

# The influence of object-relative visuomotor set on express saccades

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Express saccades are considered to have the shortest latency (70–110 ms) of all saccadic eye movements. The influence of visuomotor set, preparatory processes that spatially affect a sensorimotor response, on express saccades was examined by instructing human subjects to make a saccade to one of two simultaneously appearing spots defined by its position relative to the other. A temporal gap between fixation point disappearance and target appearance was used to facilitate the production of express saccades. For all subjects, the instruction influenced the vector of express saccades without increasing saccade latency. The effect on express saccades was only slightly weaker than that for longer latency saccades. Saccade curvature was minimal and did not depend strongly on task. Further experiments demonstrated that the effect of instruction on express saccade vector was much weaker when saccades were instructed to be made to one side of a single small spot, that the effect of instruction was equally strong when directing saccades to the less salient of two stimuli, and that an instruction could not only determine the direction of the effect but also modulate the effect's magnitude. The effect of instruction on saccade vector was no higher when blocked than when varied across trials. These results suggest that express saccades are influenced by object-relative spatial preparatory processes without increasing their reaction time and, thus, that high-level cognitive processes can influence the most reflexive of saccadic eye movements.

Keywords: saccade, express, reflex, object-centered, human, voluntary, visuomotor

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## Introduction

Saccadic eye movements can be elicited by the sudden appearance of a visual stimulus in the periphery of the visual field and generally have reaction times of around 200 ms in standard oculomotor tasks (Becker, 1989). Such sensory-driven movements are traditionally considered a “visual grasp reflex” (Fletcher & Sharpe, 1986), in that the eye is rapidly and inextricably drawn to the new object so that it can be imaged on the fovea, the portion of the retina with the greatest density of photoreceptors. The stimulus-bound nature of such responses is particularly striking when two visual stimuli in close spatial proximity suddenly appear. Such visual events tend to elicit saccadic responses that land at locations corresponding to a rough spatial average of the two target locations such that neither item is imaged on the fovea until after a second saccade (Coren & Hoenig, 1972; Findlay, 1982).

However, despite their seemingly reflexive nature, such “averaging” saccades are not immune to the effects of more high-level neural processes. He and Kowler (1989) showed that when two visual stimuli are presented close together

and subjects are instructed to make a saccade to one of the two stimuli based on its color, saccades are affected by the probability, as measured across a set of trials, of the location of the color-defined target (He & Kowler, 1989), although saccadic reaction time remains short (~180 ms). Thus, it appears that humans can bias visuomotor response *oculocentrically*, toward a particular position in space relative to the present position of the eyes.

More than 15 years since this important finding, both the temporal and spatial scope of such high-level influences on stimulus-evoked saccades remain unexplored. Temporally, it is not known whether all such reactive saccades, even those of very short latency, can be so influenced. In particular, one might expect that “express” saccades, saccades with the shortest known reaction times (monkey: 70–100 ms [Fischer & Boch, 1983], human: 80–110 ms [Fischer & Ramsperger, 1984]), would be immune to these higher level commands. Spatially, it is unknown whether visuomotor responses can be biased not only oculocentrically, to a particular position in space relative to the current angle of gaze, but also with respect to the suddenly appearing object itself, so that saccades could be made rapidly to one side or another of it.

In this study, we seek to determine whether a “visuomotor set”, established by an instruction to a subject to make a saccade to one side of a visual stimulus consisting of two neighboring small elements, can influence the vector (change of gaze angle) of express saccades. We define visuomotor set as a configuration of a sensorimotor network that affects how a visual stimulus is converted into a motor command. Several experimental findings obtained since the study of He and Kowler (1989) have provided additional motivation for examining how preparing such a visuomotor set can influence saccades with very short reaction times.

The first is evidence from monkey neurophysiological recordings in the superior colliculus during express saccades. It had long been known that for longer latency saccades, many superior colliculus neurons discharge both in response to the appearance of a visual target and immediately before a saccade (Sparks & Hartwich-Young, 1989). However, for express saccades, there is evidence that the visual response in the intermediate layers of the superior colliculus itself triggers the movement (Dorris, Paré, & Munoz, 1997; Edelman & Keller, 1996; also see Sparks, Rohrer, & Zhang, 2000, for a slightly different view). This suggests that reaction times of express saccades are as low as possible given the neural transmission and synaptic delays in the visual and movement pathways stretching from retina to striate and extrastriate cortex and then back “downstream” to the brainstem and eye muscles. Because the fastest human saccades are only slightly slower (Fischer & Boch, 1983; Fischer & Ramsperger, 1984), it is probable that they are triggered similarly. Thus, an examination of a visuomotor set’s effect on express saccades may provide the strongest test of whether volitional process can spatially influence visually triggered saccades regardless of their reaction time.

Our interest in whether object-relative representations can influence short-latency saccades arises from evidence that neurons in the supplementary eye fields (SEFs) of monkey will discharge at a higher rate prior to saccades that are made to a particular side of an object, regardless of where in the visual field that object is located (reviewed in Olson, 2003), suggesting that neurons in this area code for saccades in an object-centered coordinate frame.

In addition, recent evidence shows that object-centered representations can help guide rapid deployments of spatial attention. Kristjánsson, Mackeben, and Nakayama (2001) and Kristjánsson and Nakayama (2003) have shown that if a horizontal bar appears suddenly in an unpredictable location, and if subjects must perform a visual discrimination of an object that subsequently appears at a location on one end of the bar or on the other end, then performance on the task will be better if the object appears consistently on a particular side of the bar. This finding can be seen as an attentional analogue to the finding of He and Kowler (1989) in that a spatial response to a stimulus is not purely sensory driven but

influenced by probability of target location. However, unlike that study, the spatial information used to alter the sensory-driven response is represented in object-centered rather than oculocentric coordinates.

It is unclear, however, whether a visuomotor set implemented by following such object-relative instructions can affect saccades in a reaction-time task and specifically express saccades with their very short latencies. A finding that an object-relative visuomotor set could affect express saccades spatially would demonstrate that a high-level cognitive command can affect sensory-driven movements at their most reflexive.

