

RESEARCH NOTE

Douglas P. Munoz · Brian D. Corneil

Evidence for interactions between target selection and visual fixation for saccade generation in humans

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The present study was designed to test the hypothesis that target selection and visual fixation interact to influence saccade generation in humans. In a two-stage task, subjects were required to select a target and then fixate on it before making a saccade. The results show that saccade latencies were significantly longer when the target and fixation points were in different hemifields compared to when they were in the same hemifield. This effect was not observed when the target and fixation points were in the same hemifield but at different eccentricities. The results are consistent with the hypothesis that target selection and visual fixation interact to influence saccade generation in humans. The results also suggest that the interaction between target selection and visual fixation is not simply a function of eccentricity, but is also a function of hemifield. The results are discussed in terms of the underlying neural mechanisms that may be responsible for this interaction.

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Abstract We examined the processes controlling selective orientation, specifically the processes required for generating saccadic eye movements in humans. Before a saccadic eye movement can be initiated, active visual fixation must be disengaged from the current point of fixation and a new target selected. We investigated whether these neural processes occur independently or interactively by devising a simple, multimodal choice reaction task in which subjects were asked to direct their gaze away from a central visual fixation target to an eccentric visual target while ignoring a simultaneous auditory distractor. Subjects had more difficulty suppressing incorrect movements toward the distractor when the fixation target was extinguished prior to onset of the eccentric target than when the fixation target remained illuminated during eccentric target presentation. Subjects with the shortest saccadic reaction times produced the most incorrect movements. These results support a recent hypothesis suggesting that the processes of disengaging active visual fixation and selecting a new saccade target are interrelated and arise, at least in part, from a change of activity within the superior colliculus.

Key words Eye movement · Saccade · Visual fixation
Target selection · Human

Introduction

Saccadic eye movements are used to shift the visual axis rapidly from one target of interest to another. During each intersaccadic interval the eyes remain fixed on the target and the visual system may perform an analysis of the image. One hypothesis on the generation of saccadic eye movements states that, prior to the initiation of the impending saccade, attention must be disengaged from

the current point of fixation, a decision to make a saccade to the target must be made, and the metrics of eye rotation required to foveate the new target must be computed (Mayfrank et al. 1986; Fischer 1987; Fischer and Weber 1993). The time required to complete each of these processes contributes to the saccadic reaction time. In an experimental setting, when a fixated visual stimulus jumps to a new location, refixation saccades are triggered after about 150–200 ms (Westheimer 1954). Reaction times are increased to between 200 and 250 ms when the initial fixation target remains illuminated after the appearance of the new saccade target (overlap task; Fig. 1A), and are reduced to a minimum of about 120 ms when the initial fixation target disappears 200 ms before the new target appears (gap task; Fig. 1B) (Saslow 1967; Fischer and Ramsperger 1984; Mayfrank et al. 1986; Kalensnykas and Hallett 1987; Reuter-Lorenz et al. 1991; Wenban-Smith and Findlay 1991). The difference in saccadic reaction times between the gap and overlap conditions, a phenomenon termed the gap effect, is presumed to be related to the state of fixation at the time of target onset (Fischer 1987; Fischer and Weber 1993). In the overlap task, attention is actively engaged upon the point of fixation when the peripheral target appears. This active fixation must be broken prior to the initiation of movement, thereby increasing the reaction time. In the gap task, the 200-ms period without stimuli is thought to facilitate the disengaging of attention from fixation prior to target onset, lowering reaction latencies by reducing or removing one of the saccade-generating processes.

