The Magnitude of the Fixation Offset Effect with Endogenously and Exogenously Controlled Saccades

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Abstract

■ Two experiments examined saccadic reaction time (RT) in response to visual targets as a function of fixation offset condition (no offset; target simultaneous with offset and 200-msec offset-target SOA) in prosaccade and antisaccade tasks. The second experiment also included a condition in which saccades were made in response to verbal commands presented auditorally. To ensure that observers were equally prepared in each condition, auditory warning tones preceded target onset on every trial. The RT reduction associated with fixation offset (FOE, or gap effect) was identical with visual targets in the prosaccade task and in response to verbal signals, strongly implicating motor, rather than sensory, mechanisms in the FOE. The FOE in the antisaccade task was significant, but it was also significantly smaller than in the other tasks. We speculate that the reduced FOE in the antisaccade task may be due to the requirement to inhibit the superior colliculus when the target directed saccadic programs are, by instruction, erroneous. ■

INTRODUCTION

Saccadic latencies toward a peripheral target are reduced when the fixation stimulus is extinguished prior to target onset (Saslow, 1967). Indeed, in some conditions subjects may execute many stimulus controlled saccades within 100 msec or less of target onset (e.g., Fischer & Ramsperger, 1984; Kingstone & Klein, 1993), and the term "express saccades" coined by Fischer and colleagues (Fischer & Boch, 1983; Fischer & Ramsperger, 1984) has come to be widely used to refer to an early peak in a bimodal distribution with saccadic latencies that are thought to be due to this oculomotor reflex. Such very rapid saccades undoubtedly contribute to the reaction time (RT) reduction that accompanies fixation offset; however, because many researchers have failed to obtain results (such as a bimodal distribution of saccadic RTs) that would unambiguously classify a particular saccade as "express" (see Kingstone & Klein, 1993, for a review), in this study we will focus our attention on the reduction in latency that accompanies removal of the fixation stimulus. We will refer to this reduction (RT with fixation present, minus RT when fixation has been removed) as the fixation offset effect (FOE).

In recent years, primarily because of the work of Fischer and colleagues, there has been much interest in the psychological and neural mechanisms that might mediate this effect (e.g., Fischer & Weber, 1993; Schiller, Sandell, & Maunsell, 1987). Converging evidence suggests that the FOE depends on the reflexive orienting and fixation maintaining machinery of the superior col-

liculus (e.g., see Dorris & Munoz, 1995; Fischer & Weber, 1993; Munoz & Wurtz, 1992, 1993; Schiller et al., 1987). In this study we will explore a behavioral strategy that has contributed to this conclusion.

The FOE is observed when subjects make eye movements toward targets; but are they observed when the subject, under instructions from the experimenter, must look away from a visual stimulus? Although saccades in both cases are voluntary (in the sense that they are not obligatory), looking toward a stimulus (prosaccade) makes natural use of the saccade generating circuitry of the superior colliculus. In contrast, looking in the opposite direction (antisaccade) requires (1) the strategic generation of the appropriate saccadic parameters and (2) that any saccadic programs reflexively generated in the superior colliculus be overcome. We will use the term exogenous to refer to the psychoneural system(s) that is responsible for the control of reflexive, stimulus-driven saccades, and we will use the term endogenous to refer to the psychoneural system(s) that is responsible for the control of voluntary saccades whose metrics are not directly specified by the stimulus (see Klein, Kingstone, & Pontefract, 1992, for a discussion of this distinction). In the monkey, Schiller et al. (1987) found that superior colliculus lesions eliminated all saccades in the 100 msec range (express saccades). Guitton, Buchtel, and Douglas (1985) demonstrated that people suffering from frontal lesions had a particular difficulty making antisaccades, and they associated this deficit with lesions to the frontal eye fields (but see Pierrot-Deseillegny, Rivaud, Gaymard, & Agid, 1991, for a more precise localization of

this deficit to the prefrontal cortex). Consideration of these findings together with those of Schiller, True, and Conway (1980) that monkeys can make saccades following lesions of either the superior colliculus or frontal eye fields, but lose this ability when both areas are removed, makes it reasonable to suggest that the superior colliculus is associated with exogenous control while frontal systems are associated with endogenous control.

In this context, the proposal that the FOE is mediated by circuitry in the superior colliculus would seem to imply that there might not be a FOE with endogenously generated saccades. As we shall see, the literature on this question is characterized by methodological differences and empirical conflicts. One aim of this paper is to help resolve some of these conflicts. The main findings and possibly important methodological features of the existing studies on this question, which are reviewed below, are shown in Table 1.