## Methods

Four subjects (age range, 20 to 41 years) participated in one experiment or more; one was an author and three were naïve to the purposes of this experiment. Experiments were conducted under a protocol approved by the Institutional Review Board of City College of New York and the CUNY Medical School. All subjects provided written informed consent and had a corrected acuity of 20/20.

White stimuli (100 cd/m<sup>2</sup>) were presented at 85 Hz on an almost completely dark background (13 mcd/m<sup>2</sup>) by a computer monitor controlled by an Apple Macintosh G4 computer using custom software written in C using the Vision Shell Graphics Libraries (Comtois, 2003). To facilitate real-time control of stimulus presentation, we inactivated the operating system’s desktop interface (i.e., the “Finder”). Eye movement data were collected using video-based oculography (Eyelink II, SR Research) at a rate of 500 samples/s. Subjects were seated comfortably at a distance of 60 cm from the screen. Each subject’s head was stabilized during the experiment by the use of a bite bar made from a full-mouth dental impression mounted on head rest/bite bar system (ASL). Experiments were preceded by a 9-point (3 × 3) calibration procedure.

## Experimental procedures

The stimuli and procedures for the first experiment (two-target experiment) will be described here, many of which pertain to the three subsequent experiments as well. Methods specific to those three experiments will be described in the [Results](#) section.

### Two-target experiment

Four different trial types were used ([Figures 1A](#) and [1B](#)):

1. *One-target* trials, in which a small square fixation point (0.35°) appeared in the center of the display. Subjects were required to fixate this point for

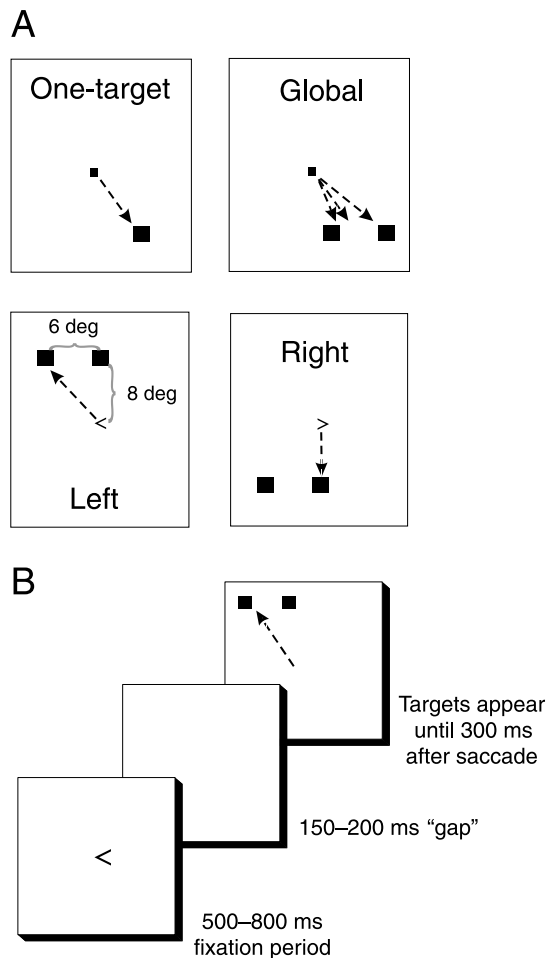


Figure 1. (A) Spatial schematics of the four tasks of the two-target experiment. (B) Temporal schematic of the saccade tasks used in the two-target experiment.

500–800 ms, after which the fixation point disappeared; 150–200 ms later, the target, a  $1^\circ$  square, appeared. This temporal gap has been known to facilitate the generation of short-latency saccades (Saslow, 1967). The target remained present until 300 ms after the end of the saccade. Subjects were required to make a saccade to the target as quickly as possible.

2. *Global two-target* trials, which are like the one-target trials except that two squares appeared separated horizontally by  $6^\circ$  and that subjects were instructed to make a saccade as quickly as possible to the stimulus configuration as a whole, rather than selecting one square as the target.
3. *Left two-target* trials, which are similar to the global trials except that the central fixation point was a less-than sign ( $<$ ;  $0.5^\circ$  wide), which instructed a saccade to be made to the square appearing on the left.
4. *Right two-target* trials, which are like the left two-target trials, except that a greater-than sign ( $>$ ) at the fixation point, instructing a saccade to the right target.

The target configuration appeared randomly centered at one of six possible locations relative to the center of the screen: two possible vertical coordinates ( $8^\circ$  above or  $8^\circ$  below) crossed with three possible horizontal coordinates ( $0^\circ$  or  $4^\circ$  left or  $4^\circ$  right). If a saccade occurred sooner than 60 ms or later than 400 ms after target appearance, or if the saccade landed outside a circular region of  $4^\circ$  radius centered at the center of the stimulus configuration, a beep sounded and the screen blanked until the next trial. Subjects were instructed not only to direct the saccade as quickly as possible toward the stimulus array but also to try to follow the instruction at the fixation point closely. Each observer participated in two sessions, each composed of 16 blocks (4 blocks per trial type) of 18 trials. Trial type was held constant within a block of trials.

## Data analysis

### Saccade latency and duration

To compute the latency and duration of each saccade, we obtained a saccade velocity trace by differentiating the horizontal and vertical components of the eye position trace by a central difference algorithm implemented in Matlab (MathWorks) and then using the Pythagorean theorem to calculate the saccadic speed as a function of time. The following algorithm for determining saccade latency was used in Matlab: The eye position trace around the time of the cue to make a saccade (either target appearance or fixation point disappearance—see below) was examined to determine the first point at which velocity exceeded  $35 \text{ deg/s}$ . Next, the trace was evaluated backward in time until the first point below  $5 \text{ deg/s}$  was found. Latency was calculated as the difference in time between the appearance of the target and this point. The end of the saccade was determined in an analogous manner but with time being reversed.

Given that the stimuli were presented on a CRT, on which the time of appearance of a stimulus on the monitor depends on its vertical position, we took into account the vertical position of the stimuli when calculating saccade latency.