How does this change in reaction latency and presumed differences in states of visual fixation, observed between the overlap and gap paradigms, affect the capabilities of a human subject to select the correct saccade target? To examine the interaction between the processes of visual fixation and selection of the next saccade target we devised a multimodal choice reaction task. Human subjects were asked to look as quickly as possible from a central visual fixation point (FP) to an eccentric visual target (T) and ignore a simultaneously presented auditory stimulus. The T appeared in the overlap (Fig. 1A) and

D. P. Munoz (✉) · B. D. Corneil
MRC Group in Sensory-Motor Physiology,
Department of Physiology, Botterell Hall,
Queen's University, Kingston, Ontario, Canada K7L 3N6;
Fax no: +1-613-545-6840; e-mail: doug@biomed.queensu.ca

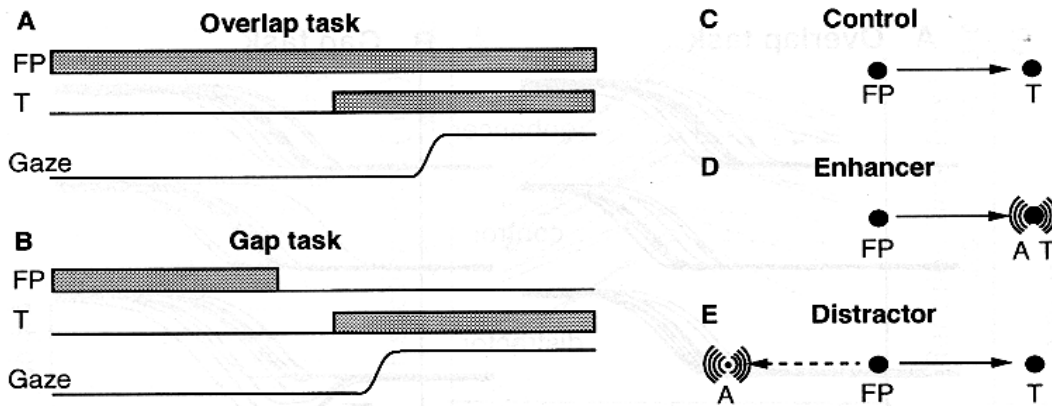


Fig. 1A–E Schematic representation of the experimental paradigms. **A** In the overlap task, the fixation point (*FP*) remained illuminated while the eccentric visual target (*T*) came on. **B** In the gap task, the *FP* was turned off 200 ms prior to *T* onset. **C** In the control condition, only *T* appeared either 40° to the right or left of the *FP*. **D** In the enhancer condition, a suprathreshold auditory stimulus (*A*) was presented simultaneously with *T* at the same location. **E** In the distractor condition, *A* and *T* were presented simultaneously, but on opposite sides. The control, enhancer, and distractor conditions were randomly intermingled among the overlap and gap tasks. **C–E** *Solid lines* represent correct movements, and the *dashed line* signifies an incorrect movement

gap (Fig. 1B) conditions and was either presented alone (control; Fig. 1C) or together with a suprathreshold auditory stimulus (*A*), located at the same site as the visual target (enhancer; Fig. 1D) or on the opposite side (distractor; Fig. 1E). Auditory stimuli were used as distractors because the afferent delay for transmission of auditory information into the central nervous system is less than the visual afferent delay. For example, auditory information reaches the deeper layers of the cat superior colliculus in about 10 ms only (Wise and Irvine 1983; Middlebrooks and Knudsen 1984; Hirsch et al. 1985), while it takes about 60 ms for visual information (Syka et al. 1979; Peck et al. 1980; Meredith et al. 1987; Guitton and Munoz 1991). Therefore, information specifying the location of the auditory stimulus would reach the superior colliculus before information specifying the location of the visual target. The presentation of the auditory cue could lead to several possible outcomes: (1) it could have no effect on subject performance; (2) it could modify the saccadic reaction times; or (3) in the case of the distractor, it could lead to the generation of directional errors if subjects incorrectly look to the auditory cue and not the visual target (dashed line in Fig. 1E). We wanted to compare subject performance in the distractor-overlap and distractor-gap conditions in which fixation was either actively engaged or disengaged, respectively, when the targets were presented. We found that subjects had difficulty selecting the correct target only in the distractor-gap condition.