As far as we know, Klein (1977) was the first to combine the removal of the fixation point with the antisaccade task. In his study the fixation point was present throughout the trial or was extinguished *simultaneously* with target onset (0-msec offset-target SOA). Peripheral markers were used (to provide a "landing place" for the antisaccades) and catch trials were included to discourage anticipatory eye movements. In his second experiment saccadic latencies in prosaccade and antisaccade tasks were compared in both simple (all eye movements in one direction regardless of the side of the stimulus, which was the brightening of one of the peripheral markers) and choice tasks. Saccadic latencies were longer in the antisaccade than prosaccade conditions, and all conditions showed a reduction in saccadic RT when the fixation stimulus was removed. In the choice task (in this paper we will focus on the choice task where the saccade direction cannot be specified until the target appears) the FOE was nonsignificantly larger in the antisaccade than in the prosaccade condition. However, because there were many more errors in the antisaccade task with the fixation removed (11%) than with fixation present (4%), it is possible that the

absence of a reduced FOE in the antisaccade task may have been due to a speed-accuracy tradeoff. It should also be noted that only three subjects were tested in this experiment.

Reuter-Lorenz, Hughes, and Fendrich (1991, Exp. 2) compared the no offset condition with one in which the fixation point was extinguished *200 msec prior* to target onset (200-msec offset-target SOA) in both prosaccade and antisaccade tasks. They did not use peripheral markers and they presented an auditory warning tone prior to target onset on every trial. In the prosaccade task prior fixation offset reduced RT by approximately 35 msec. The 8-msec FOE in the antisaccade task was not significant.

In comparing these two studies it is useful to note that in their prosaccade tasks Klein (1977) and Reuter-Lorenz et al. (1991) obtained FOEs of similar magnitude even though Klein used simultaneous fixation offsets and Reuter-Lorenz et al. used a 200-msec interval between fixation offset and target onset. Moreover, when compared with the FOE obtained in some published studies (e.g., over 100 msec in Saslow's thesis; 91 msec in Fischer & Weber, 1992, see Table 1), their FOEs of about 30-35 msec are very much smaller. This discrepancy can be explained by assuming that a portion of the FOE reported in many previous studies (those using a positive interval between fixation offset and target onset and no warning tone) is attributable to the warning signal property of the offset event (cf. Klein & Kingstone, 1993). Recognizing this possible confound, Reuter-Lorenz et al. (1991) used the tone to equate the subject's alertness and temporal uncertainty in the no offset and offset conditions. Klein's (1977) use of a target that appeared simultaneously with fixation offset may have accomplished the same thing as it takes about 200-400 msec for a subject to make optimal use of a warning signal.

Fischer and Weber (1992) investigated the FOE in both prosaccade and antisaccade tasks using no peripheral markers, no warning tone, and subjects who had previously received extensive training in the former condition. They ran the 200-msec offset-target SOA (often

Table 1. Summary of the Literature Comparing the Fixation Offset Effect with Pro- and Antisaccades[a]

Study	N	Warning tone?	Prosaccade			Antisaccade		
			No offset	0	200	No offset	0	200
Klein (1977)	3	No	279.7	249.7	—	333.7	288.7	—
Reuter-Lorenz et al. (1991)	5	Yes	185.0	—	150.0	230.0	—	222.0
Fischer and Weber (1992)	4	No	216.0	—	125.2	231.0	—	182.9/170.6[b]
Reuter-Lorenz et al. (1994)	10	No	262.3	—	197.1	312.2	—	280.5
		Yes	230.2	—	187.2	258.1	—	243.7

[a] Reaction times are shown as a function of whether the fixation stimulus remains present (no offset), is removed when the target appears (0),

referred to as gap condition) and no offset (overlap) conditions in separate blocks, and, in the context of this study, their subjects were given more trials with the antisaccade task than with the prosaccade task. The FOEs in both the pro- and antisaccade tasks were significant, and, as noted above, much larger than in the previously described studies. The FOE in the antisaccade task appears to be smaller than in the prosaccade task, but this difference was not explicitly tested.

