisaccade latencies decreased to well below baseline performance (Fig. 1c). However, antisaccade latencies increased when the discrimination task was presented simultaneous to or shortly after the saccade target moved (100 to 200 ms later). Although the interfering effects of the secondary task on the prosaccades were consistent with previ-

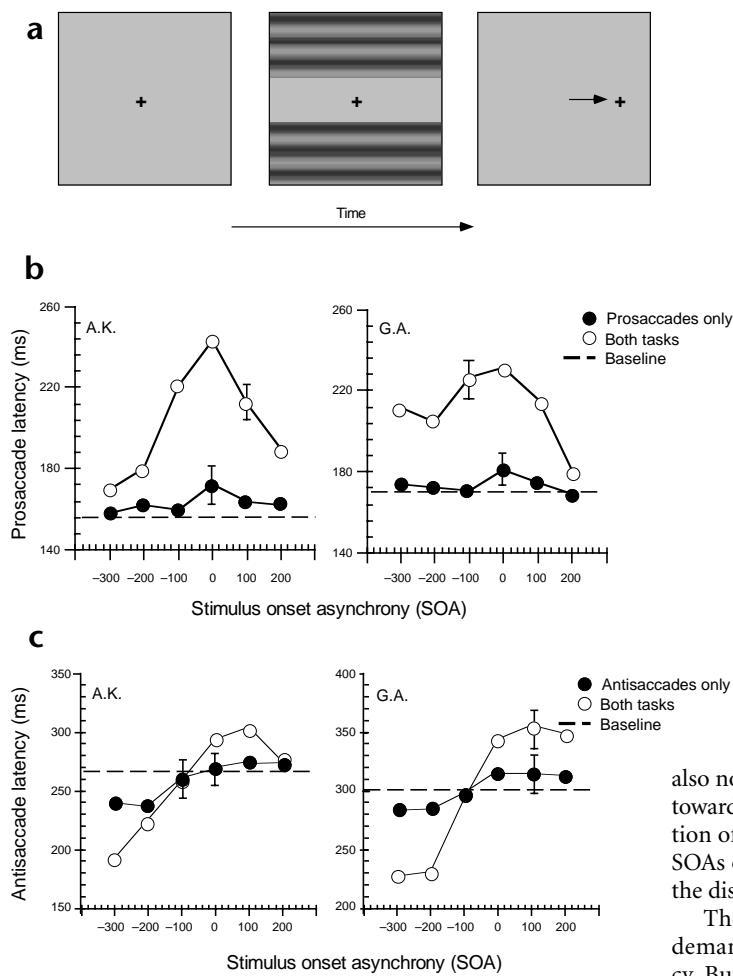


Fig. 1. Stimuli and results for experiment I. Data are shown for two representative observers. Similar results were also obtained for three other observers. (a) A trial started with the appearance of the fixation cross followed by its displacement and the presentation of the stimuli for the discrimination task. The task was to make a prosaccade or antisaccade as soon as the saccade target was displaced and to judge which of two sinusoidal gratings was of higher spatial frequency. The response to the discrimination task was to be given only after the saccade was completed. Within each prosaccade or antisaccade block, the two tasks were presented at six different times relative to each other (6 different SOAs). They ranged from -300 ms (discrimination stimulus appeared 300 ms before the saccade target moved) to +200 ms (the target moved 200 ms before the discrimination stimulus was presented). In the figure, the discrimination task appears before the target displacement ($SOA < 0$). (b) Prosaccade latencies as a function of SOA. Black circles denote trials when only the prosaccades were to be made but the stimuli for the discrimination were still presented. White circles denote the trials on which both the saccade and discrimination tasks were to be performed. Dashed lines denote baseline prosaccade performance (measured without the presence of the grating stimuli). Error bars show the largest standard error for each condition. (c) Antisaccade latencies as a function of SOA. The different symbols denote conditions similar to those described for Fig. 1b above.

also no systematic variation in the number of reflexive saccades toward the saccade target in the antisaccade condition, as a function of SOA (Table 1). The prosaccade latencies were slowest at SOAs of 0, most likely due to interfering effects of the onset of the discrimination stimulus.