### Measurement of saccade endpoint and effect of instruction

Occasionally, glissades (postsaccadic smooth movements of the eye) and short-latency movements were observed close to the end of a saccade. Because we did not wish our estimates of the effect of instruction to be corrupted by such movements, we adopted a conservative measure of saccade endpoint by calculating the mean eye position window in a narrow (10 ms) window centered on the end of the saccade as determined above. To obtain an estimate of the effect of the instruction, we calculated, for each saccade, the amount that the saccade endpoint deviated to the right or left of the centroid of the target configuration. To minimize the effects of small errors due to calibration, for a set of movements directed to target arrays of a particular centroid position, we took into

account the average landing position of one-target saccades to that position by calculating the mean distance between saccade endpoint and target position and then adjusting the measured saccade endpoints in the two-target tasks by this amount. Finally, we noted that in the left and right two-target tasks, initial eye position occasionally strayed as much as a degree in the direction of the instruction. As we did not wish this presaccadic movement to influence our measure of the effect of instruction on the saccade, we calculated the gaze displacement with respect to the eye position at the beginning of the saccade.

### Saccade curvature

If the effect of the instruction did not become manifest until late into the saccade, a curved saccade might result. To assess this possibility, we defined saccade curvature as the maximum perpendicular distance of any point on the saccade trajectory from a straight line connecting the start and endpoints divided by the distance between the two points (Smit & Van Gisbergen, 1990). We then assigned a sign to this value depending on whether the curvature toward the end of the saccade was toward the right (+) or the left (−).

### Data inclusion and definition of “express saccade”

In rough agreement with previous results (Fischer & Ramsperger, 1984; Kalesnykas & Hallett, 1987), we found that saccades with latencies less than 70 ms tended to be directed at random rather than at the visual target array, whereas saccades with latencies longer than 80 ms were almost always directed toward the target array. Therefore, we eliminated saccades from our data set that had latencies <80 ms.

We generally found that histograms of saccade latency did not break down into separate “express” and longer latency peaks, as has been found by others (Kalesnykas & Hallett, 1987; Kingstone & Klein, 1993). However, as most of our analyses depend on a definition of express saccade, we adopted an upper bound of 110 ms. This is quite arguably conservative, with a smaller value than that used in any other study of human saccades that we know of (reviewed in Delinte, Gomez, Decostre, Crommelinck, & Roucoux, 2002) and consistent with all other studies that we know of that claim to have elicited express saccades (e.g., Fischer & Ramsperger, 1984, 1986; Fischer et al., 1993; Weber, Biscaldi, & Fischer, 1995).

## Results

### Two-target experiment

There was a strong effect of instruction on the endpoint of the saccade, including that for express saccades,

whereas little or no effect of instruction was found on saccade latency. Sample trajectories of express saccades for two subjects are shown in Figure 2. Saccades in the left task had endpoints to the left of endpoints in the global task, which were, in turn, to the left of endpoints in

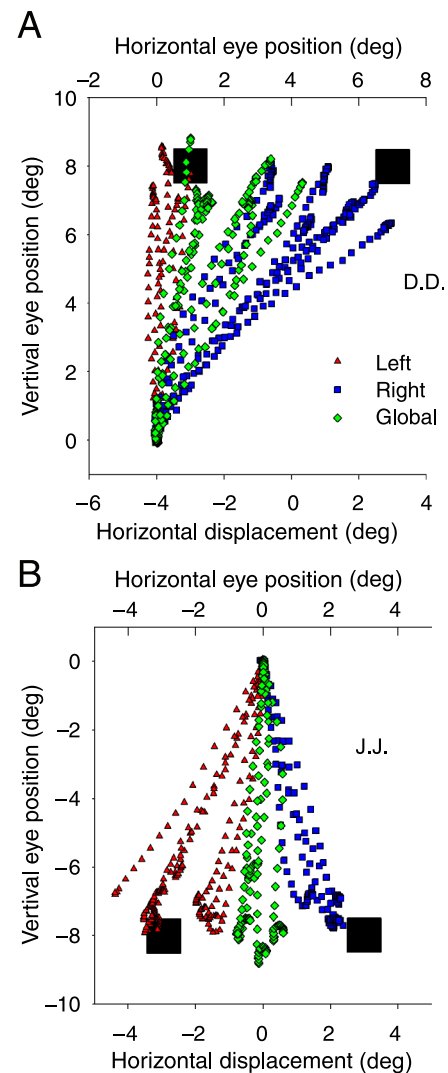


Figure 2. Sample eye movement traces in the left, global, and right two target tasks of the two-target experiment. (A) All movements made in one recording session in the 3 two-target tasks when the two targets appeared up and to the right of the fixation point are shown. Movements in the three tasks are color coded. Black squares indicate the location of the two stimuli. Every sample of the eye position trace between saccade initiation and saccade termination is shown (sampling rate: 500 Hz). Displays of traces have been shifted with respect to the actual data such that movements begin at the same location. The axis title, “Horizontal displacement” refers to the displacement of the endpoint of the saccade from the midpoint between the two targets. (B) All movements made in one recording session in the 3 two-target tasks when the two targets appeared down and below the fixation point are shown for another subject. Other conventions are as described in Panel A.

the right task. As evident in Figure 2, express saccades did not “follow” the instruction completely. Movements tended not to reach the desired target but generally landed somewhere between the center of the two stimuli and the instructed goal. We will define a displacement as positive if the saccade landed to the right of the midpoint of the two squares and negative if to the left. Overall, across all saccades of all latencies for all the three subjects, displacement relative to the endpoints of one-target saccades was  $-1.6^\circ$  in the left task and  $+2.0^\circ$  in the right task; both values were significantly different from  $0^\circ$  (no effect of instruction; Figure 3A). This effect was nearly as strong when just considering express saccades (latencies  $<110$  ms, left:  $-1.47^\circ$ , right:  $+1.9^\circ$ ).