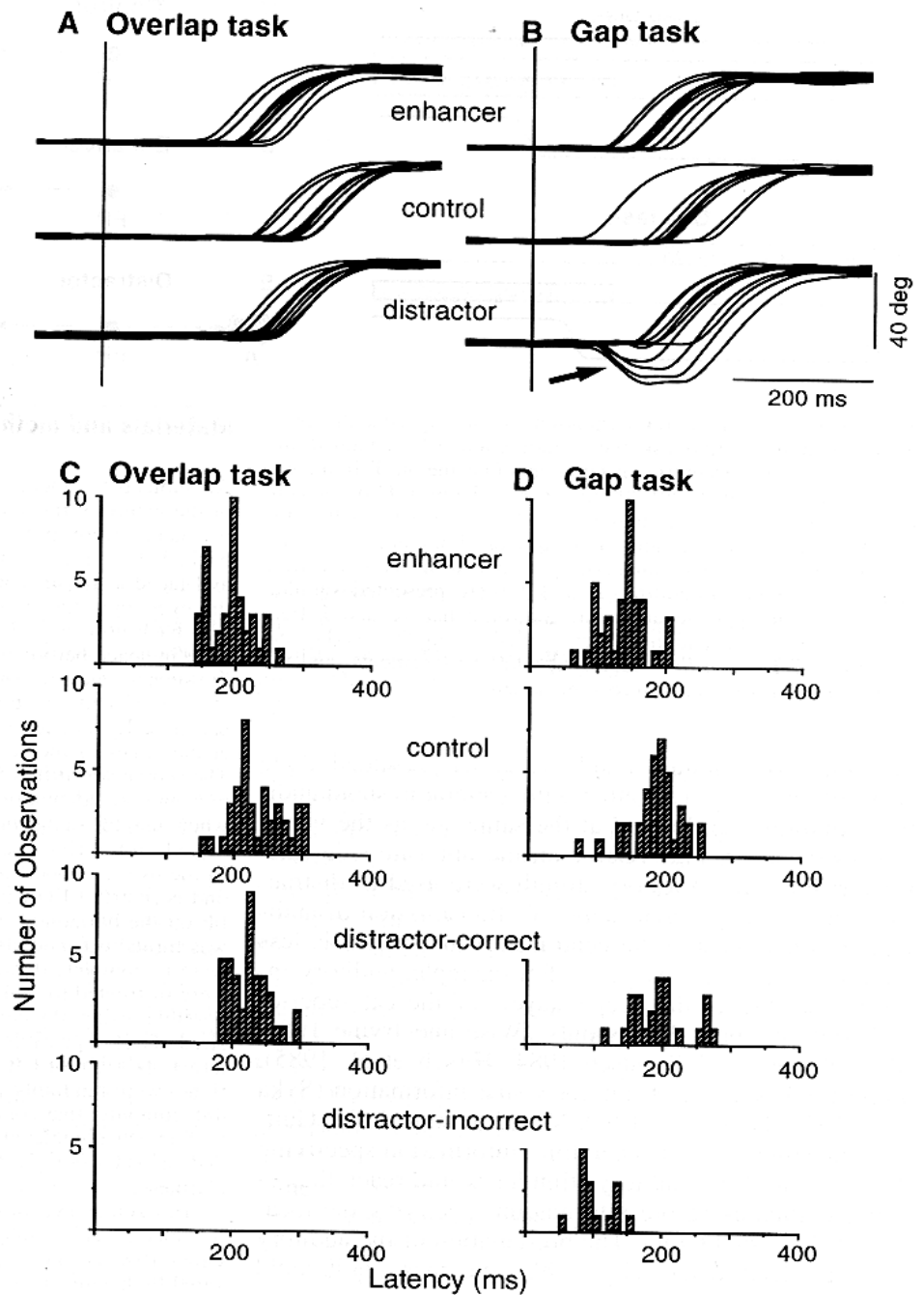
Materials and methods

All subjects (12 men, 5 women, aged 21–35 years) were informed of the nature of the study and consented to participate before experiments were initiated. Subjects were seated in a straight-backed chair in the center of a sound-attenuated, light-tight room and faced a translucent visual screen that was 86 cm in front of the eyes, onto the center of which a light-emitting diode (LED) was back-projected (*FP*). The *FP* served to center the subject's gaze in space before each trial. The experiments were performed in silence and darkness except for the presence of LEDs (5.0 cd/m²) and tone pips (75 dB, 2 kHz) from small buzzers. The eccentric LEDs and buzzers were mounted in small boxes placed at the edges of the screen at the same vertical height as the *FP*. The screen was diffusely illuminated (1.0 cd/m²) between trials to prevent dark adaptation. The background lights were extinguished when the *FP* came on, signifying the start of a trial. The *FP* stayed on for 1000 ms before one of two visual events occurred. In the overlap condition (Fig. 1A), the *FP* stayed on while a second eccentric LED came on either 40° to the right or left of the *FP* on the horizontal meridian. In the gap task (Fig. 1B), the *FP* was turned off, and after a gap of 200 ms, in which the subjects were in complete darkness, the eccentric LED came on. Subjects were instructed to look at the eccentric visual target as quickly as possible, using any combination of eye and head motion they desired. Twelve possible trial combinations (gap or overlap; visual target 40° right or left; and control, enhancer, or distractor conditions) were randomly interleaved in each block of 120 trials by a 486 computer that controlled the experiment and digitized the data. Subjects completed three to six blocks of trials of 10 min each, and breaks were given between each block to maintain subject alertness.

