The effect of object-centered instructions in Cartesian and polar coordinates on saccade vector

Jay A. Edelman

Department of Biology, The City College of New York, New York, NY, USA

The Graduate Center, The City University of New York, New York, NY USA ✉

Alexa M. Mieses

Department of Biology, The City College of New York, New York, NY, USA

Kira Konnova

Department of Biology, The City College of New York, New York, NY, USA

David Shiu

Department of Biology, The City College of New York, New York, NY, USA

Express saccades (ES) are the most reflexive saccadic eye movements, with very short reaction times of 70–110 ms. It is likely that ES have the shortest saccade reaction times (SRTs) possible given the known physiological and anatomical delays present in sensory and motor systems. Nevertheless, it has been demonstrated that a vector displacement of ES to spatially extended stimuli can be influenced by spatial cognition. Edelman, Kristjansson, and Nakayama (2007) found that when two horizontally separated visual stimuli appear at a random location, the spatial vector, but not the reaction time, of human ES is strongly influenced by an instruction to make a saccade to one side (either left or right) of a visual stimulus array. Presently, we attempt to extend these findings of cognitive effects on saccades in three ways: (a) determining whether ES could be affected by other types of spatial instructions: vertical, polar amplitude, and polar direction; (b) determining whether these spatial effects increased with practice; and (c) determining how these effects depended on SRTs. The results demonstrate that both types of Cartesian as well as polar amplitude instructions strongly affect ES vector, but only modestly affect SRTs. Polar direction instructions had sizable effects only on nonreflexive saccades where the visual stimuli could be viewed for several hundred milliseconds prior to saccade execution. Short- (trial order within a block) and long-term (experience across several sessions) practice had little effect, though the effect of instruction increased with SRT. Such findings suggest a generalized, innate ability of cognition to affect the most reflexive saccadic eye movements.

Introduction

All movement results from a combination of perceptual information and internal, or top-down, commands. Spinal reflexes, even those mediated by direct pathways located entirely within the spinal cord, can be squelched by an inclination not to move (Capaday, Forget, Fraser, & Lamarre, 1991; Evarts & Tanji, 1974; Wolpaw, 1997). Postural reflexes are influenced by behavioral context, both conscious and unconscious (Horak, Diener, & Nashner, 1989). Responses to visual stimuli are also under high-level influence. The saccadic eye movement system has been used as a model system for understanding how perception and cognition control movement, and thus can provide a useful tool for understanding how cognition can affect reflexive responses. Saccades can be made reflexively in response to suddenly occurring sensory stimuli, voluntarily, as observed in experiments studying decision, memory, or other cognitive processes, and automatically, as observed during the searching and scanning of the visual world (Leigh & Zee, 2015). Human saccades elicited by the sudden appearance of visual stimuli have reaction times ranging from 80 to several hundred milliseconds,

depending on factors such as the task parameters, properties of the visual stimuli, subject demographics, and familiarity of subjects with the task (Leigh & Zee, 2015).

The stimulus-bound nature of such reactive saccades is apparent when two visual stimuli are presented in spatial and temporal proximity. Saccadic responses to such stimuli tend to land in between the two stimuli rather than directly on one stimulus or the other. Such responses have been termed "averaging saccades" (Coren & Hoenig, 1972; Findlay, 1982). However, these responses are not strictly stimulus bound, but can be affected by cognition. He and Kowler (1989) demonstrated in a task where subjects were instructed to make a saccade to one of the two stimuli, defined by color, that the probability of the location of the target stimulus could affect saccade endpoint. Such saccades had a reaction time of less than 200 ms (He & Kowler, 1989).

Our lab has extended this finding to provide evidence that the spatial endpoints of reflexive saccadic eye movements with very short reaction times can be influenced by what we termed "visuomotor set," preparatory processes that alter the way visual responses are processed spatially into motor commands (Edelman, Kristjansson, & Nakayama, 2007). Moreover, this cognitive command need not dictate a saccade to a specific location in space, but could instead direct it towards a particular position within an object. Such object-centered instructions have been shown to modulate activity in areas of the primate brain including the supplementary eye fields (Olson, 2003) and to influence rapid spatial attentional deployment to extended objects (Kristjansson, Mackeben, & Nakayama, 2001). In our task, subjects were instructed, by means of a central fixation point, to make a saccade to the left or right of two visual stimuli that were separated horizontally. The two stimuli appeared randomly at one of several locations on the display. Thus, this instruction was object-centered, in that subjects did not know the location in space to which to make the saccade, but knew where to make a saccade to with respect to the stimulus array. The instruction was found to alter saccade vector without increasing saccade reaction time (SRT; Edelman et al., 2007).

Most surprisingly, such instructions influenced the vector of express saccades (ESs), saccades that have the shortest latency of all saccadic eye movements (B. Fischer & Boch, 1983; B. Fischer & Ramsperger, 1984), while leaving their ultrashort latencies intact (Edelman et al., 2007). This is particularly surprising given that the latencies and neurophysiology of ESs (Edelman & Keller, 1996) suggest that they have close to the minimum reaction time possible for saccades given the conduction and propagation delays in the neural

pathways starting in the retina, continuing through visual and extrastriate cortex, and progressing through saccade-related areas in the brainstem such as the superior colliculus before innervating the eye muscles (Leigh & Zee, 2015). Thus, following the instruction does not involve a separate, time-consuming process interceding between the sensory and motor processes involved in ES generation, but must instead involve the setting of synaptic weights or levels of neural activity in advance of the appearance of the visual stimuli. We refer to this ensemble of preparatory activity as "visuomotor set."

The finding that an object-centered horizontally oriented visuomotor set can alter ultrashort sensorimotor reflexes raises the question of whether other types of visuomotor set, involving other directions or instantiated within other coordinate systems, can have such an influence. Assuming that such mechanisms can influence sensorimotor reflexes during more naturalistic behavior, an exploration of how different types of visuomotor set can influence sensorimotor reflexes can yield a broader insight into how spatial cognitive processes can interact with perceptual processes to guide rapid movement.