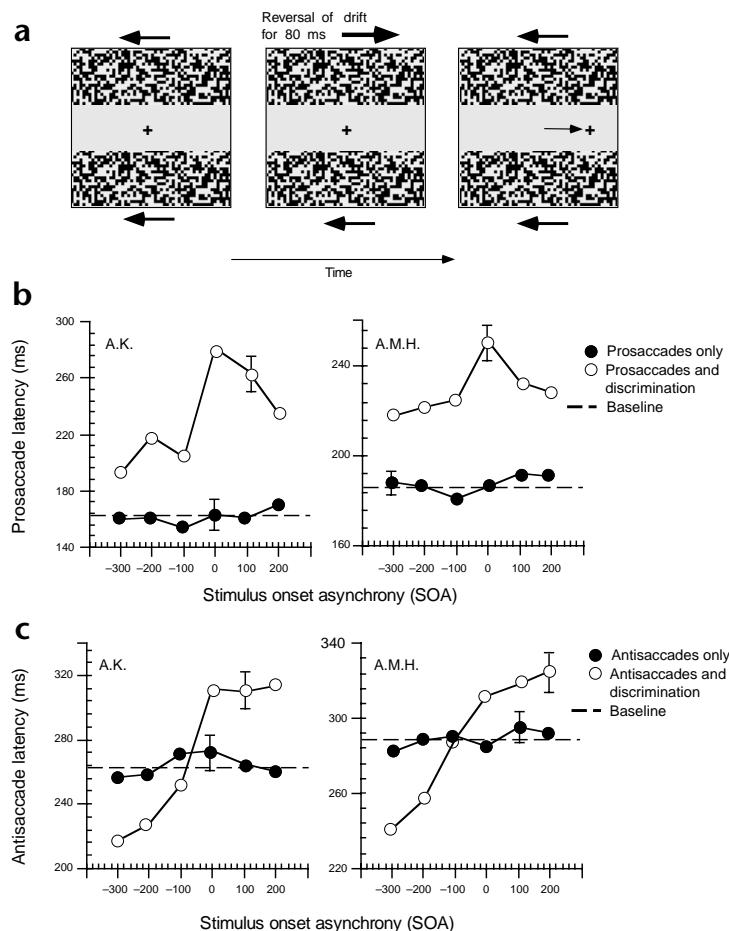
These results suggest that the presentation of an attention-demanding task before an antisaccade can decrease its latency. But how do we explain the attenuated pattern of the same results in the control condition, in which an antisaccade is to be made but the discrimination task is to be ignored? The grating stimulus by itself leads to a small reduction in antisaccade latencies (black circles, Fig. 1c). Abrupt onsets of stimuli can capture attention involuntarily^{20,21}, and this capture can be modulated by the expectations of the observer^{22–24}. It is possible that the phenomenon of speeded antisaccades is sensitive to involuntary diversions of attention as well as task-related diversions. This may have occurred in the control condition because the grating onset was abrupt and highly visible. To address this issue and to generalize the results more fully, we conducted an experiment in which an involuntary attentional diversion was less likely.

Table 1. Percentage of erroneous prosaccades in the antisaccade condition during performance of secondary discrimination tasks.

SOA (ms)	Experiment number		
	1	2	3
-300	3.1	2.6	3.2
-200	3.3	2.7	4.0
-100	3.5	3.1	3.9
0	4.3	4.1	3.7
100	3.4	4.3	4.1
200	3.3	4.2	3.3

Data are for the first three experiments, averaged across subjects.