In an attempt to understand the differences between their earlier work and Fischer and Weber's finding, Reuter-Lorenz, Oonk, Barnes, and Hughes (1995) manipulated whether or not an auditory warning tone was presented prior to target onset. The FOE was larger in the prosaccade task than in the antisaccade task whether the tone was present or absent. Both the pro- and antisaccade FOEs were more than doubled when the warning tone was absent. In contrast to Reuter-Lorenz et al. (1991), the antisaccade FOE in the tone condition (14.4 msec) was significant. The larger FOE observed by Reuter-Lorenz et al. (1995) in the antisaccade task when no warning tone was used is consistent with the findings of Fischer and Weber (1992) who did not alert subjects prior to target onset.[1] Thus, fixation point offsets act to alert the subject that the target is about to occur and when the auditory warning signal serves this purpose a purer measure of the FOE (one not contaminated by the warning signal component) is provided.

As can be seen in Table 1, the evidence indicating whether a FOE occurs in an antisaccade task, and if so whether the effect is the same as or less than in a prosaccade task, is inconsistent. Using peripheral markers and a 0-msec offset-target SOA, Klein (1977) obtained an FOE in the antisaccade task. Using a 200-msec offset-target SOA, Reuter-Lorenz et al. (1991) failed to observe an FOE in the antisaccade task when a warning tone was used, but later observed this effect (Reuter-Lorenz et al., 1995) whether or not a warning tone was used. In all studies with the exception of Klein (1977), the FOE was clearly larger in the prosaccade task but the magnitude of the FOE in the antisaccade task is highly variable across studies. Klein's unusual finding might be attributed to his use of peripheral markers, the high errors in the antisaccade task with 0-msec offset-target SOA condition (suggesting a possible speed-accuracy tradeoff), and/or to a combination of chance and low power.

EXPERIMENT 1

The present study investigated whether endogenously generated saccades (i.e., antisaccades) show an FOE and, if so, whether this effect is different in magnitude from that shown with exogenously generated saccades (prosaccades). To make contact with the literature described earlier, we compared a no offset condition with 0- and 200-msec offset-target SOA conditions (with all three occurring randomly in the same block of trials). An auditory warning signal, presented at a fixed interval prior to the saccadic target, was used to equate the three offset conditions for alertness and temporal uncertainty. Target location (4° to the left and right of fixation) was varied randomly. Whether the task was to move toward (prosaccade) or away from (antisaccade) visual targets was factorially combined with the presence vs absence of peripheral markers, and the four combinations were run in separate blocks.

RESULTS AND DISCUSSION

A four-way analysis of variance (ANOVA) [task (pro-/anti-), presence of markers (markers/no markers), offset condition (200/0/no offset), visual field (left/right)] was performed on the RT data (see Table 2). The effect of task was significant [$F(1,7) = 11.18, p < 0.025$] with prosaccades faster than antisaccades (247.3 vs 297.9 msec) as was the effect of fixation offset [$F(2,14) = 43.13, p < 0.001$]. Planned comparisons indicated that the 200-msec offset-target SOA condition (246.8 msec), 0-msec offset-target SOA condition (269.5 msec), and no offset (301.5 msec) conditions differed from each other. There were no main effects or interactions involving the presence of peripheral markers or the location of targets. The absence of an interaction ($F = 1.67$) between task and offset condition suggests that reductions in saccadic latency across conditions were similar in the prosaccade and antisaccade tasks. Contrast analyses indicated that all three offset conditions differed significantly from each other in both prosaccade and antisaccade tasks. Although the reduction in saccadic latency between the 0-msec and no offset conditions was larger in the prosaccade (40.6 msec) than antisaccade (23.4 msec) task, this difference was not significant. The additional effect of extinguishing fixation 200 msec prior to target onset (compared to the simultaneous condition) was similar in both prosaccade (21.5 msec) and antisaccade (23.8 msec) tasks.

The percentage of errors and anticipations were subjected to four-way ANOVAs (same factors as above). In the error analysis there was a significant effect of task [$F(1,7) = 20.66, p < 0.005$] with more errors being made in the antisaccade (5.99%) than prosaccade (1.43%) condition. Planned comparisons on the significant effect of offset condition [$F(2,14) = 10.94, p < 0.005$] revealed that more errors were made in the 200-msec offset-target SOA condition (7.42) than in the 0-msec offset-target SOA (2.54) or no offset (1.17) conditions, which did not differ from each other. A significant task by fixation offset interaction [$F(2,14) = 7.17, p < 0.01$] was due to a particularly high error rate in the antisaccade task with the 200-msec target-offset. A four-way ANOVA performed on the anticipations (which averaged 7.75%) did not reveal any significant main effects or interactions.