In the current study, we used the basic procedure of the previous study but tested whether other types of instruction can influence ESs without increasing their reaction time. We tested whether instructions expressed in vertical Cartesian coordinates, namely to make a saccade to the upper or lower part of a visual stimulus array, can affect ESs. We also tested whether instructions given in polar coordinates of amplitude and direction could have such an influence. In addition, we examined whether learning or practice could enhance the effect over short or long time periods and how the extent of the effect increases with SRT.

Methods

Subjects

All research was approved under a protocol submitted to The City College of New York Institutional Review Board. Research conduct adhered to the Declaration of Helsinki. Four subjects (ages: 20–35 years, two female) participated in these experiments. One subject was an author on this paper; all others were naive as to the purpose of these experiments. All subjects were trained to make ESs prior to testing (see below), but none had experience on the object-centered instruction tasks.

General methods

Eye position was measured at 500 Hz by the Eyelink II eyetracker (SR Research, Kanata, ON, Canada). Subjects' heads were stabilized using a bite bar made of dental acrylic. Visual stimulus presentation and data collection were performed on a Mac G4 computer (Apple, Cupertino, CA) running routines from the Vision Shell library (Comtois, 2003). Visual stimuli were presented on a Compaq P1200 CRT monitor (Compaq, Palo Alto, CA) 55 cm from the subject. Stimuli were all white with a luminance of 100 cd/m^2. Sessions begin with a calibration procedure using a 3 × 3 grid, and a drift correction was performed between every block of trials.

Stimuli and procedure

Training procedure

Prior to beginning the main set of experiments, all subjects were trained to make ESs. The subjects participated in several sessions of "gap" eye movement trials until 2/3 of their trials had latencies in the ES range (<120 ms). In each session, subjects performed 288 trials, arranged in 18 blocks of 16 trials. Each trial began with a white square fixation stimulus at the center of the screen (0.5°). Subjects were required to fixate this stimulus within 500 ms of its appearance and then hold fixation until the presentation of the target stimulus elicited a saccade. The target square (1°) appeared 500–800 ms after fixation began; 150–200 ms before the appearance of a peripheral target, the fixation stimulus disappeared (i.e., gap task; Saslow, 1967). The target could appear in the four horizontal and vertical cardinal directions at an eccentricity of 9°. Subjects were instructed to make a saccade to the stimulus as quickly as possible, within 400 ms of target appearance. They then were required to maintain fixation of the target for 300 ms, after which it disappeared. Intertrial intervals were 700 ms. Any violations of these requirements, which were monitored in real time, resulted in the sounding of a beep and an immediate termination of the trial.

Experiment 1

The purpose of this experiment was to test the effect of eight spatial object-centered visuomotor sets (left, right, up, down, near, far, clockwise, counterclockwise) on ES vector. There were nine different trial types; in each the shape of the fixation point indicated the object-centered instruction. One task was a standard control task, identical to the training task described above. Here, the task was simply to make a saccade to the single target. The target could appear in the four horizontal and vertical directions at an eccentricity of 9°.

In the eight spatial instruction tasks, a target array of four white squares arranged in a diamond shape appeared (see Figure 1). As in the case for the one-target control task, the stimulus array was centered randomly in one of the four horizontal and vertical directions at an eccentricity of 9°. Each of the four squares was 1°. on a side, and the separation between the centers of the left and right squares and between the top and bottom squares was 5°. The temporal properties of the experiment procedure for these tasks were identical of those of the control trials. Instruction was indicated by the nature of the central fixation stimulus. These eight spatial instruction tasks (with their fixation stimuli) were (a) left ("v" shape pointing to the left, like a less than sign), (b) right ("v" shape pointing to the right, like a greater than sign, (c) up ("v" pointed up), (d) down ("v" pointed down), (e) near ("N"), (f) far ("F"), (g) clockwise ("CW"), and (h) counterclockwise ("CCW"). Note that due to the diamond shape configuration of the stimuli, as well as the possible positions of the stimuli (right, up, left, down), the location of the stimulus indicated by the instruction was always unambiguous. For convenience, given the nature of some of our analysis procedures the left and right instructions will be referred to as horizontal instruction types, the up and down instructions as vertical instruction types, the near and far instructions as polar amplitude instruction types, and the CW and CCW tasks as polar direction instruction types.

As in the training task above, each experimental session consisted of 18 blocks of 16 trials each, for a total of 288 trials. Instruction (or single-target trials with no instruction) was consistent within each block, and blocks of each of the nine trial types (eight different instructions plus the single target trials) were run twice in each session, with order counterbalanced. Each session, including set-up and calibration, lasted approximately 30 min. Four sessions were run across 2–3 weeks.