Fig. 2. Stimuli and results for experiment 2. Data are shown for two representative observers. Similar results were obtained for two other observers. (a) A trial started with the appearance of the fixation cross along with two random-dot patterns drifting in the same direction at the same speed. At some unpredictable time, one of the drifting random dot patterns reversed its direction of drift for 80 ms before resuming its drift in the same direction as before. The two tasks were presented at six different times relative to each other (6 different SOAs) ranging from -300 to 200 ms. In the figure, the discrimination task is presented before the target displacement (SOA < 0). (b) Prosaccade latencies as a function of SOA. Black circles denote trials when only the prosaccades were to be made but the stimuli for the discrimination were still presented. White circles denote the trials on which both the saccade and discrimination tasks were to be performed. The dashed lines denote prosaccade performance measured without the grating stimuli. Error bars show the largest standard error for each condition. (c) Antisaccade latencies as a function of SOA. The different symbols denote conditions similar to those described for Fig. 2b above.



Secondary task with no luminance changes

In this experiment, the saccade task was the same as before, but the discrimination task did not involve a strong luminance onset. Two random dot patterns drifted in the same direction at the same speed above and below the saccade stimulus (Fig. 2a). At an unpredictable time, one pattern reversed its direction of drift for 80 ms and then continued in the same direction as before. The observers indicated which of the two patterns reversed direction. As in the previous experiment, the reversal could occur at any one of six different SOAs relative to the displacement of the saccade target. The average luminance of the drifting patterns was constant throughout each trial. Here we expected to replicate the pattern of results seen in Experiment 1, but more cleanly, as the discrimination task was less likely to divert attention in the control condition.

As expected, prosaccade latencies increased at all SOAs relative to baseline in the dual task condition (Figs. 2b and c). Also, confirming our basic finding, antisaccade latencies decreased at SOAs of -300 to -100 ms and increased at the SOAs of 0 to 200 ms. Antisaccades in the control condition, where the secondary task was to be ignored, were at baseline and did not depend on SOA, suggesting that an involuntary diversion of attention by the grating discrimination task was responsible for the small speed-up of antisaccades in the control condition of experiment 1. Thus, we conclude that the speed-up of antisaccades depends on performance of the secondary task, not merely its presentation.

Small luminance changes of saccade target

So far, the results have shown a paradoxical shortening of antisaccade latencies if attention is diverted away from fixation and deployed for the comparison of stimuli in the upper and lower visual hemifields. This might suggest that diversion of attention from fixation is responsible for the phenomenon. Removal of attention from fixation, for example, has been shown to speed prosaccades, leading to the phenomenon of express saccades^{25,26}. A possible broader conclusion, however, is that removal of attentional resources from the programming of saccades, whatever the cause, is critical. One way to explore this is to manipulate visual attention without presenting stimuli in the periphery. Most direct would be to require observers to pay greater attention to the target responsible for eye movement control itself, namely the stimulus controlling gaze direc-

tion. In the third experiment, we investigated this by requiring a visual discrimination at the point of fixation.

Again, the observers made prosaccades or antisaccades when the saccade target was displaced. The discrimination task was to indicate whether the target became briefly (for 80 ms) lighter or darker (Fig. 3a). As before, prosaccade latencies increased at all SOAs when the secondary task was performed (Fig. 3b, white circles). Antisaccade latencies, however, decreased to below baseline levels when the secondary task was presented before the target displacement, but increased when the task was presented with or right after target displacement (Fig. 3c, white circles). These results were confined to the trials in which the task was to be performed; when the same stimulus configuration was presented when observers were asked to ignore the secondary task, saccade latencies were similar to the baseline performance (Fig. 3b and c, black circles).

These results show that attentional disengagement from eye-gaze targets was not responsible for the observed effects on prosaccade and antisaccade latencies. Even though the visual discrimination was confined to the fixation, the results were similar to the previous two experiments. In all cases, there was a clear decrease in antisaccade latency when attention was tied up with a visual discrimination task right before the target displacement. The exact locus of the discrimination is thus not critical for the observed result. These results exclude the possibility that the speeded antisaccades are simply due to the withdrawal of attentional resources from the saccade target at a critical time, because, as the saccade target is also the discrimination stimulus, attention is presumably bound to the saccade target at all times.