Although influenced by the instruction given before target appearance, saccades were nonetheless strongly stimulus driven. For saccades with latencies longer than 75 ms, less than 2% were made in a vertical direction opposite the targets. Although saccades were considered

as “correct” if they landed anywhere between the two targets (see the Methods section), the horizontal component of the saccade displacement was strongly dependent on the horizontal position of the target array, although the slope of this relationship was significantly higher in the one-target task than in the other tasks for all three subjects. Across the three subjects, the mean slope of this relationship was 0.78 in the left task, 0.68 in the right task, 0.75 in the global two-target task, and 0.90 in the one-target task. The tightness of this correlation (Pearson product–moment correlation,  $R$ ) was very strong for all four tasks: left,  $R = .93$ ; right,  $R = .93$ ; global,  $R = .94$ ; one target,  $R = .99$ .

Overall, latencies in the 3 two-target tasks, as well as in the control one-target task, were highly similar. Across the three subjects, mean latency was 107 ms in the left task, 106 ms in the right task, 110 ms in the one-target task, and 112 ms in the global two-target task. Latencies in the left or right task did not exceed those in the global task for any

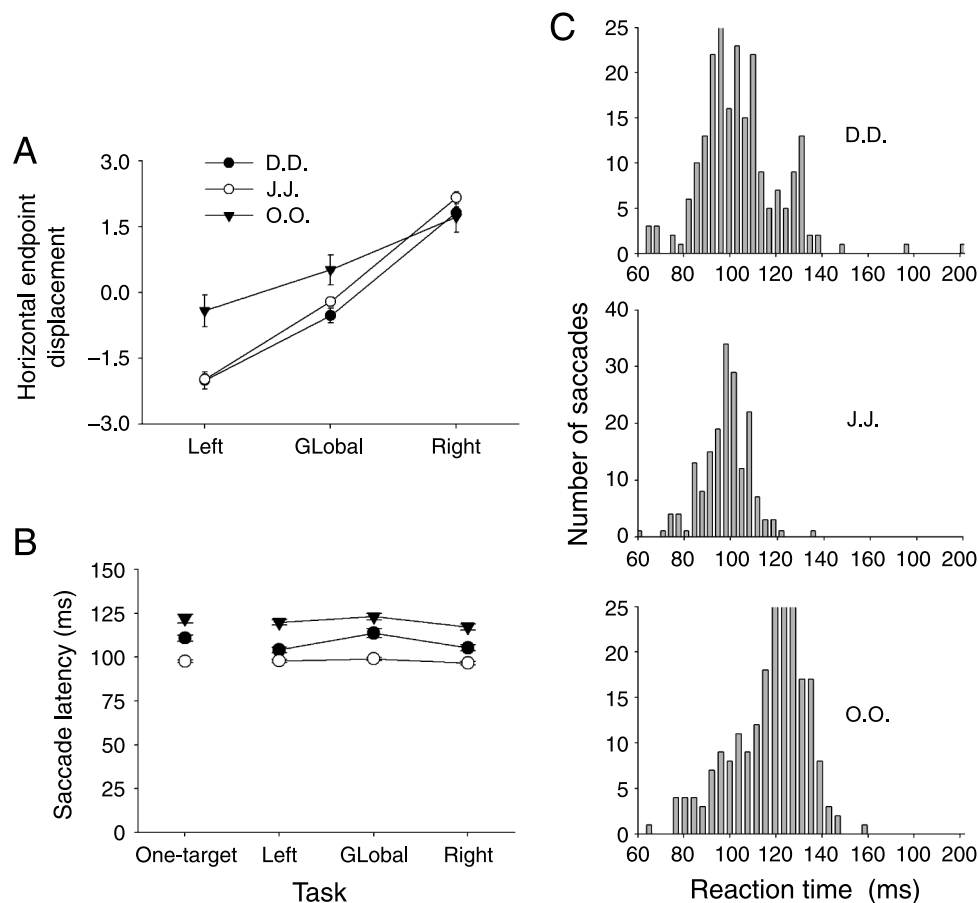


Figure 3. (A) Average horizontal displacement of express saccade endpoint is shown for the three subjects in the 3 two-target tasks (left, right, and global) of the two-target experiment. Horizontal deviation is measured with respect to the midpoint of the two targets such that a positive number indicates that the saccade landed to the right of the two targets. Bars indicate standard error of the mean. (B) Average saccade latency of all saccades is shown for each of the three subjects for the each of the three saccade tasks of the two-target experiment. Bars indicate standard error of the mean. (C) Latency histograms for all saccades in the left two-target and right two-target tasks combined for each of the three subjects.

of the three subjects (Figure 3B). The production of anticipatory saccades was less than 8% for all three subjects.

Saccade latency histograms for all three subjects gave only slight evidence for bimodality, in agreement with many previous studies of human saccades elicited by the gap paradigm (Kalesnykas & Hallett, 1987; Kingstone & Klein, 1993; Reuter-Lorenz, Hughes, & Fendrich, 1991; Wenban-Smith & Findlay, 1991) but not with others (Carpenter, 2001; Fischer & Ramsperger, 1984; Fischer et al., 1993; Jüttner & Wolf, 1992). For all three subjects, few saccades were observed with latencies less than 75 ms, but with at least a modest number of saccades starting at around 80–90 ms, thus having similar, or even faster, latencies than the fastest seen in studies that did show a separate population of express saccades (Figure 3C). Note that this time range is only slightly higher than that shown for express saccades in monkeys, in which bimodality is almost always clearly seen. For these reasons, we feel that we are justified at least in referring to the fastest of our saccadic responses as express saccades.

The effects of instruction were evident for even the shortest latency saccades for all three subjects. Saccade latencies were binned for each subject (see Figure 4), and, for saccades in the lowest latency bin, the effect of instruction for the left one-target task was compared with that for the right one-target task. These effects were significant for each of the three subjects ( $p < .001$ ).

Indeed, there was, at most, a modest speed–accuracy trade-off, manifested as a larger effect of instruction with longer saccade reaction times. Across all three subjects, saccades with latencies longer than 110 ms had values indicative of a slightly greater effect of instruction than that for express saccades (left:  $-1.7^\circ$ , right:  $2.6^\circ$ ; see Figure 4). For each of the three subjects, for saccades in the left and right one-target tasks, we compared the strength of effect in the shortest latency bin as defined in Figure 4 with that of the longest latency bin. Subject D.D. had a significantly greater effect for longer latency saccades in both left and right tasks, whereas subject J.J. showed an increased effect in the right task and subject O.O. showed no significant effect.