Horizontal eye movements were measured using bitemporal d.c. electrooculography (EOG), and filtered and amplified with a Grass P18 d.c. preamplifier. Horizontal head rotation was measured by having subjects wear a hockey helmet attached to a low-torque potentiometer. The potentiometer signal was first calibrated to known angles of rotation. Subjects then maintained fixation upon a stationary spot of light and deviated their heads to the right and left. The gain of the EOG signal was adjusted to be equal and opposite to that of the potentiometer signal.

Signals from both eyes and head were filtered, amplified, and digitized at a rate of 500 Hz. Digitized data were stored on a hard disk and subsequently analyzed off-line on a Sparc 2 workstation. Gaze (eye position in space) was reconstructed off-line by adding the calibrated eye- and head-position signals together. Gaze saccades were scored as correct if they were in the direction of the visual target or incorrect if they were directed away from the visual target. Reaction times were measured from target onset to the onset of the gaze saccade. Gaze shifts to auditory or visual targets initiated less than 80 ms or 120 ms, respectively, after target onset were classified as anticipatory (Kalesnykas and Hallett 1987) and were excluded from computation of mean reaction times. Gaze shifts with reaction times greater than 500 ms were also excluded, due to lack of subject alertness.

Fig. 2A–D Data collected from one subject when the visual target was located 40° to the right. **A,B** Individual gaze traces in the overlap and gap tasks, respectively, from one block of trials. Traces are aligned on target onset (vertical line). Arrow points to directional errors. **C,D** Histograms of reaction times for movements in the overlap and gap tasks, respectively, from four blocks of trials (bin width 10 ms)