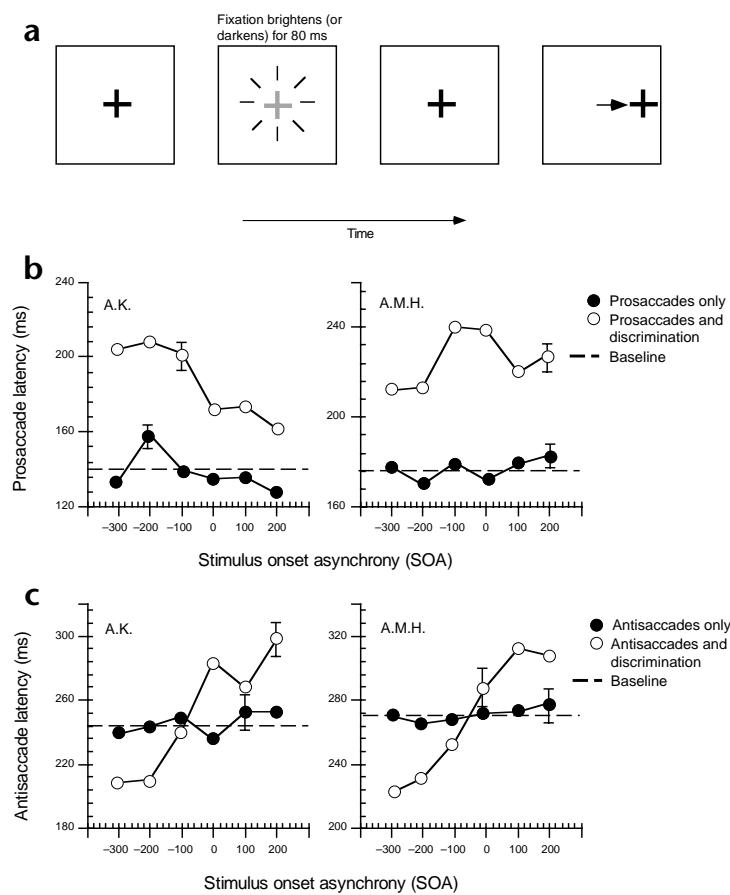


Fig. 3. Stimuli and results for experiment 3. Data are shown for two representative observers. Similar results were obtained for two other observers. (a) A trial started with the appearance of the fixation cross at the center of the screen. The two tasks (saccade displacement and the brightening or darkening off the fixation cross for 80 ms) were presented at six different times relative to each other (6 different SOAs) ranging from -300 to 200. Observers made either pro- or antisaccades and also judged whether the fixation point brightened or darkened. In the figure, the discrimination task is presented before the target displacement (SOA < 0). (b) Prosaccade latencies as a function of SOA. Black circles denote trials when only the prosaccades were to be made but the stimuli for the discrimination were still presented. White circles denote the trials on which both the saccade and discrimination tasks were to be performed. Dashed lines denote baseline prosaccade performance measured without the presentation of the secondary task stimuli. Error bars show the largest standard error for each condition. (c) Antisaccade latencies as a function of SOA. The different symbols denote conditions similar to those described for Fig. 3b above.

than prosaccades, one might expect that they would be more susceptible to attentional disruption. Yet such an account ignores the competitive nature of antisaccade programming. The eye movement system must refrain from making the more natural movement, the prosaccade^{5–7}. There is thus room for more complex and perhaps paradoxical interactions.