Express saccade trajectories showed some variability when directed toward the left or right. Generally, they were quite straight (Figure 2) and, overall, mean curvatures were very small in all four tasks (left:  $-0.011$ , right:  $0.028$ , global:  $0.002$ , one target:  $0.002$ , see the Methods section), although for two of three subjects, differences between curvature for the left and right tasks were statistically significant. However, across the three subjects, there was no consistent relationship between saccade latency and the amount of curvature.

These results suggest that a visuomotor set established by an object-relative instruction can influence the vector of express saccades. The next experiment provides insight as to whether this instruction is implemented by a high- or low-level neural mechanism.

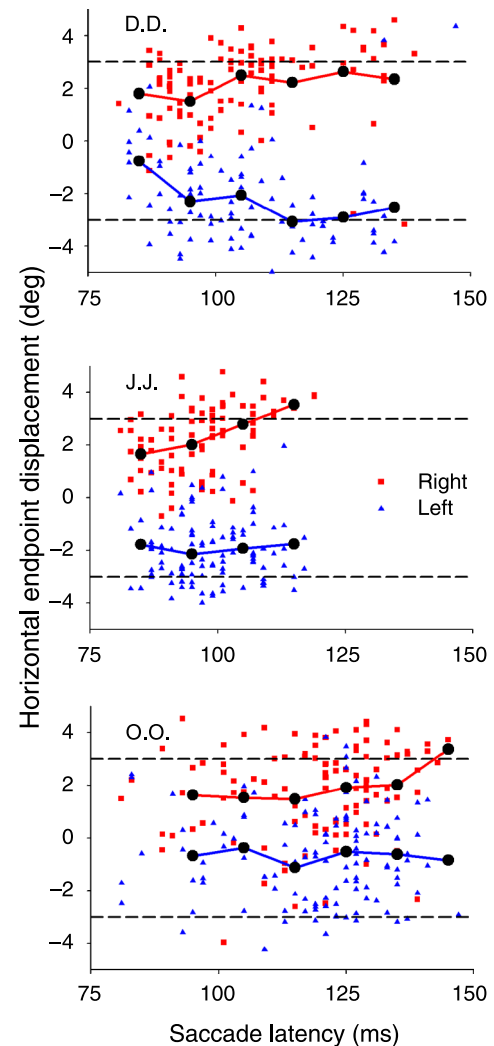


Figure 4. Scatter plots showing relationship between saccade endpoint displacement and saccade latency in the left two-target and right two-target tasks in the two-target experiment for the three subjects. Solid lines indicate binned averages for bins of 10 ms width starting at 80 ms, except for subject O.O., in which the leftmost bin consists of all saccades with latencies between 80 and 100 ms.

### Is the effect of object-relative visuomotor set merely a preprogrammed offset to a stimulus-driven express saccade?

One possible explanation of the above results is that upon receiving the instruction, subjects first preprogram a left or right saccadic vector displacement. The subsequent presentation of the visual stimulus then elicits a reflexive, stimulus-bound motor program to generate a saccade toward the spatial average of the suddenly appearing stimuli. Finally, the saccadic system computes a vector sum of the preprogrammed (left or right) vector and sensory-elicited vector to obtain the final motor command.

If this were the case, then the saccade vector will depend on the instruction and the geometric center of the target array but not on the spatial extent of the target array.

An alternative to this scheme is that no saccade vector is preprogrammed in response to the instruction; instead, the signals arising from the instruction interact with the ensemble of stimulus-evoked activity distributed on a visuomotor map. If true, the size of the effect of the instruction should be dependent on the spatial extent of the visual stimulus evoking the saccade.

### One- versus two-target experiment

To address this question, we ran a “one- versus two-target” experiment using not only the four tasks of the two-target experiment, but also an additional two tasks in which the appearance of one square elicited the saccade and subjects were instructed to make a saccade to a position to the left or right of a single square target into visual space not bounded by visual stimuli (Figure 5A). Data were collected from three subjects. In the left one-target trials, only one square appeared and subjects were instructed (using a centrally located “<” as a fixation point) to make a saccade 3° to the left of the square. A corresponding right one-target task used a central “>” to direct saccades 3° to the right of the square. Immediately after the beginning of the saccade, the original target disappeared and two targets appeared, one 3° to each side of the former position of the single target. The purpose of this was to provide postsaccadic visual feedback to the subject equivalent to that received in the two target tasks. Trials of the six different types were run randomly intermixed not only because it would make subjects adopt the same strategy for the one-target and two-target trials but also to examine whether not keeping the instruction constant from trial to trial would reduce the effect of the instruction compared to that observed in the two-target experiment described above, where instruction was held constant throughout a block.

In all three subjects, the effect of the instruction on express saccade vector was significantly reduced when the stimulus consisted of only one square (Figure 5B). Overall, the effect of instruction on saccade vector (right condition minus left condition) was reduced by 64% when there was one target rather than two. For two of the three subjects, a one-way ANOVA followed by multiple comparisons showed that deviations on the two-target tasks were significantly greater than those for the one-target tasks for both subjects. For the third subject, who made fewer express saccades, the difference between the right one-target and right two-target conditions reached significance, but the difference between the corresponding leftward conditions did not, although the trend was in the same direction. Saccade latencies averaged across all three subjects, like those in the two-target experiment, had very little dependence on task (range = 103.2 to 107.8 ms).