Experiment 2

The purpose of this experiment was to test the effect of object-centered visuomotor sets when reaction times were greater than those in the ES range—in particular to show the time range in which these effects reached an asymptote. In terms of object-centered instruction, trial types (control + eight different instructions) were identical to those of Experiment 1. The temporal properties of stimulus presentation and behavioral requirements were identical to that of Experiment 1, except that the interval between the disappearance of the fixation stimulus and the appearance of the target stimuli could range from 100 ms (gap) to −150 ms (overlap). Subjects were instructed to make a saccade
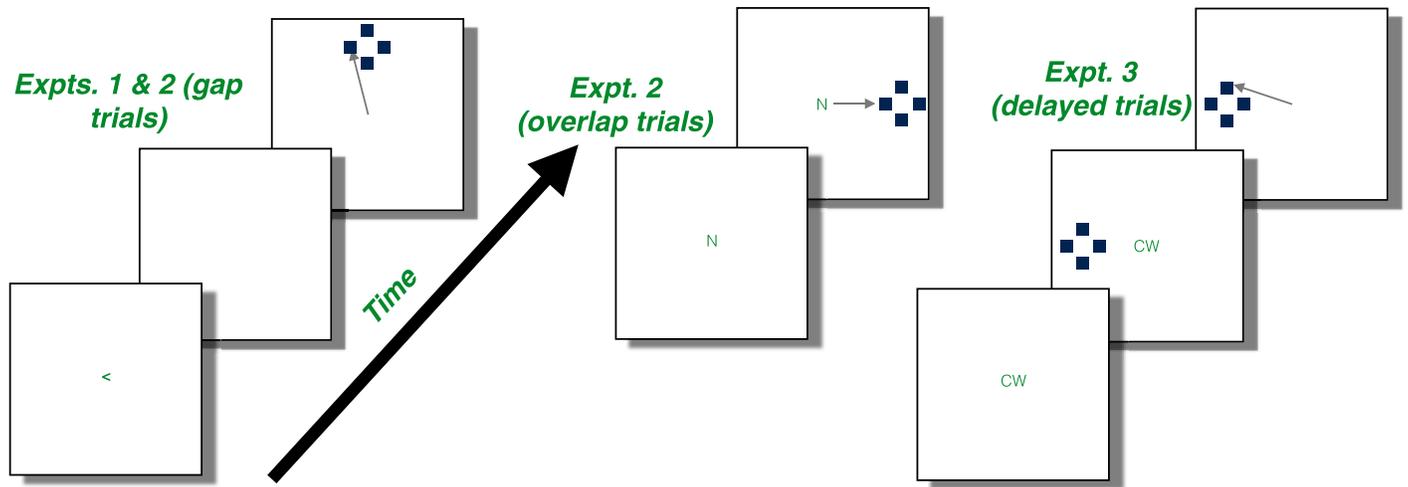
Figure 1. Schematics of the three trial types used in this experiment. Far left: Gap trials were used in Experiment 1 and some trials of Experiment 2. In these trials, the screen was blank in between the presentation of a central fixation and a peripheral target array. Sample trial shown used "<" as a central fixation point, prompting the subject to make a saccade to the leftmost of the four stimuli, wherever they appeared. Center: Overlap trials were used in some trials in Experiment 2. In these trials, the peripheral target was presented while the central fixation stimulus remained visible. In this sample trial, an "N" served as central fixation stimulus, prompting the subject to make a saccade to the nearest (closest) of the four stimuli. Right: Delayed trials were used in Experiment 3. In these trials, the central fixation stimulus remained visible for a variable amount of time after the target array appeared. The disappearance of the fixation stimulus cued the subject to make a saccade to the peripheral target array. In the trial shown, a "CW" indicated that a subject should make a saccade to the clockwise-most target.

to the target array as soon as it appeared, regardless of whether the fixation point disappearance or the target appearance occurred first. The number and structure of trials, blocks, and sessions was identical to that of Experiment 1.

Experiment 3

The purpose of this experiment was to examine how the effect of the instruction with longer intervals between the appearance of the target stimuli and the temporal cue to make a saccade. The control and object-centered tasks are similar to those of the other tasks, except that the tasks are run in an instructed delay format (B. Fischer & Boch, 1981), with target appearance preceding fixation point disappearance for 200, 400, 600, or 800 ms, and with the disappearance of the fixation point being the cue to make a saccade. The number and structure of trials, blocks, and sessions were identical to that of Experiments 1 and 2.

Data analysis

Data analysis was performed using routines from Matlab (Mathworks, Natick, MA). All stated statistically significant differences were significant at $\alpha = 0.05$. Our general approach was to run analysis of variance (ANOVA) and multiple comparison tests using one or more of our independent variables as fixed factors and subject as a random factor. We also examined data trends on an individual subject basis to ensure that any differences were not driven by only one or two subjects. This approach allowed us to use every saccade in our dataset in our analysis and have effects that approach, but not reach, statistical significance on the individual level still contribute when assessing the effect across all subjects. Saccades with reaction times less than 75 ms were deemed anticipatory saccades and were not analyzed further.

Calculation of saccade metrics

To compute the start and end of each saccade, a saccade velocity trace was obtained by differentiating the horizontal and vertical components of the eye position trace by a central difference algorithm implemented in Matlab and then using the Pythagorean theorem to calculate radial velocity as a function of time. We then used Matlab routines to estimate the eye position trace just after the time of the cue to make a saccade (either target appearance or fixation point disappearance; see below) to determine the first point at which velocity exceeded 35°/s. Next, the trace was evaluated backward in time until the first point below 15°/s was found. The end of the saccade was determined in an analogous manner, but with time reversed.
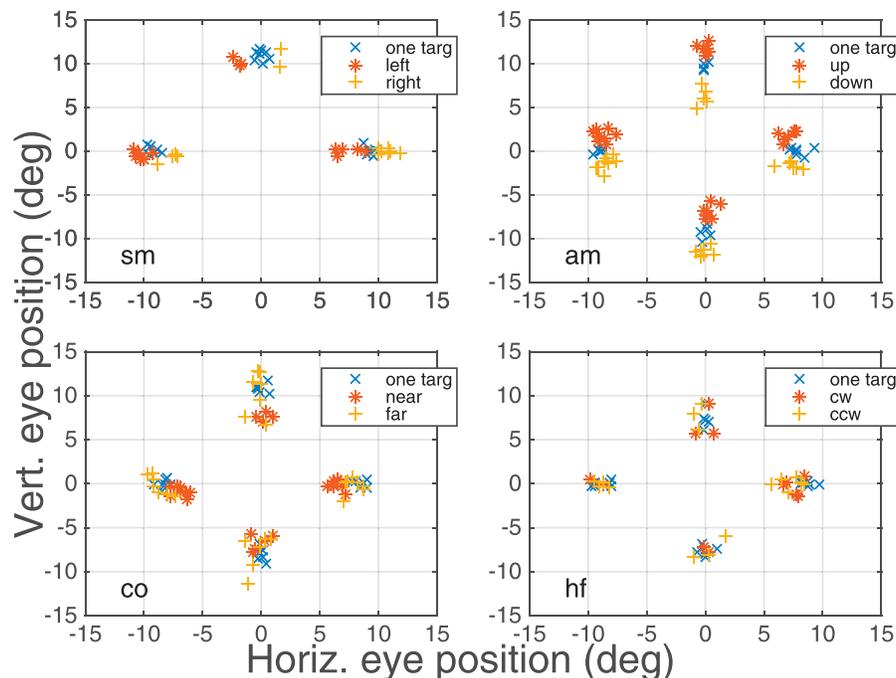
Figure 2. Endpoints of individual ESs (SRT < 120 ms) following directional instructions to stimulus arrays and of ESs to one target are shown for sample data for the four different instruction types from one of the four subjects (shown by initials) in Experiment 1. Top left: horizontal – left/right; top right: vertical – up/down; bottom left: polar amplitude – near/far; bottom right: polar direction – CW/CCW. In same cases (e.g., top left), ESs in a particular direction, usually downward, were not observed.