Therefore, we hypothesize that withdrawal of attention by the addition of a secondary task can interfere with the generation of prosaccades. This is evident in all four experiments in which the subject was instructed to make prosaccades. If the reflexive preparation of a prosaccade inhibits the initiation of an antisaccade, attention withdrawal from that process can lead to the paradoxical speeding up of the antisaccade (Fig. 5). When the antisaccade is to be made, the secondary task interferes with the reflexive prosaccade, so that an attention-demanding disengagement from that reflex is not needed. This results in faster antisaccades (Fig. 5d) but slower prosaccades (Fig. 5b) because the inhibited reflexive saccade would be the correct response for the prosaccade task, and thus, a longer time is required to make a successful prosaccade to the displaced stimulus.

The model predicts that antisaccade latencies should be reduced when the visual discrimination stimulus is presented before the saccade target, which accords with our results for SOAs of -200 to -300 ms. When the eye movement stimulus is presented first, however, the attention allocation to the visual task must occur at the second stage of antisaccade preparation or later. Under such conditions, the model predicts an increase in antisaccade latency because the visual task can no longer affect the inhibitory process but instead interferes with the generation of a saccade in the opposite direction from the stimulus (the second stage of antisaccade preparation), just like in the preparation of a regular prosaccade. Our results at SOAs of +100 to +200 ms show this increase. The model, therefore, accounts well for the different effects of the secondary task on antisaccades as a function of SOA. It is also possible that an explanation with more emphasis on sensory aspects, yet also focusing on competitive interactions between pro- and antisaccades, could account for the results. The secondary task could attenuate the sensory response to the saccade target, which would delay the prosaccade and thus increase the speed of antisaccade generation. Further research is needed to resolve this issue.

Relative timing

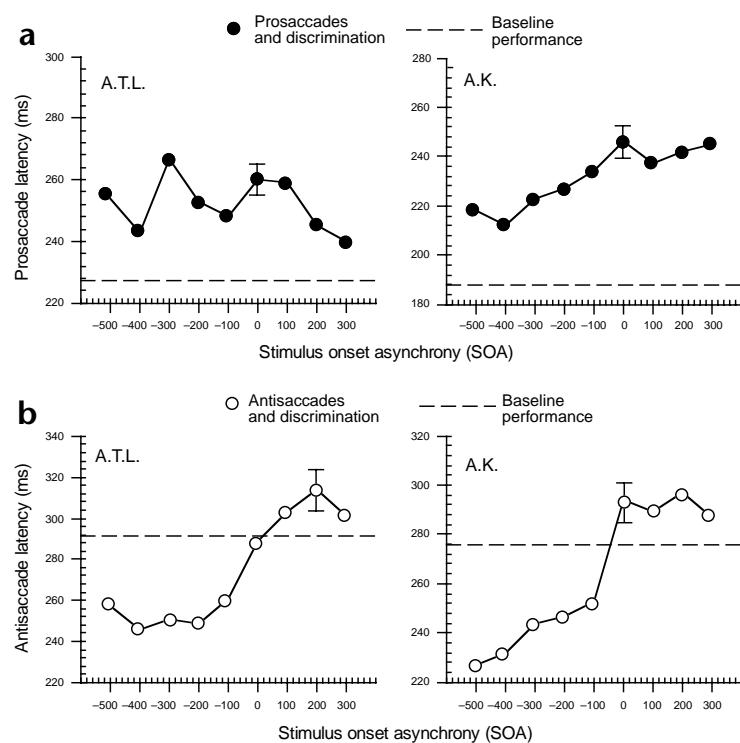
One potential complicating factor is that prosaccades and antisaccades occur at different times relative to the attentional response. As such, it may be problematic to make a direct comparison of prosaccades and antisaccades in terms of a hypothetical mediating process that affects each differently. Yet our results show that there are at least two intervals (100 ms apart) in which the visual stimulus preceded the eye movement stimulus and the results were similar (SOAs, -300 and -200 ms in all 3 experiments). To address this issue more fully, however, we extended the range of SOAs from -500 to +300 ms. If the results were confounded by the different time courses of the preparation of pro- and antisaccades, the speed-up of antisaccades at negative SOAs and the slowing down of prosaccades at all SOAs should only have been observed at a restricted range of SOAs, as we are sampling a greater range than the possible range of differences in the relative timing of pro- and antisaccades.