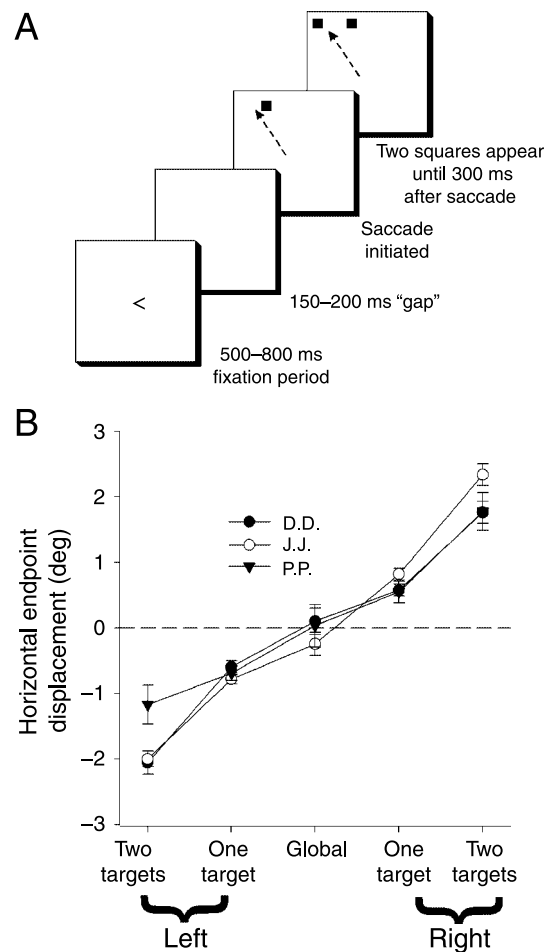


Figure 5. (A) Spatial and temporal schematics shown for the two additional saccade tasks (left one target and right one target) used in the one- versus two-target experiment. (B) Results of the one- versus two-target experiment. Mean horizontal saccade endpoint displacement is shown for three subjects in the two-target tasks and the one-target tasks. Saccade displacement indicates distance from saccade endpoint to the midpoint of the two targets (two-target tasks) or from the single target (one-target tasks) such that a positive value indicates the shift was to the right. Standard error bars are shown.

Express saccade trajectories in the one-target tasks had virtually no curvature, showing little or no indication of movement toward the ends of the expected stimuli followed by a recurvature toward the target (mean curvature across both subjects: left one target, 0.019; right one target, 0.007; left two targets,  $-0.018$ ; right two targets, 0.056). This suggests that subjects did not program a saccade to one side of the target and then adjust the vector once it was evident that only one target was visible, but rather that the movement was more or less stimulus driven for its entire extent.

The overall effect of instruction (right condition minus left condition) for the two-target tasks for the two subjects who participated both in this experiment and the preceding

one was 14% higher in this experiment, in which trials of different types were run intermixed, than that found for the two-target tasks in the first experiment, in which trials of a particular instruction were run in separate blocks.

### Can “bottom-up” differences in visual stimuli overwhelm the effect of visuomotor set?—The unequal-salience experiments

In the preceding experiments, the two targets were identical. Is it possible that when the two targets differ in salience, saccades will be directed to the more salient target, regardless of the instruction? In other words, is it possible that the instruction has an effect only when it can break a “sensory tie”? Or can an instruction help direct a saccade to the less salient of two stimuli?

A third, two-part experiment tested this by repeating the tasks used in the two-target experiment above but with trials (nonsymmetric trials) in which one stimulus was bigger than the other ( $2^\circ$  vs.  $0.5^\circ$ , unequal-size experiment, Figure 6A) or of higher luminance ( $100 \text{ cd/m}^2$  vs.  $12.5 \text{ cd/m}^2$ , unequal-luminance experiment) than the other. By means of the central fixation stimulus, saccades were directed to the less salient target, which could appear on the left or on the right. For comparison, we ran trials with the same stimulus configuration but had the same instruction as the global tasks of the first two experiments in that subjects were instructed to respond to the stimulus array as a whole, rather than attempt to direct a saccade to one item or the other. We also reran the four trial types of the two-target experiment (symmetric trials).

In the unequal-size experiment, we found no evidence that the effect of instruction on saccade vector was weaker when saccades were directed to the less salient target. If anything, the effect of instruction was somewhat stronger when saccades were directed to the less salient target (Figure 6B). For each of two subjects, we conducted a two-way ANOVA to compare the left and global tasks and a second to compare the right and global tasks. One factor was instruction (left or right); the second was target array configuration (symmetric or nonsymmetric). We found that both factors were significant for each subject for each experiment for each test. The average effect of instruction on saccade vector (global minus left or right minus global) was  $2.4^\circ$  when the stimuli were nonsymmetric and  $1.9^\circ$  when the stimuli were symmetric. As in the first two experiments, we found virtually no effect of task on saccade latency, with average latencies ranging from 94 to 99 ms across the two subjects.

Similar results were found in the unequal-luminance experiment, although the effect of instruction on target vector was more similar in the symmetric and nonsymmetric conditions, suggesting additivity of the two factors of instruction and stimulus salience on saccade

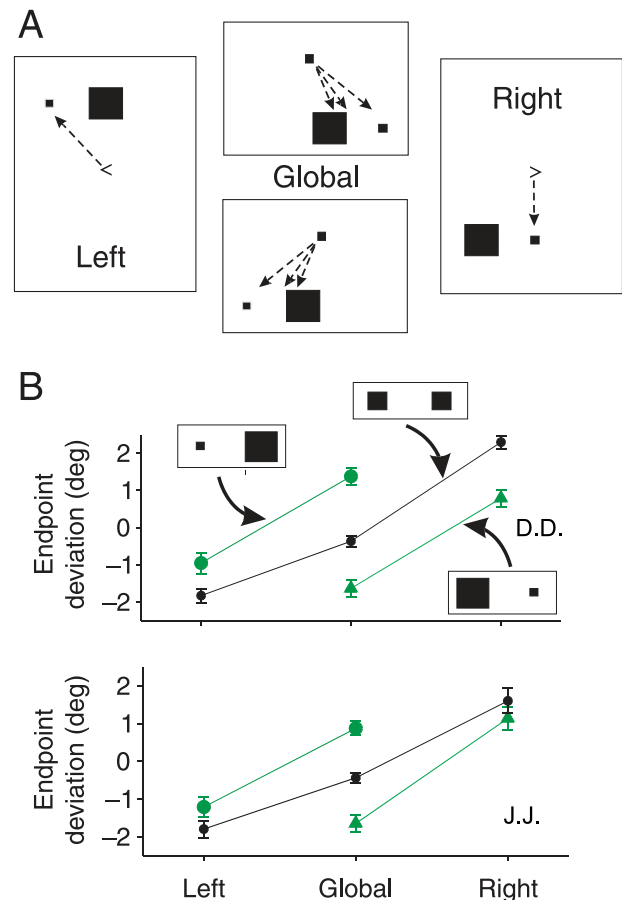


Figure 6. (A) Spatial schematic of the four tasks introduced in the unequal-size experiment: left size asymmetry, right size asymmetry, global/left (bottom center), and global/right (top center). The fixation point (<, >, ■) instructed the subject to make a saccade to, respectively, the left target, the right target, or the target array as a whole. Note that in the left and right tasks, the subjects were directed to make a saccade to the smaller of the two targets. (B) Results of the unequal-size experiment. Mean horizontal saccade endpoint displacement is shown for two subjects for trials in which targets are different in size. For comparison, data from tasks in which the two targets are identical are also shown. Schematics of the spatial arrangement of stimuli indicate the corresponding data. Other conventions are as described in Figure 5B.