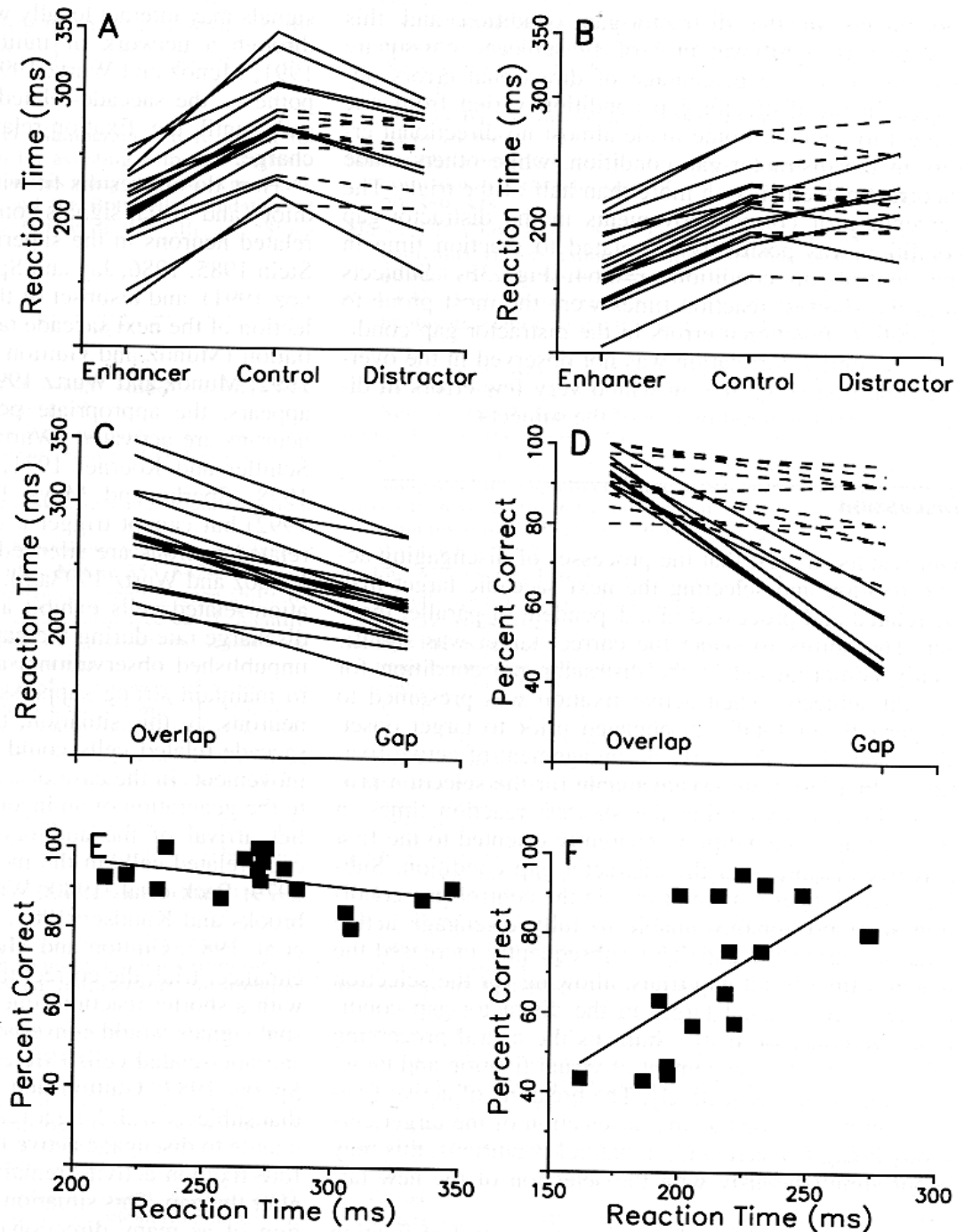
Results

The various behavioral conditions produced characteristic distributions in the saccadic reaction times of all subjects. Figure 2 illustrates results obtained from a representative subject. The location of the auditory stimulus strongly influenced subject performance in both the overlap (Fig. 2A,C) and the gap (Fig. 2B,D) tasks. The subject reacted to target onset sooner in the enhancer than in the control conditions. The subject also had difficulty suppressing incorrect movements to the auditory stimulus in the distractor condition and occasionally generated directional errors. These errors were confined to distractor-gap trials (arrow in Fig. 2B) and were trig-

gered at shorter latencies than the gaze shifts to the correct visual target in this condition (Fig. 2B,D). The direction errors were triggered by the onset of the distracting auditory stimulus. Such movements were not anticipatory because they were not present in the other gap trials (control-gap, enhancer-gap).

Figure 3A,B summarizes the mean reaction times of 17 subjects for correct movements to the right in the various overlap and gap conditions. Significant differences were assigned to probabilities of less than 0.05 using the Student's *t*-test. Gaze shifts were triggered after significantly shorter times in both enhancer-overlap (Fig. 3A) and enhancer-gap (Fig. 3B) tasks in all subjects. Approximately half of the subjects (8/17) also produced signifi-