Whether measured using the 0-msec or 200-msec offset conditions we have obtained a significant FOE in the

Table 2. Reaction Time (RT), Errors, and Anticipations in Experiment 1

	Prosaccades			Antisaccades		
	No offset	0	200	No offset	0	200
Peripheral markers						
RT	287.3	246.9	231.0	331.4	303.7	283.1
%Error	0.8	1.6	3.9	2.3	3.9	10.2
%Anticipation	7.8	6.2	6.2	7.8	7.0	7.8
No peripheral markers						
RT	275.7	234.9	207.7	311.5	292.3	265.3
%Error	0.0	0.0	2.3	1.6	4.7	13.3
%Anticipation	9.4	7.8	3.9	6.2	11.7	10.9
Overall						
RT	281.5	240.9	219.4	321.5	298.0	274.2
%Error	0.4	0.8	3.1	1.2	4.3	11.7
%Anticipation	8.6	7.0	5.1	7.0	9.4	9.4

antisaccade task. This finding is in agreement with those of Fischer and Weber (1992), Klein (1977), and Reuter-Lorenz et al. (1995), who also observed an FOE in the antisaccade task. Although the FOE was larger in the prosaccade task than in the antisaccade task, this difference was not significant. Considering the direction of this effect and its similarity to the pattern observed in Reuter-Lorenz's two studies, one purpose of the second experiment was to obtain further data in these conditions to provide a more powerful test of the interaction. A second purpose was to explore saccadic performance, and determine the relative magnitude of the FOE, in a condition where generation and control of saccades might be completely endogenous (as would be the case with saccades made in response to verbal commands).

EXPERIMENT 2

Subjects in Experiment 2 were tested on three tasks in separate blocks. The pro- and antisaccade tasks from Experiment 1 were repeated (to provide additional evi-

dence on the relative magnitude of the FOE in these two tasks), and the third task involved subjects making saccades to the verbal commands "left" and "right presented auditorially." We reasoned that saccades in response to these verbal commands should depend upon purely endogenous programming, and were interested in comparing the magnitude of the FOE in this condition with those in the pro- and antisaccade tasks. Because the presence of peripheral markers had no effect in Experiment 1, and because they would be useful to subjects doing the verbal task (especially those subjects exposed to this task before the two visual ones), peripheral markers were used in all conditions.

RESULTS AND DISCUSSION

A three-way analysis of variance (ANOVA) [task (pro-saccade, antisaccade,verbal), offset condition (200/0/no offset), visual field (left/right)] was performed on the RT data (see Table 3). The main effects of task [$F(2,22)$ = 25.42, p < 0.0001] and offset condition [$F(2,22)$ = 26.72, p < 0.0001] were significant, as was the interaction

Table 3. Reaction Time (RT), Errors, and Anticipations in Experiment 2

	Prosaccades			Antisaccades			Verbal		
	No offset	0	200	No offset	0	200	No offset	0	200
RT	274.7	245.3	231.1	309.0	297.2	288.8	362.6	323.8	319.0
%Error	0.5	0	1.0	4.7	5.2	7.8	2.6	5.7	10.9
%Anticipation	7.3	9.9	7.8	4.7	6.2	2.6	10.9	6.2	6.2

between these two factors [$F(4,44) = 3.57, p < 0.05$]. Subjects were significantly faster in the prosaccade task than in the antisaccade task and were significantly faster in the antisaccade task than in the verbal task. To understand the interaction, separate three-way ANOVAs were performed on the no offset and 0-msec offset-target SOA conditions and on the 0-msec and 200-msec conditions. In both analyses there were significant effects of task and fixation offset. A significant interaction between task and fixation offset was found when no offset and the simultaneous offset conditions were compared [$F(2,22) = 4.92, p < 0.05$] but not when 0 and 200 were compared ($F = 1.05$). Planned contrasts indicated that the 0-msec fixation offset effect (no offset minus 0 msec) was greater than zero in both the prosaccade (29.4 msec) [$F(1,11) = 19.19, p < 0.05$] and verbal (38.8 msec) [$F(1,11) = 23.34, p < 0.05$] tasks but not in the antisaccade task (11.8 msec) [$F(1,11) = 3.02, p > 0.05$]. When measured using the 200-msec offset-target condition, the FOE in the antisaccade task (20.2 msec) was significant [$F(1,11) = 6.10, p < 0.05$].