Results

Experiment 1: Gap task

ES yield was high in the gap task, showing that the gap, in combination with the pre-experimental training, was effective. Eight and a half percent of trials were not analyzed because subjects did not follow procedures correctly; 68% of these errors were anticipatory saccades, where subjects initiated saccades less than 75 ms after target appearance, indicating that they were not visually driven. Of the analyzed trials, 66.7% were ESs (reaction times < 120 ms). Instructions given in Cartesian (horizontal – left vs. right or vertical – up vs. down) or polar amplitude coordinates (polar amplitude – near vs. far) resulted in large effects on saccade landing point for ESs (reaction times < 120 ms), although, as in the case for Edelman et al. (2007), this effect was not complete, as ESs tended to land in between the intended target and the center of the stimulus array. In contrast, there was little influence of polar direction instructions (CW vs. CCW) on the vector of ESs. Examples of these effects are portrayed in Figure 2. The effect of instruction on saccade vector was quantified by performing, for each of the four pairs of opposing instruction types (horizontal, vertical, polar amplitude, polar direction) a two-factor AN-OVA, with instructional effect as the dependent variable, instruction (e.g., left vs. right) as a fixed factor and subject as a random factor. For the horizontal, vertical, and polar amplitude instruction pairs, we found highly significant effects of instruction (see Table 1). Note that for the polar amplitude instructions there was a bias towards shorter amplitude saccades, as saccades in the near condition tended to land much further from the midpoint between the two targets than those in the far condition, where saccades tended to land near the midpoint. This asymmetry between near and far may have contributed to a slightly weaker effect seen in the polar amplitude instructions compared to the horizontal and vertical instructions. This asymmetry was much smaller for the horizontal and vertical instruction types (Table 1).

Dependence of saccade vector and reaction time on instruction type

The relative dependence of ES vector on the type of instruction—horizontal, vertical, polar amplitude, and polar direction—had a remarkably constant pattern across the four subjects, with vertical having the greatest effect, followed by horizontal and polar amplitude, with, as described above, little effect in the polar direction instruction types. This was confirmed statistically by calculating a rectified value of instruction for each saccade type, so that saccades directed to the instructed target had a value of 1 and saccades

	Ins1	Ins2	SS_{Inst}	F	p_value
Horizontal right (Ins1) v. left (Ins2)	0.46 (0.37)	−0.58 (0.41)	158	68.3	0.0036
Vertical up (Ins1) v. down (Ins2)	0.63 (0.47)	−0.73 (0.44)	296	64.4	0.004
Polar amplitude far (Ins1) v. near (Ins2)	0.02 (0.53)	−0.62 (0.45)	63.8	39.7	0.008
Polar direction CW (Ins1) v. CCW (Ins2)	0.00 (0.50)	0.08 (0.51)	5.3	20.2	0.0188

Table 1. Mean (*SD*) normalized instruction effects on saccade endpoint for express saccades in Experiment 1. *Notes*: These values were signed such that the values corresponding to the "Ins1" instructions (right/up/far/CW) had a positive value if the saccades followed the instruction (with a value of +1.0 if the instruction was followed perfectly, with the saccade landing in the middle of the correct square) and the "Ins2" instructions (left/down/near/CCW) had a negative value if they followed the instruction (with a value of −1.0 if they followed the instructions perfectly). Statistics from ANOVA of main effect of task (Ins1 vs. Ins2) on normalized endpoint effect are also shown. CW = clockwise; CCW = counterclockwise.

directed to the midpoint of the target array had a value of 0. For each pair of instructions we then averaged the rectified values of the instruction effect (e.g., for vertical, the rectified values of up and down instructions were averaged). We then conducted a two-factor ANOVA with instruction type as a fixed factor and subject as a random factor, followed by a multiple comparisons procedure. A main factor of instruction type was found (SS = 198, *df* = 3, *F* = 66, *p* < 0.0001), and the multiple comparisons procedure showed significant differences for all pair-wise comparisons. Figure 3 illustrates that this pattern, vertical > horizontal > polar amplitude > polar direction, was found for all four subjects.

It is possible that the cognitive demands of object-centered spatial instructions increase SRT relative to
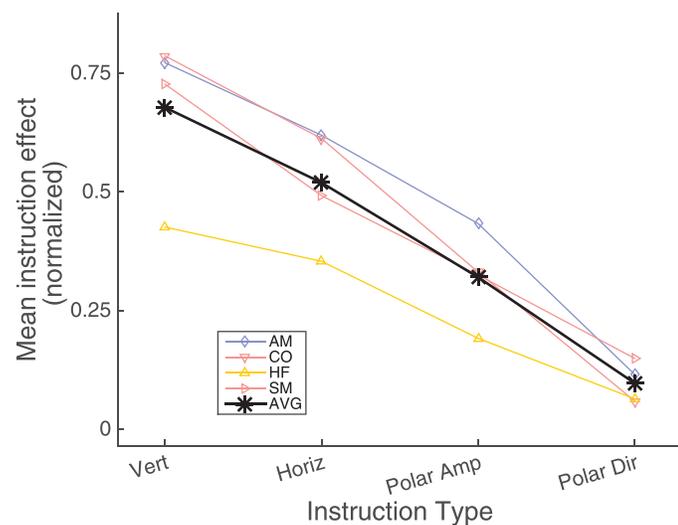