Fig. 3A–F Summary data collected from 17 subjects when the visual target was presented 40° to the right. Each line represents one subject. *Solid lines* represent significant differences between points, while the *dashed lines* represent nonsignificant differences. **A, B** Mean reaction times in the different overlap and gap conditions, respectively (Student's *t*-test, $P < 0.05$). **C** Comparison of mean reaction times in the control-overlap and control-gap conditions (Student's *t*-test, $P < 0.05$). **D** Comparison of the percentage of correct responses in the distractor-overlap and distractor-gap conditions (chi-square test, $P < 0.05$). **E** Plot of mean reaction time in the control-overlap versus percentage of correct responses in the distractor-overlap condition. Each point represents data from one subject. For the linear regression line, correlation coefficient = -0.40 , slope = -0.06 , y-axis intercept = 109.08 . **F** Plot of the mean reaction time in the control-gap versus percentage of correct responses in the distractor-gap condition. For the regression line, correlation coefficient = 0.64 , slope = 0.41 , y-axis intercept = -18.57 .



cantly shorter latency responses in the distractor-overlap condition (Fig. 3A). None of these reductions in reaction time, however, were as great as those attained in the enhancer-overlap condition. We speculate that the onset of the auditory stimulus in both enhancer-overlap and distractor-overlap conditions may have facilitated the breaking of active fixation, thereby reducing reaction times in these conditions, as other studies have demonstrated a reduction in the latency of saccades to visual targets following the onset or offset of a nonspecific auditory cue (Ross and Ross 1980; Rueter-Lorenz et al. 1991). This effect was minimized in the gap task (Fig. 3B), in which the disengagement of active fixation may have preceded target onset. In the distractor-gap condition, only 2 of 17

subjects demonstrated significant decreases, while 4 of 17 subjects had significant increases over control values. Similar results were obtained when the visual target was located 40° to the left.

All subjects were significantly faster in the control-gap condition than in the control-overlap condition (Fig. 3C), as previously documented (Saslow 1967; Fischer and Ramsperger 1984; Mayfrank et al. 1986; Kalensnykas and Hallett 1987; Reuter-Lorenz et al. 1991; Wenban-Smith and Findlay 1991). Coupled with this reduction in reaction time in the gap task was a decrease in the percentage of correct movements in the distractor-gap as compared to the distractor-overlap condition (Fig. 3D). All but two subjects generated fewer correct

movements in the distractor-gap condition and this change was significant in 7 of 17 subjects (chi-square test, $P < 0.05$). The percentage of directional errors observed in the distractor-gap condition varied from one subject to another. Some made almost no directional errors in the distractor-gap condition, while others made incorrect movements on more than half of the trials. The percentage of correct movements in the distractor-gap condition was positively correlated to reaction time in the control-gap condition ($r = 0.64$; Fig. 3F). Subjects with the shortest reaction times were the most prone to generating directional errors in the distractor-gap condition. A similar correlation was not observed in the overlap condition (Fig. 3E), in which very few errors in direction were triggered by any of the subjects.

Discussion

Our results suggest that the processes of disengaging active fixation and selecting the next saccadic target may be related and processed in a dependent or parallel manner. The ability to select the correct target was significantly compromised in the distractor-gap condition for several subjects, when active fixation was presumed to be partially or totally disengaged prior to target onset. The trade-off of this early disengagement of active fixation is that less time was available for the selection process. Subjects exhibiting the shortest reaction times in the control-gap condition apparently oriented to the first perceived stimulus in the distractor-gap condition. Subjects with longer reaction times in the control-gap condition were presumably unable to fully disengage active fixation during the gap. This subsequently increased the reaction time in all gap trials, allowing for the selection of the correct visual target in the distractor-gap condition. We conclude that in humans the neural processing related to the disengagement of visual fixation and target selection occur interactively. The breaking of active fixation can be regarded as the unselection of the target currently being foveated and, in natural conditions, this may occur simultaneously with the selection of the new target.