vector. The average effect of instruction on saccade vector was  $2.1^\circ$  when the stimuli were nonsymmetric and  $2.0^\circ$  when the stimuli were symmetric. Average latencies ranged from 95 to 105 ms.

### Can visuomotor set direct saccades to more than two possible locations in a stimulus array?—The four-target experiment

Finally, we wished to assess the spatial specificity of the instruction. Are subjects simply able to make movements



to one side of a stimulus array or to another, based on its spatial extent, or can subjects follow instructions with more specificity? We tested this by presenting a target array consisting of four squares, two spaced by  $3^\circ$  flanked by two spaced by  $6^\circ$ , and instructing subjects to make saccades to one of the four targets (near left, near right, far left, or far right) by use, again, of a central fixation point (“<”, “>”, “<<”, or “>>”, respectively, Figure 7A). If subjects could not only make a saccade indiscriminately to the left and right but also modulate the extent of the deviation from the center of the array, then saccades in the far-right and far-left conditions should land farther away from the center of the stimulus array than saccades in the near-right and near-left conditions.

This is exactly what we found. For express saccades, deviations were nearly twice as large in the far conditions as in the near conditions for the two subjects (Figure 7B). A one-factor ANOVA on task (far left, near left, global, near right, far right) followed by a multiple comparison procedure showed that the effect of instruction on saccades in any task was significantly different

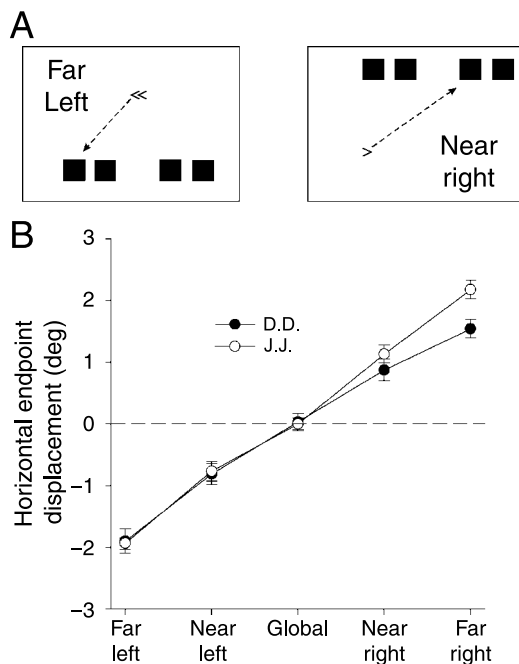


Figure 7. (A) Spatial schematic of two of the six tasks used in the four-target experiment. The fixation point (<<, >>) instructed the subject to make a saccade to, respectively, the far-left target or the near-right target. Other tasks used in the four-target experiment are described in the Methods section. (B) Results of the four-target experiment. Mean horizontal saccade endpoint displacement is shown for two subjects in the far, near, and global tasks for data collected in the four-target experiment. Saccade displacement indicates distance from the saccade endpoint to the midpoint of the four targets such that a positive value indicates that the eye landed on the right of the midpoint. Standard error bars are shown.

from those in the other four tasks for both subjects. Interestingly, as in the previous experiments, neither near nor far instructions were completely effective, as saccades tended to land in between the center of the array and the desired target. This is consistent with the idea that the effect is proportional to the deviation dictated by the instruction and that the incomplete effects of instruction observed in these experiments are not due to an inherent maximum effect of the instruction. Again, latencies did not depend on task, and amounts of saccade curvature were modest and not task dependent.

## Discussion

We found that the vector of express saccades could be altered by an object-relative visuomotor set so as to land near one side of an extended visual stimulus without any increase in reaction time. The spatial instruction that established the set had an effect almost as strong for express saccades as for saccades of longer latency. The effect of instruction was substantial, frequently reaching more than 50% of the distance between the center of the visual stimulus array and the desired target (two-target experiment, Figures 2 and 3). The effect increased modestly with increasing saccade latency (Figure 4). The curvature of such saccades was small and only modestly greater than that of saccades with no specific instruction. There was no evidence that the effect of the instruction depended on curvature on a saccade-by-saccade basis. The instruction's effect was greatly reduced when subjects were instructed to make a saccade to one side of a single small stimulus (one- vs. two-target experiment, Figure 5), suggesting that the effect of the instruction depends upon the spatial extent of the target array. The effect of instruction was robust, evident even when saccades were directed to a target of lesser saliency, suggesting that the instruction's effect was not simply to break a saliency tie when two stimuli were equivalent (unequal-saliency experiment, Figure 6). Finally, not only the direction (left or right) of the effect on saccade vector but also its magnitude were modulated by the instruction (four-target experiment, Figure 7).

### The influence of visuomotor set on express saccades

These results show that top-down cognitive commands can influence express saccades. While Findlay (1982) found that saccades elicited by the presentation of two neighboring visual stimuli were generally directed between the two targets, He and Kowler (1989) demonstrated that such “averaging” responses need not be purely stimulus bound, which shows that if subjects were

directed to select a target in a two-target array based on color, with the pair of stimuli always appearing in the same location but with the target switching from side to side, saccadic responses of a relatively short latency (~180 ms) were altered by the probability of the target's location. Our results extend these findings by showing that such high-level influence need not be due to an oculocentric bias, as we show that an object-centered bias can have a similar effect. Moreover, we show that this bias can influence express saccades, the shortest latency saccadic eye movements. There has been a report that high-level influences can affect averaging saccades of express latency (Weber, Latanov, & Fischer, 1993), but in that study, subjects were instructed simply to make a saccade to the closer of two targets that had the same direction, an instruction presumably not difficult to implement given that reflexive saccades tend to be hypometric, and that when two targets are presented separated in eccentricity, movements tend to land closer to the near target (Findlay, 1982), even without an instruction.