Figure 3. Mean instructional effect of ES endpoint in Experiment 1 for the four instructional trial types (horizontal / vertical / polar amplitude / polar direction) are shown for each of the four subjects and for the grand average of the four subjects. Mean instruction effect was calculated by averaging the mean rectified normalized effects for the two tasks within a task pair (e.g., left and right). If saccades followed directions perfectly then the mean rectified normalized instruction effect would be 1.0 (see text for additional details).

that of a simple SRT task. However, as this was not found to be the case in Edelman et al. (2007), we did not expect to find it here. Indeed, at most a modest effect on reaction time was found across the wider range of tasks in the present study. Mean reaction times across the four subjects ranged from 110 ms in the one-target task to 117 ms in the CCW task.

As in previous work (Dafoe, Armstrong, & Munoz, 2007; Goldring & Fischer, 1997; Previc, 1998), we found a dependence of SRT on target direction, with downward saccades having the longest SRT. Across all instruction types, mean SRT and percentage ESs for all analyzed trials were as follows: rightward: 101 ms, 89%; leftward: 104 ms, 89%; upward: 122 ms, 52%; and downward: 130 ms, 44%. Since ES yield was higher in certain directions, it's possible that asymmetries in the instructional effect within a pair of instructions may contribute to the results described above. To account for this, we recalculated the values shown in Table 1 by first calculating subaverages for saccades in each of the four directions, and then averaging these four sub-averages together. The results were very similar to those shown in Table 1.

Influence of reaction time on the effect of instruction

While instruction had little effect on reaction time, it is possible that the effect of instructions increased for saccades of greater reaction time. Our data indicated that this was the case for the horizontal, vertical, and polar amplitude instruction types in Experiment 1. Examples of this dependence are portrayed in Figure 4 and the differences are summarized in Figure 5.

To quantify the dependence of instructional effect on reaction time, we compared the effect of instruction on saccades with less than 100 ms reaction time (fast gap) with those of more than 120 ms reaction time (slow gap). For the data for each of the four instruction types we ran a two-factor ANOVA with rectified instruction effect as the dependent variable, latency group (fast gap vs. slow gap") as a fixed factor, and subject as a random factor. For the horizontal and vertical
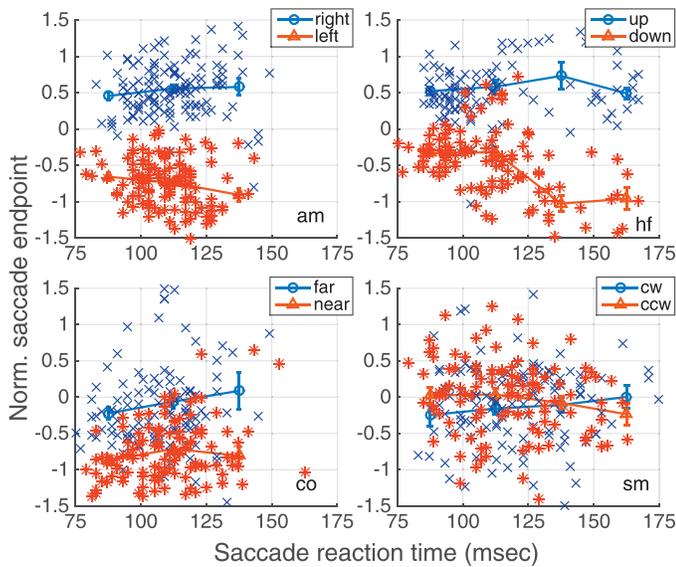
Figure 4. Example data of normalized saccade endpoints for the four instructional trial types as a function of SRT in Experiment 1. Top left: horizontal – left/right; top right: vertical – up/down; bottom left: polar amplitude – near/far; bottom right: polar direction – CW/CCW. Each data point represents a single saccade and each plot shows data for a single session. Lines are binned averages for the corresponding instruction. Bin size is 25 ms.
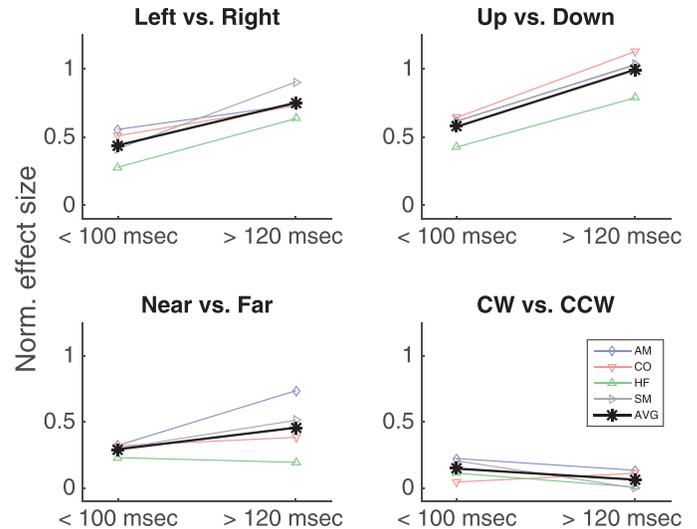

Figure 5. Means of normalized rectified effect size for the fast ESs (SRT < 100 ms) and slower saccades (SRT > 120 ms) for Experiment 1. Data for each subject and grand average of all subjects are shown.

instruction types we found significant main effects of latency group (horizontal: SS = 12.6, $df = 1$, $F = 19.3$, $p = 0.021$; vertical: SS = 20.4, $df = 1$, $F = 243$, $p < 0.001$), while for polar amplitude and polar direction instruction types we did not find a significant main effect, though for polar amplitude we found a significant interaction between latency group and subject (horizontal: SS = 3.42, $df = 3$, $F = 3.82$, $p = 0.01$), indicating that for some subjects the effect was increasing with reaction time (Figure 5).