Separate three-way ANOVAs (same factors as above) were conducted on the eye movement error and anticipation data. A significant effect of task [$F(2,22) = 5.09, p < 0.05$] was due to fewer errors in the prosaccade (0.5) than antisaccade (5.9) or verbal (6.4) tasks. A significant main effect for offset condition [$F(2,22) = 4.28, p < 0.05$] was found and contrast analyses indicated that significantly more errors were made in the 200-msec offset-target SOA condition (6.6) than in the simultaneous (3.6) or no offset (2.6) conditions. The overall percentage of anticipations was 6.89, but no significant main effects or interactions were observed in the ANOVA.

Four important findings are apparent in the RT data from this experiment: (1) the FOE with simultaneous offsets was larger in the prosaccade task than in the antisaccade task [confirming the findings of Reuter-Lorenz et al. (1995), and the nonsignificant trend in E1], (2) the FOE with a 200-msec offset-target SOA condition gap in the antisaccade task was significantly greater than zero, (3) the FOE in the 200 msec offset-target was exactly the same magnitude (43.6 msec) in the prosaccade task and in the purely endogenous verbally directed saccades, and (4) compared to the 0-msec offset condition, RT decreased by the same amount in all three tasks when the fixation offset preceded the command signal by 200 msec.

GENERAL DISCUSSION

The pattern of results in the pro- and antisaccade tasks was very similar in the two experiments. To optimize the power of these two experiments a four-way ANOVA [experiment (1/2), task (pro-, antisaccade), offset condition (200/0/no offset), visual field (left/right)] was performed on the RT data from the pro- and antisaccade tasks in both experiments. In this analysis, the RTs from

experiment 1 were first collapsed across the conditions with and without peripheral markers, a factor that the reader may recall did not impact on the results from that experiment. As expected there were main effects of task [$F(1,18) = 32.63, p < 0.0001$] and offset condition [$F(2,36) = 55.23, p < 0.0001$]. The interaction between task and offset condition was significant [$F(2,36) = 5.06, p = 0.0116$]. Visual inspection of these data, presented in Figure 1 (filled symbols), suggests that this interaction was due to a smaller difference in latency between no offset and the 0-msec offset-target SOA condition in the antisaccade than in the prosaccade condition. This was confirmed by statistical analyses that revealed (1) that gap condition and task interacted when no offset and 0 were compared [$F(1,18) = 6.34, p = 0.0215$] and (2) that these factors were additive when 0- and 200-msec offset conditions were compared ($F < 1$). Thus the combined results of these experiments demonstrate that an FOE is observed in an antisaccade task but is smaller than the FOE observed with the prosaccade task, a finding consistent with most of the studies reviewed in Table 1.

We have additionally shown that the FOE for saccades generated endogenously in response to verbal commands is identical in magnitude to that for prosaccades generated exogenously in response to abruptly onset visual targets.[2] This finding appears to settle the long-standing issue (Klein, 1977) of whether removal of fixation has its effect primarily on sensory (Reulen, 1984) or motor (Reuter-Lorenz et al., 1991) mechanisms. There is no overlap in the sensory processing of the visual targets and the auditory verbal commands, hence the equality of the FOEs in the prosaccade and verbal tasks strongly implies that fixation offset affects postsensory stages such as motor programming and/or execution and does not affect the accrual of sensory information.

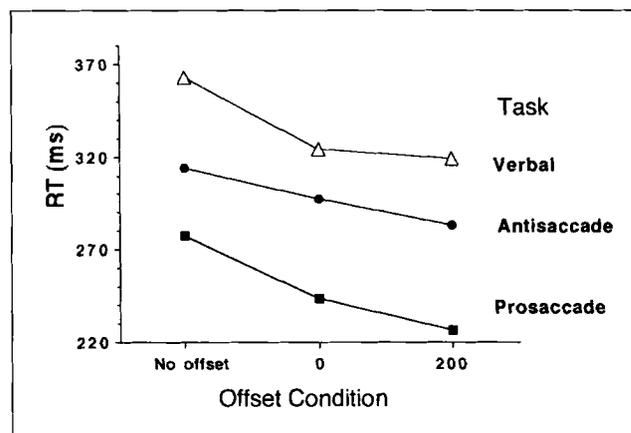The reduced size of the FOE in the antisaccade task

Figure 1. Saccadic reaction time (RT) as a function of fixation offset condition and task. The data from the prosaccade (square) and antisaccade (circles) tasks of both experiments have been collapsed and are represented using filled symbols to distinguish them from the data from the verbal task (open triangles) from the second experiment.