The results from this fourth experiment (Fig. 4) are similar to our previous findings. The speed-up of antisaccades is evident even at SOAs of -500 ms, as is the slowing effect on prosaccades at all SOAs, and on antisaccades at positive SOAs. These results exclude the possibility that the different time courses of pro- and antisaccades have a confounding effect in the experiments.

DISCUSSION

Visual attention is usually viewed as a limited resource, for which different tasks are thought to compete^{27–30}. It is therefore surprising that antisaccades can be faster with increased attentional load. Because antisaccades require more attentional processing

Fig. 4. The results from experiment 4. Apart from the larger range of SOAs tested (-500 to $+300$ ms), the methods were similar to methods in the second experiment, where the discrimination task was to judge changes in drift direction of a random-dot pattern. (a) Results for the prosaccades. (b) Results for the antisaccades. White circles denote saccade latencies when the discrimination task was also performed. Dashed lines denote baseline performance. Error bars show the largest standard error for each condition.



The neurophysiology of antisaccades

The frontal and supplementary eye fields (FEF and SEF) in the prefrontal cortex, along with the superior colliculus (SC) in the midbrain, have been implicated as key regions in the control of saccadic eye movements^{31–33}. These areas project to brain stem premotor nuclei that control eye movements. It has been suggested that the SC is responsible for reflexive saccades, whereas the FEF and SEF are involved in the voluntary control of saccades^{34–39}. Activity in the SEF is correlated with goal-directed, purposeful eye movements but not with unmotivated spontaneous movements⁴⁰. Furthermore, neurons in the SEF fire more before antisaccades than before prosaccades⁵. This activity might reflect the mechanism by which the command for an antisaccade prevents reflexive prosaccades. It was previously suggested that the suppression of a reflexive saccade may be executed through the reduction of excitatory drive from neurons in the FEF⁴¹. This drive reduction may be accomplished by the SEF neurons identified previously⁵, and may eventually influence the activity of neurons in the SC that control saccade generation⁴². The activity of those neurons differs according to whether a pro- or antisaccade is to be made.

These findings accord with the proposed scenario that antisaccades require reflex inhibition as well as subsequent saccade generation. It is possible that the secondary tasks in our experiment, when presented 100 to 300 ms before the saccade target is displaced, block the reflexive prosaccade, perhaps by suppressing excitatory input from the FEF to the SC. This, in turn, would make the suppression of this reflex unnecessary, allowing faster antisaccades because the disengagement process is cut short.

Our results may be useful in understanding the processes required for the generation of saccadic eye movements. An outstanding question is whether the principles we determined for pro- and antisaccades will hold for other competing, mutually exclusive motor responses. A protocol similar to the present one

may allow examination of the organization of motor routines and their dependence on attention.

METHODS

Stimuli and procedure. Stimuli were presented on a 67-Hz CRT screen with 8-bit grayscale resolution, controlled by a PowerPC Macintosh computer. The viewing distance was 50 cm. A bite-bar was used to stabilize head position. Observers participated in at least 120 trials under each of the four conditions of each experiment (prosaccades or antisaccades; with performance of the discrimination task, or without its performance with the discrimination stimuli still presented). The four conditions were always run on separate blocks. Baseline performance was measured on 60 trials for each observer for each experiment in the same recording session.