However, as was the case for Edelman et al. (2007) we found that even saccades with the shortest reaction times were affected by instruction. We repeated our analysis of the instruction effect shown in Table 1 (nonrectified) comparing our pairwise analysis (left vs. right, up vs. down, etc.) for each of the four instruction types for just the saccades with reaction times less than 100 ms. We found significant effects for all four instruction types, including polar direction, though the effect size for polar direction was smaller than that for the other instruction types (Table 2), and statistical significance, even across this large data set, was marginal.

Effect of order in block and experience across sessions

In these experiments, like those of Edelman et al. (2007), we ran blocks of 16 trials that were identical in instruction. We also ran subjects in four identical experimental sessions (of 288 trials each). We thus wished to determine whether short- and long-term experience with following these instructions could increase the object-centered effects. Generally, we found only slight effects of trial history and session history. To examine trial history, we quantified this by dividing our data sets by trial order within a block into early trials for Trials 1–8 in a block and late trials for Trials 9–16 within a block. For examining session history, we divided the data into early sessions for Sessions 1–2 and late sessions for Sessions 3–4. For each of the four instruction types we then conducted two-way ANOVAs in which rectified instruction effect was the dependent variable, trial order (or session order) was a fixed effect, and subject was a random effect.

For the polar amplitude instruction type (near vs. far) we found a highly significant effect of trial order within a block (M SS = 1.98, $F = 78$, $df = 1$, $p < 0.001$) with a greater effect in later trials. Otherwise the effects of trial and session order were quite modest. For polar amplitude instructions, the effect of session order had a small effect that bordered on significance (M SS = 1.27, $F = 8.8$, $df = 1$, $p = 0.053$). We found generally that both trial order and session order had at most modest effects on the size of the instruction effect. For the horizontal instruction type, the effect of session was about 10%, but still statistically significant (see Table 3). There were no significant effects of either trial order nor session order for vertical and polar direction instruction types.

	Ins1	Ins2	SS$_{Inst}$	F	p value
Horizontal right (Ins1) v. left (Ins2)	0.33 (0.36)	−0.54 (0.35)	48.9	49.6	0.006
Vertical up (Ins1) v. down (Ins2)	0.52 (0.29)	−0.63 (0.43)	73	105	0.002
Polar amplitude far (Ins1) v. near (Ins2)	0.07 (0.40)	−0.51 (0.35)	20.2	162	<0.001
Polar direction CW (Ins1) v. CCW (Ins2)	0.14 (0.48)	−0.15 (0.49)	3.89	11.6	0.037

Table 2. Mean (*SD*) normalized instruction effects on saccade endpoint for express saccades with reaction times less than 100 ms in Experiment 1. *Notes*: Statistics from ANOVA of main effect of task on normalized endpoint effect are also shown. For other conventions see Table 1. CW = clockwise; CCW = counterclockwise.

Experiment 2: Gap/overlap task

In order to more fully understand how the effects of object-centered instruction evolve with time, we ran subjects on a gap/overlap task where the time between fixation disappearance and target appearance could range from a 100-ms gap to a 150-ms overlap. Use of gaps mixed with overlaps yielded a much larger range of SRTs, allowing a clearer picture of how the object-centered effect depended on reaction time.

As was the case for Experiment 1, the effect of task instruction on reaction time was statistically significant, though very modest. Mean reaction times across the four subjects ranged from 141 ms in the far task to 156 ms in the one-target task. Also as in Experiment 1, we found the pattern of instruction type on the object-centered effect on saccade vector to be consistent across subjects, with again vertical instructions having the largest effect, followed by horizontal, and polar amplitude. The effect of polar direction was slight at best (Figure 6).

There was a substantial speed/accuracy tradeoff within the range of reaction times observed for these saccades (100–200 ms), except for the polar direction instructions. As reaction time varied from subject to subject, but had probability distributions that were similar in shape, for display and analysis purposes we divided each subject's dataset into quartiles based on reaction time, yielding four reaction time epochs (Figure 6). The effect of epoch and instruction type on object-centered effect was then found by conducting a three-way ANOVA with rectified object-centered effect as the dependent variable and instruction type and epoch as fixed factors, and subject as a random

factor. Given that the data from the polar direction task were clearly different from that of the other tasks, we excluded these trials from the analysis, and thus analyzed only data from the horizontal, vertical, and polar amplitude instruction types. We found significant main effects of task ($F = 20$, $df = 2$, $p = 0.002$) and of epoch ($F = 8.6$, $df = 3$, $p = 0.005$). A multiple comparisons procedure analyzing the effect of epoch showed pairwise differences for all epochs, except for the comparison between the third and fourth epochs. These differences appeared to be driven by larger increases in effect with reaction time for the vertical instructions, an intermediate increase for the horizontal instructions, and a smaller effect in the polar amplitude instructions. Generalized across the tasks, multiple comparisons indicated a significant difference between the first and third epochs for all four subjects. In particular, the polar amplitude effect appeared to decrease overall between the third and fourth quartiles of reaction time. Also, the one subject (HF) who tended to have a smaller effect of instruction also appeared to have less of a speed–accuracy trade-off.