is not (contrary to our original hypothesis) due *merely* to the endogenous nature of the task since the size of the FOE observed in the verbal task, which is surely endogenous, was not reduced. If endogenous programming is responsible for decreasing the size of the FOE in the antisaccade task, then a comparable decrease should have been observed in the verbal task. The reduction of the FOE in the antisaccade task in comparison to the verbal task would appear to be dependent on the requirement to orient in the direction opposite to that of a visual stimulus. In this case (antisaccades) accurate performance may depend upon *inhibiting* reflexive eye movements generated by the superior colliculus to initiate an endogenously generated saccade in the opposite direction. Therefore, we speculate that the reduction of the magnitude of the FOE in the antisaccade task is due to the requirement for the reflexive machinery of the superior colliculus to be inhibited to perform accurately in that task.

Our interpretation of these findings can be described with reference to the functional diagram of the saccadic system presented in Figure 2. We assume three subsystems important in the control of saccades. One subsystem, which we refer to as exogenous (EXO), is responsible for the reflexive programming and rapid execution of saccades to visual targets. It is located primarily in the superior colliculus and it is probably useful to consider the posterior parietal cortex as a cooperating partner in its functioning (see, e.g., Pierrot-Deseillegny et al., 1991). This system contains the neural machinery [fixation cells in the rostral pole of the superior colliculus that have been hypothesized (cf. Munoz & Wurtz, 1993) to exert inhibitory control upon saccade cells in the superior colliculus and, via excitatory activation of the inhibitory omnipause neurons, in the brain

Figure 2. Diagram illustrating functional interactions between endogenous (ENDO) and exogenous (EXO) systems for controlling the execution of saccades (SAC). See text for explanation and details.

stem] that is primarily responsible for the FOE. A second system, which we refer to as endogenous (ENDO), is responsible for the strategic programming and execution of saccades when the colliculus-based "winner-take-all" algorithm would not be appropriate. It is located primarily in frontal cortex, including the frontal eye fields, supplementary eye fields (Schlag & Schlag-Rey, 1987), and prefrontal cortex and it is probably useful to consider other structures such as the caudate nucleus and substantia nigra pars reticulata as functionally related to this system. The third subsystem, which is the final common path for the control of saccades (SAC), is located in the brain stem oculomotor nucleii. It receives, from both the endogenous and exogenous systems, saccadic command parameters and "braking" signals via the omnipause neurons.

In the prosaccade task the visual input reaches both the endogenous and exogenous systems, but the exogenous control system is largely responsible for the generation of saccade parameters and signals that lead to foveation of the target.[3] When the fixation point is present the fixation system in the superior colliculus acts as a brake on the movement system through inhibitory projections within the superior colliculus and excitatory projections to the inhibitory omnipause neurons in the SAC. Removal of fixation disinhibits these systems, hence reducing saccadic latencies.

In the verbal task the imperative signal is interpreted outside of the systems shown in Figure 2. Information about where to direct the saccade eventually reaches the endogenous control system (including the frontal eye fields, prefrontal cortex, and supplementary eye fields) and saccadic program parameters generated there are transmitted in parallel to the superior colliculus (EXO) and brain stem (SAC) (Segraves & Goldberg, 1987; Schlag, Schlag-Rey, & Dassonville, 1992). As with prosaccades, in the presence of fixation the saccade command must overcome inhibition originating in the fixation system of the rostral pole of the superior colliculus. We assume that the efficacy of this inhibitory subsystem depends on the degree to which the superior colliculus itself may be inhibited and that whether performing saccades toward targets or in response to verbal commands, there is little or no net inhibition of the superior colliculus at the time of the imperative signal.