### Possible neural mechanisms implementing the effect of visuomotor set on express saccades

Olson (2003) has shown that the SEFs carry a signal that codes for visual stimuli or impending saccades in an object-centered coordinate frame. The strong connections from the SEFs to the superior colliculus (Shook, Schlag-Rey, & Schlag, 1990) could, thus, serve as an anatomical substrate for the effects found here. Although it has been shown that the saccadic system can use object-centered representations to program saccades of longer latency in a context when accuracy, not speed, is emphasized (He & Kowler, 1991), the present results provide the first direct evidence that suggests that object-centered signals such as those found in the SEFs can facilitate visuomotor reflexes.

An important clue for determining the nature of the neural mechanism that implements this visuomotor set is the finding that the effect of the instruction is much greater when the saccade was elicited by two targets rather than one (one- vs. two-target experiment). This indicates that the power of the visuomotor set depends upon the spatial extent of the object (here, either a one-element or multielement stimulus array). Therefore, the effect of instruction is not merely due to a left or right motor bias signal that one might expect to find in brain stem regions that code for horizontal components of saccades (Scudder, Kaneko, & Fuchs, 2002). Instead of directly operating on a purely motor area in the saccadic system, the signal representing the instruction seems to operate on a visual or a visuomotor representation of the stimulus.

What might this visuomotor representation look like? Neurophysiological recordings in the superior colliculus have shown that visual activity and motor activity are essentially merged for express saccades in monkey (Dorris et al., 1997;

Edelman & Keller, 1996; Sparks et al., 2000). Moreover, express saccades to two targets (for which no instruction is given) are accompanied by a spatially broad, possibly bimodal distribution of activity in the superior colliculus, with much more spatial spread than that observed for saccades to one target (Edelman & Keller, 1998).

Given the time constraints during the execution of an express saccade, it is likely that the top-down signal potentiates saccade-related areas such as the superior colliculus prior to the appearance of the visual stimuli. This potentiation may alter the profile of the broad distribution of saccade-related activity resulting from two targets. Indeed, the reason why the effect of the instruction in the one-target tasks is smaller may be that there is a much more spatially confined distribution of activity to modulate. A saccade that successfully landed well away from one target might have to be generated predominantly by non-visually evoked activity—activity that presumably arises as a result of cognitive processes occurring somewhat later than visually driven activity (see Edelman & Goldberg, 2001, 2003).

Turning our attention back to the two-target case, it is unclear how the spatial potentiation of visuomotor activity is accomplished. Given the nature of the object-centered instruction, the mechanism is likely to have a greater computational complexity than that of cortical influences on skeletomotor reflexes, in which the gains of a small set of sensorimotor circuits are modulated (Capaday, Forget, Fraser, & Lamarre, 1991; Colebatch, Gandevia, McCloskey, & Potter, 1979; Evarts & Tanji, 1974; Hammond, 1956; Wolpaw, 1997), or of that of oculocentric biases affecting saccades, as such influences presumably require simply the modulation of input–output gains at one or more locations on an oculocentric neural map (Basso & Wurtz, 1998; Dorris & Munoz, 1998; He & Kowler, 1989; Paré & Munoz, 1996).

A mechanism that accounts for the results described here may also account for the results of (Kristjánsson et al., 2001; Kristjánsson & Nakayama, 2003) who demonstrated that attention can quickly be allocated to one side of a suddenly appearing stimulus. Subjects were required to perform a visual discrimination of a visual element that could appear on either side of a horizontal bar. They found that performance was facilitated when the side at which the discriminandum appeared was repeated across trials, indicating object-centered priming. In contrast, we found that the effect of instruction on saccade endpoint in the two-target tasks was similar when trial types were run intermixed (one- vs. two-target experiment), as they were when trial types were blocked (two-target experiment). The difference between these effects of trial sequence may be a consequence of differences in the way high-level processes affect saccade and attentional systems, or they may result from the explicit instruction given in our task. Our results on the effects of trial sequence suggest that this explicit instruction can be implemented rapidly, within several hundred milliseconds after the instruction is received.

## The influence of visuomotor set on reflexive saccades during normal visual behavior

It has long been known that skeletomotor reflexes can be modified by higher level neural commands to maintain posture in different behavioral contexts (Horak, Diener, & Nashner, 1989; Marsden, Merton, & Morton, 1981). It has been theorized that “preflexes”, configurations of sensorimotor networks established prior to the onset of a sensory stimulus, can influence sensorimotor reflexes so that they facilitate or at least not hinder ongoing behavior (Loeb, Brown, & Cheng, 1999). Similarly, for normal saccadic behavior, the ability to modify reflexive saccades may be more useful than an obligatory link between sensory stimuli and motor commands. Outside of the laboratory, suddenly appearing stimuli are rarely simple points of light but generally objects with some spatial extent that appear coming out of occlusion, such as from behind a tree or a building. Rapid visual processing of the behaviorally significant part of an object may be facilitated if saccades and attention are directed to a particular part of the object, rather than to the geometric center of the suddenly appearing stimulus, as a tight and inflexible sensorimotor coupling would entail (see Kristjánsson, 2006, for further discussion). Establishment of a visuomotor set prior to the appearance of a visual stimulus can enable such responses.

There has long been a debate on the extent to which saccadic eye movements in reaction-time tasks are, on the one hand, stimulus bound and, on the other, affected by expectation, instruction, practice, and other cognitive processes (Kowler, 1990; Robinson, 1986; Steinman, 1986). By showing that a visuomotor set can spatially influence what are arguably the most reflexive saccadic eye movements, our results reveal that these views are not necessarily at odds but rather that their reconciliation may explain ecologically adaptive elements of visuomotor behavior.

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