Experiment 3: Overlap task with instructional delay

In Experiment 3, unlike Experiments 1 and 2, the disappearance of the fixation point was the cue to make the saccade. The interval between visual target presentation and saccade initiation, which we will define as "saccade latency," was increased by keeping the fixation point illuminated after target presentation

	Session # diff. (Ins 2 − Ins1)					Trial order diff. (Ins 2 − Ins 1)				
Instruction/effect	Early	Late	SS$_{Inst}$	F	p value	Early	Late	SS$_{Inst}$	F	p value
Horizontal	0.97	1.09	0.70	29	0.002	1.01	1.06	0.14	0.63	0.48
Vertical	1.35	1.37	0.02	0.02	0.9	1.36	1.34	0.04	0.06	0.81
Polar amplitude	0.55	0.72	1.27	8.84	0.053	0.53	0.74	1.98	77.9	<0.001
Polar direction	0.07	0.09	0.06	0.86	0.41	0.10	0.07	0.02	0.08	0.79

Table 3. Session and trial order effects – difference in normalized effects of instruction type on saccade endpoint for express saccades in Experiment 1. *Notes*: See Table 1 for conventions pertaining to the values shown in the early and late columns. Statistics from ANOVA of main effects of session and trial order are also shown.
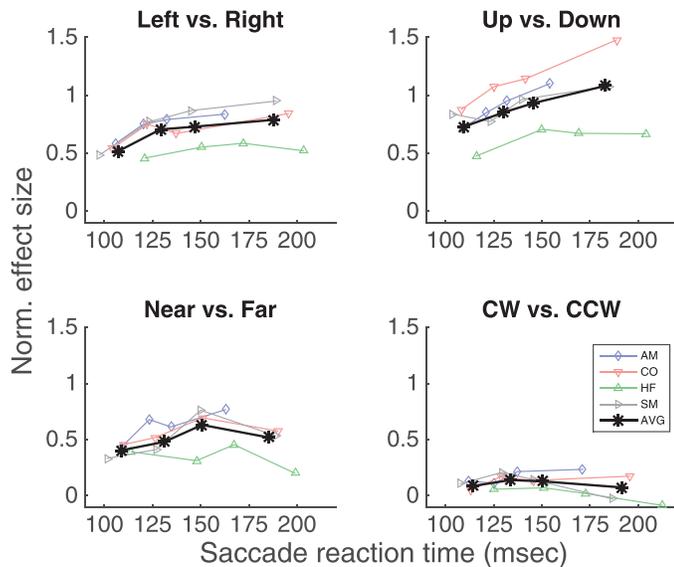
Figure 6. Normalized effect size as a function of reaction time for the four instruction types in Experiment 2. Data are binned for each subject by reaction time quartile. See Figure 3 for conventions pertaining to the difference in normalized effect size.
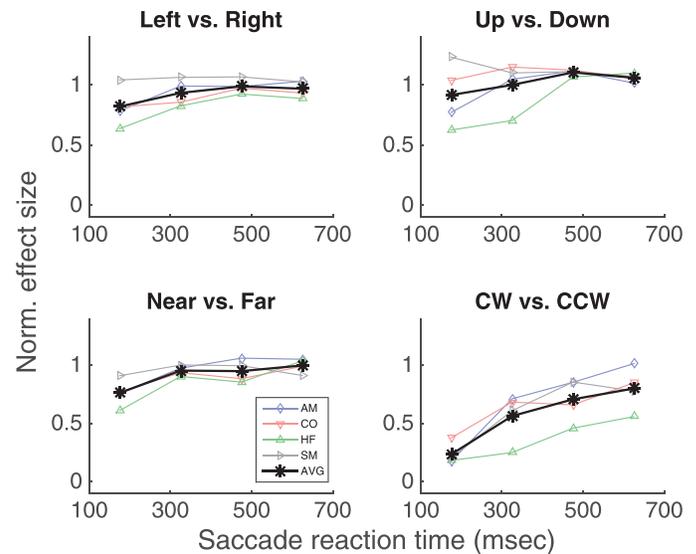

Figure 7. Difference in means of normalized effect size as a function of reaction time for the four instruction types in Experiment 3. Reaction time is binned at 200 ms intervals. See Figure 3 for conventions pertaining to the difference in normalized effect size.

and asking subjects to refrain from making a saccade until the fixation point disappeared, which occurred 200, 400, 600, or 800 ms after target appearance (stimulus-onset asynchrony [SOA]).

Our main motivation for this experiment was determining how the effect of instruction depended on the time between target appearance and saccade initiation. Since there were four, broadly spaced SOAs, we analyzed the role of latency on instruction effect by dividing our data into four groups based on the SOA (Figure 7). For the vertical, horizontal, and polar amplitude instructions, the effect appeared to reach a maximum at an SOA somewhere between 300 and 500 ms, corresponding to saccade latencies (time between stimulus presentation and saccade initiation) of 450–700 ms. Note that at higher SOAs the effect strength reached 1.0 for these instructions, indicating that saccades were made directly to the instructed target. The differences between the effects of horizontal, vertical, and polar amplitude instructions appear to be much smaller here than in Experiment 2, as the effects asymptote at larger SOAs.

As the effect of epoch on instruction effect was roughly similar for the vertical, horizontal, and polar amplitude instruction types, we analyzed the effect epoch by conducting a three-way ANOVA using all saccades from the vertical, horizontal, and polar amplitude data sets and with normalized instruction effect as the dependent variable, epoch and instruction type as fixed factors, and subject as a random factor. We found a significant main effect of epoch ($F = 3.9$, *df*

$= 3$, $p < 0.05$) and a main effect of instruction type that bordered on significance ($F = 4.7$, *df* $= 2$, $p = 0.059$). A multiple comparisons procedure analyzing the effect of epoch showed pairwise differences between the first epoch and all subsequent epochs, and a difference that bordered on significance ($p = 0.057$) between the 500- and 700-ms epochs.

Meanwhile, in this larger saccade latency range a substantial effect of the polar direction (CW vs. CCW) instruction pair was finally observed, with large differences found between the earlier and later epochs. We analyzed this by conducting a two-way ANOVA on all saccades with the polar direction data set with normalized instructional effect as the dependent variable, epoch as a fixed factor, and subject as a random factor. We found a substantial effect of epoch on the effect of instruction ($F = 17$, *df* $= 3$, $p < 0.001$). Multiple comparisons revealed significant differences between the first and all subsequent epochs and between the second and fourth epochs.

Discussion

The results of these experiments build upon the earlier work of Edelman et al. (2007) to show the generality of object-centered instructions on saccadic eye movements across instructions expressed in different coordinate frames, how the effect of instruction evolves with SRT (or latency), and how the extent of

effects depends upon short- and long-term experience with the instruction.