In contrast, in the antisaccade task we assume that the superior colliculus is tonically inhibited by the endogenous control subsystem in advance of the target stimulus.[4] This inhibition, once thought to originate in the frontal eye fields (Guitton et al., 1985) apparently originates in the prefrontal cortex (Pierrot-Deseillegny et al., 1991). The saccade parameters are computed (on the basis of the visual input combined with the instructional set) and, as with the verbal task, then transmitted by the endogenous control system in parallel to the superior colliculus (EXO) and brain stem (SAC). The inhibition of the superior colliculus is maintained and, therefore, the
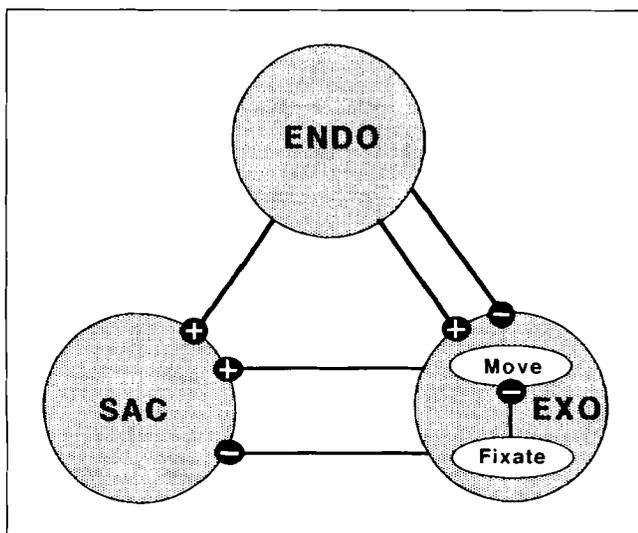
FOE is reduced because there will be less inhibition from the fixation system to be overcome by the endogenously generated saccadic program. It is also possible that inhibition of the exogenous system is removed sometime after the target is presented, perhaps while the saccade parameters are simultaneously delivered to the superior colliculus—which then would play a functional role in the production of the saccade. We think this is unlikely for two reasons: (1) following such release there would be many errors as the original exogenously generated saccadic program might often win out over the endogenously generated one, and (2) if inhibition of the colliculus were released then we would not expect the FOE to be reduced in comparison with the verbal or prosaccade tasks.[5]

Our speculative proposals should, of course, be tested. We will pursue this in behavioral experiments. There are several assumptions and proposals we have made that might be assessed in neuropsychological or neurophysiological studies, some of which are described below. For example, if the frontal eye fields are responsible for endogenously generating saccadic program parameters, and saccades in the verbal task were so generated, then the ability of patients with lesions involving the frontal eye fields to make saccades to verbal commands should be disrupted. According to our proposals, in monkeys with superior colliculus lesions, pro- and antisaccades might show identical FOEs. Assuming that the prefrontal cortex's role in importance for resisting incorrect reflexive glances in the antisaccade task is via the substantia nigra pars reticulata's inhibitory control of the superior colliculus, then antisaccade performance in monkeys with lesions of the prefrontal cortex (but sparing the frontal eye fields, which may be necessary for generating the saccade parameters) should be improved by chemical or electrical activation of the substantia nigra pars reticulata. The evidence we have marshalled in support of the proposal that inhibition of the exogenous system is necessary for correct performance of the antisaccade task is indirect and subject to counterargument. Direct evidence on this question, such as might be provided by single cell recordings from the colliculus during the antisaccade task, would be desirable. Another approach would be to measure the threshold stimulation required to elicit saccades from the frontal eye fields and superior colliculus at various points of time in relation to fixation offset and target onset in animals performing the antisaccade and prosaccade tasks.

METHODS

Experiment 1

Subjects

Eleven Dalhousie University graduate and undergraduate students with normal or corrected-to-normal vision participated in the experiment on a volunteer basis. The data from three subjects were excluded because of extremely high eye movement errors or anticipations (greater than 31% in any condition). It should be noted that preliminary analyses indicated that the results of the study did not change when these subjects were included in the sample.

Apparatus, Design, and Procedure

Visual stimuli were presented on a 604 oscilloscope in a dark room and subjects were dark-adapted for several minutes before the experiment began. Subjects sat with their head placed in a chin rest that was 46 cm from the oscilloscope screen. Eye positions were calibrated prior to each block of stimuli so that erroneous eye movements, blinks, and anticipatory movements could be identified.

Subjects began each trial by pressing a thumbswitch with one hand, at which time an Eyetrac 210 eye movement monitor began sampling the horizontal position of the left eye every 2 msec. After 1300 msec a 100-msec warning tone (1500 Hz) was turned on 300 msec (and turned off 200 msec) prior to the appearance of the target, which was a 0.5° diameter circle centered 3.7° to the left or right of fixation. The oscilloscope, thumbswitch, and Eyetrac monitor were interfaced with a MBD 11-23 computer, which was used to present stimuli and record responses.

A central fixation point (i.e., plus sign) was presented at the beginning of each trial. There were four types of experimental blocks of trials generated by the factorial combination of saccade task (pro- and anti-) and presence/absence of target markers. During the prosaccade task subjects made a saccade as quickly as possible to the left or right in the direction of the visual target (i.e., empty circle) when it appeared. In the antisaccade task subjects were instructed to make a saccadic eye movement in the direction opposite the visual target. In half the stimulus blocks for each task dots were displayed in the left and right periphery to mark the possible target locations (and when it appeared, the target stimulus was centered around the dot). Presentation of the four blocks was pseudorandomized: half the subjects completed both prosaccade blocks followed by both antisaccade blocks, whereas the remaining half were tested in the reverse order. Within a task the order of marking conditions was also counterbalanced across subjects.