A recent hypothesis describing the control of fixation and saccade generation has been proposed (Munoz and Guitton 1989, 1991; Munoz and Wurtz 1993a,b) that is based upon single-cell recording studies in the superior colliculus of alert animals. Fixation-related neurons in the intermediate layers of the rostral superior colliculus discharge tonically during active visual fixation and pause for saccades (Peck 1989; Munoz and Guitton 1989, 1991; Munoz and Wurtz 1993a,b). This pattern of activity is reciprocal to that of the collicular saccade-related cells, which are silent during active visual fixation and discharge a burst of action potentials during saccades of a specific amplitude and direction (Schiller and Koerner 1971; Wurtz and Goldberg 1971, 1972; Sparks et al. 1976; Sparks 1978; Sparks and Mays 1980). These findings led to the hypothesis that fixation and saccade

signals may interact locally within the superior colliculus through a network of inhibition (Munoz and Guitton 1991; Munoz and Wurtz 1993a,b). According to this hypothesis, the saccade-related cells cannot trigger a saccade until the fixation-related cells reduce their discharge.

How do our results fit with this hypothesis? Both auditory and visual signals converge directly onto saccade-related neurons in the superior colliculus (Meredith and Stein 1985, 1986; Jay and Sparks 1987; Guitton and Munoz 1991), and a subset of these cells may signal the selection of the next saccade target well before saccade initiation (Munoz and Guitton 1991; Glimcher and Sparks 1992; Munoz and Wurtz 1992). After an eccentric target appears, the appropriate population of saccade-related neurons are activated (Wurtz and Goldberg 1971, 1972; Schiller and Koerner 1971; Sparks et al. 1976; Sparks 1978; Sparks and Mays 1980, Glimcher and Sparks 1992) but cannot trigger a movement until the fixation-related neurons are silenced (Munoz and Guitton 1991; Munoz and Wurtz 1993a,b). In monkey experiments, fixation-related cells exhibit a transient reduction of their discharge rate during the gap period (Dorris and Munoz, unpublished observations) and consequently are unable to maintain strong suppression over the saccade-related neurons. In this situation, the first sensory input to the saccade-related cells could trigger a reflexive orienting movement. In the case of a distractor trial, this may lead to the generation of an incorrect response, due to the earlier arrival of the auditory information activating saccade-related cells in the incorrect colliculus (Syka et al. 1979; Peck et al. 1980; Wise and Irvine 1983; Middlebrooks and Knudsen 1984; Hirsch et al. 1985; Meredith et al. 1987; Guitton and Munoz 1991). In the case of an enhancer trial, the correct movement would be generated with a shorter reaction time because the auditory and visual signals would converge onto the same population of saccade-related cells (Meredith and Stein 1986; Jay and Sparks 1987; Guitton and Munoz 1991). We speculate that subjects with longer reaction times in gap trials were unable to disengage active fixation completely and therefore fixation activity remained in the superior colliculus after the gap. This situation would not lead to the generation of as many directional errors in the distractor-gap condition because of the continued suppression of the saccade-related cells, allowing for eventual selection of the correct visual target.

The central nervous system must select the most behaviorally relevant stimuli from a mass of incoming sensory input, and proper assessment of these stimuli may be associated with an orienting movement. We have shown that in the generation of saccadic gaze shifts, the ability to select the correct target target is related to the current state of active visual fixation. According to the collicular model (Munoz and Guitton 1991; Munoz and Wurtz 1993a,b), the level of fixation-related cell activity in the superior colliculus is critical for suppressing unwanted saccades. The variations in subject performance seen in this study suggests differing behavioral strate-

movements in the distractor-gap condition and this change was significant in 7 of 17 subjects (chi-square test, $P < 0.05$). The percentage of directional errors observed in the distractor-gap condition varied from one subject to another. Some made almost no directional errors in the distractor-gap condition, while others made incorrect movements on more than half of the trials. The percentage of correct movements in the distractor-gap condition was positively correlated to reaction time in the control-gap condition ($r = 0.64$; Fig. 3F). Subjects with the shortest reaction times were the most prone to generating directional errors in the distractor-gap condition. A similar correlation was not observed in the overlap condition (Fig. 3E), in which very few errors in direction were triggered by any of the subjects.

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gies. One possible source of this variation may be the higher cortical centers projecting to and controlling the output of the fixation-related cells of the superior colliculus.

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