The saccade target in the first, second and fourth experiment was a white (51.3 candelas per square meter (cd/m^2)) cross on a gray ($21.4 \text{ cd}/\text{m}^2$) background that was displaced by 8.1 degrees. The gratings in the first experiment (Fig. 1a) had a contrast of 60% and varied in spatial frequency from 0.4 to 0.8 cycles/degree. The mean luminance of the gratings was the same as the gray background ($21.4 \text{ cd}/\text{m}^2$). The minimum spatial frequency difference between the two gratings on each trial was 0.1 cycles/degree. The gratings appeared for 80 ms at 6 (or 9 in the fourth experiment) different SOAs relative to the saccade target displacement (Fig. 1b and c). The drifting random dot patterns used in the second experiment (Fig. 2a) contained white ($51.3 \text{ cd}/\text{m}^2$) or black

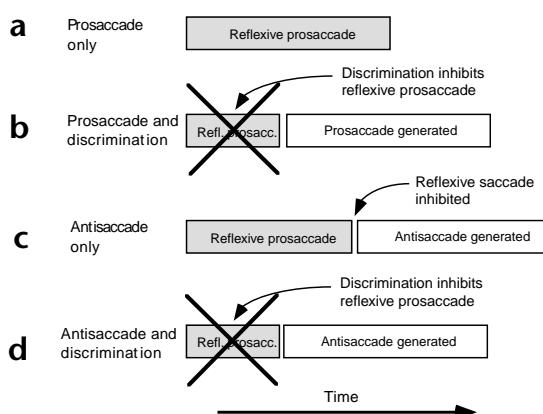


Fig. 5. A proposal for a functional explanation of the results. (a) When a prosaccade is to be performed on its own, the task is completed relatively fast. (b) When a discrimination task is to be performed concurrently with the prosaccade, a reflexive saccade toward the stimulus is inhibited so that the time taken to accomplish the task is longer than it would be otherwise. (c) When an antisaccade is to be performed on its own, latencies are relatively long, as not only must a voluntary saccade be made away from the stimulus, but a reflexive prosaccade towards the stimulus needs to be inhibited as well. (d) When both an antisaccade and a discrimination are to be made, the secondary task interferes with the reflexive prosaccade, allowing faster generation of the voluntary antisaccade.



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(0.5 cd/m²) dots subtending 6 arc min. The patterns drifted at a rate of 7 degrees/s. Either the upper or lower pattern reversed its direction of drift for 80 ms at six different SOAs relative to the target displacement. The discrimination task in the third experiment was to decide whether the saccade target itself brightened or darkened (for 80 ms). The luminance of the target was 40.2 cd/m²; the luminance was 51.3 cd/m² when the target brightened and 5.6 cd/m² when it darkened. In the fourth experiment, the methods were similar to those described for the second experiment except that we tested 9 different SOAs, ranging from -500 to +300 ms. In all four experiments, observers were instructed to make either prosaccades to the displaced stimulus, or antisaccades of equal size in the opposite direction from the target. They were asked to make the saccades as fast as possible and to respond to the discrimination task, by pressing the appropriate key, only when the saccade was completed. Observers were informed by an auditory signal whether their response to the discrimination task was correct or incorrect. The experiments were run in a darkened room. The only visible light came from the CRT display.

Eye movement recording. An Ober2 infrared reflection system was used for eye movement recording, sampling eye position with a temporal resolution of 250 Hz (experiment 1) and 500 Hz (experiments 2, 3 and 4). To linearize eye position with the measurements of the system, the eye position was calibrated at the start of each recording session.

Data analysis. The eye tracking records were analyzed offline to obtain the latency and amplitude (not reported here) of the saccadic eye movements. Saccades with latencies two standard deviations above the mean latency were dropped from the analysis, as were saccades that landed more than two standard deviations away from the average landing point. For any given block of 60 trials, no more than 4.1% of the trials were dropped from the analysis.

Observers. Although we presented data for only two representative observers for each experiment, five observers participated in the first experiment, four in the second and third experiment and two in the fourth experiment. All had normal or corrected to normal vision and were 28–36 years old. All observers except for authors A.K. and Y.C. were unaware of the purpose of the experiment. Before data collection, observers were trained on both the pro- and antisaccade task with the secondary discrimination task, for at least 200 trials.

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