In all blocks three fixation offset conditions were randomly intermixed: The fixation point was extinguished 200 msec prior to or simultaneously with target onset or was not extinguished. In the experimental blocks there were 16 trials in each offset condition, 8 with left side targets and 8 with right side targets. Subjects completed a prosaccade and antisaccade practice block that consisted of 12 trials with each offset condition presented equally prior to beginning the corresponding experimental blocks.

Subjects received visual feedback after completing each trial. If the correct saccadic response was made the latency was presented on the screen. However, if the saccade was made in the wrong direction then "EYE ERROR" was presented. Similarly, if blinks, anticipatory (prior to the target onset), or slow (greater than 900 msec) responses were made then one of the following messages appeared, as appropriate: "BLINK?," "TOO SOON," "TOO SLOW." Trials were aborted and coded as misses if no eye movement was detected within 900 msec of the imperative signal.

Experiment 2

Subjects

Twelve new subjects, recruited as above, were used in this experiment.

Design and Procedure

The design for the experiment was the same as the previous one with two exceptions. Peripheral markers were present in all blocks (since no significant differences from their presence or absence in the periphery were observed in Experiment 1). Second, another task condition was included in the design, which involved verbal commands. In this condition, the direction of eye movement was indicated by an electronic voice (Dectalk) that said either "left" or "right." The order of presentation for the three tasks was counterbalanced across subjects.

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Notes

1. It should be noted that even when they did not use a tone, Reuter-Lorenz et al.'s (1995) observers did not show as large an FOE as did Fischer and Weber's (1992). This might be due to the fact that Reuter-Lorenz et al. mixed no offset and 200-msec offset-target SOA conditions, whereas Fischer and Weber blocked these conditions. Alternatively, this difference may be due to the high level of training in the Fischer and Weber study.
2. Recently Abrams, Oonk, and Pratt (1995) compared endogenously generated saccadic latencies in overlap and 200-msec offset-target SOA conditions. The imperative signal was a high or low tone to which the subject made leftward and rightward saccades (respectively) to rectangular markers that were part of the fixation display. They obtained an FOE of about 20 msec in this situation, demonstrating, as does our Experiment 2, that endogenously generated saccades do show a fixation offset effect. Abrams et al. (1995) do not report what the magnitude of the FOE would have been with exogenously directed saccades, so their study cannot be used to confirm or disconfirm our finding of identical FOEs in these two conditions.
3. This is suggested by the fact that the average and modal latencies for visually responsive neurons are much shorter in the superior colliculus (Goldberg & Wurtz, 1972) than in the frontal eye fields (Bruce & Goldberg, 1985) and the prefrontal

cortex (Funahashi, Bruce, & Goldman-Rakic, 1990); see also note 4), and by the findings that saccade initiation is greatly delayed by superior colliculus lesions (Schiller et al., 1987) while frontal lesions have little impact on visually guided saccades (Schiller et al., 1980).
4. Although it is possible that the endogenous control systems inhibit the exogenous control system in response to the visual signal, we think it is more likely the inhibition is instituted in advance. First, since the subject knows in advance that she or he is required to look away from the target, performance will be most efficient if the reflexive system can be inhibited before the stimulus. Second, chronometric analysis of the visual responses of single cells in the different systems, as well as the minimum latency of goal-directed saccades (80 msec in the monkey), suggests that stimulus-released inhibition would be too late to prevent a reflexive foveation of the stimulus. The latencies of visual responses of cells in the frontal eye fields and prefrontal cortex are too slow (range = 60-150+, median = 92 in the frontal eye fields, Bruce & Goldberg, 1985; range = 37-309, mean = 134, median = 116, mode = 80-100, in the prefrontal cortex, Funahashi et al., 1990) in relation to the visual afferent time to the superior colliculus (range = 40-50, Goldberg & Wurtz, 1972) to prevent the rapid, reflexive machinery of the superior colliculus from reaching the point of no return.
5. Kopecz, K. (1995). Saccadic reaction time in gap/overlap paradigms: A model based on integration of intentional and visual information on neural dynamic fields. *Biological Cybernetics, 35*, 2911-2925.

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