We found that instructions given in vertical coordinates (up vs. down) had an effect on ES vector that was even stronger than that of horizontal (left vs. right) coordinates (used in Edelman et al., 2007). Instructions given in terms of polar amplitude (near vs. far) were also effective in influencing ESs, even though the coordinate frame was non-Cartesian. These object-centered effects were clearly evident even for saccades less than 100 ms in reaction time. However, instructions given in terms of polar direction (CW vs. CCW) had only a small effect on saccades with reaction times less than 200 ms.

An analysis of how the effect of object-centered instruction depended on reaction time indicated that effect increased with increasing reaction time and reached an asymptote at saccade latencies of around 400 ms for the horizontal, vertical, and polar amplitude instruction types. In contrast, polar direction effects were apparent only with reaction times above 300 ms, and gradually increased before reaching an asymptote at a reaction time of around 800 ms. Edelman et al. (2007) previously examined effects of horizontal Cartesian instructions on ESs, showing also that the effect could be adjusted in amplitude and was dependent on the size of the visual stimulus. Given the degree of radial isotropy in the visual and oculomotor systems, it is not surprising that the vertical instructions had a similar effect, though it was notable to find that this was larger than the horizontal effect. One possible reason for a larger vertical effect is the functional significance of altitude, namely the distinction of up versus down, as opposed to horizontal position, where there is less functional distinction between left and right.

The effect with the polar amplitude instructions appeared to be smaller than the horizontal and vertical instruction effects. One possible reason for the reduction in amplitude is it may be difficult to make a saccade that overshoots a visible target. Indeed, saccades to suddenly appearing visual stimuli tend to be hypometric (Leigh & Zee, 2015). We thus would expect to find a near/far asymmetry in our data set, where the effect on near saccades was stronger that of far saccades. One previous study showed that when two stimuli are presented on an isodirectional line (such that the two stimuli have the same polar angle, but different eccentricities) and subjects are instructed to make saccades to the closer target, subjects are able to do so even for ESs (Weber, Latanov, & Fischer, 1993). This result is thus similar to our results in the near condition of Experiment 1, although they did not run a condition similar to our far condition.

Why do the polar direction conditions have different results from the other conditions?

The results in the polar direction conditions were strikingly different from the other three instruction conditions. Only a small effect of polar direction instruction was evident for ESs, and for any reaction time saccades in general. Only in the instructed delayed task (Experiment 3) did instruction begin to substantially influence saccade vector, with a full effect of polar direction not evident until approximately 500 ms after the target array appeared. This is reminiscent of data from a previous study of mental rotation during saccade programming (M. H. Fischer, Deubel, Wohlschlager, & Schneider, 1999), where subjects were required to use mental rotation to program a saccade displaced in polar direction from a suddenly appearing visual stimulus. This link with mental rotation can be confirmed with further experiments varying the polar angle distance between the two stimuli and testing if this systematically influences the ability of the instructions to influence saccades.

One explanation for why polar direction instructions were so ineffective on reactive saccades may be that brain mechanisms do not exist that can encode an object in terms of relative polar angle. It is known that locations on objects can be encoded in object-centered reference frames in terms of horizontal and vertical position (Olson, 2003). Such Cartesian encoding seems intuitive given our daily experience in the visual world. There is also considerable experimental evidence of this encoding, as it has been observed or inferred with a variety of neurophysiological, psychophysical, and clinical studies (Olson, 2003). As visual search of an object may prefer the exploration of close or far locations depending on characteristics of the visual scene, having a representation encoded in terms of near and far with respect to the current gaze angle may also serve behavior. In contrast, other than playing roulette, watching a Ferris wheel, or making spatial judgments regarding the hands of an old-fashioned analog clock, it is more difficult to see how the encoding of parts of objects with respect to the CW or CCW position of the object is useful in the real world.

One possible confound in this experiment is that the Cartesian instructions were indicated by arrows while the polar instructions were indicated by letters, adding a linguistic component that could result in different mechanisms of encoding, and possibly lengthening the time required to encode the polar instructions. The trial structure is likely to have mitigated any such differences, since instruction types were held constant within a block, so that encoding only needed to be switched once per block. It should be noted that we make no claim as to how these instructions are encoded, and it is quite possible that there is a linguistic component in

encoding both polar and Cartesian instructions and that the nature of this encoding is different across individuals.

The effect of practice and trial order

The analysis of session and trial order indicated that the effect of instructions on ES vector was evident with no training on the object-centered tasks. Effect on trial order within a block of trials (object-centered instruction was held constant within a block) was minimal, except for the polar amplitude instruction type, and the influence of session number on the effect (across the four sessions) was small. These results suggest that the ability to use these object-centered instructions to influence saccadic eye movements is hard-wired into the human sensorimotor system, or that at the very least it can arise during the development of normal visuomotor function and does not require specialized training or practice. This suggests that the ability to guide saccades to particular parts of suddenly appearing visual objects may be a commonplace visuomotor behavioral skill. The small effect of trial order within a block of trials in the polar amplitude instruction is reminiscent of short-term saccade adaptation, in which saccade vector changes across repeated trials in which a target is stepped to a new position during a saccade made to it (Leigh & Zee, 2015). Indeed, a recent study has shown amplitude adaptation even when saccade targets appear in different directions, as is the case here (Rolfs, Knapen, & Cavanagh, 2010). Conversely, if indeed there was a connection between saccade adaptation and this instruction effect then our data would predict that such global adaptation would not be seen in a task analogous to the Cartesian tasks used here.

Neurophysiology

Olson et al. (reviewed in Olson, 2003) described signals in the supplementary eye fields (SEF) that can represent visual or motor activity in object-centered coordinates. The SEF projects strongly to both the superior colliculus (SC) and the frontal eye fields (FEF), areas well known to play a major role in the production of saccadic eye movements. One explanation of the effects of instruction found here and in Edelman et al. (2007) is that such an object-centered signal could enhance or diminish saccade-related signals in brainstem areas, such as the paramedian pontine reticular reformation (PPRF) or mesencephalic reticular formation, in which horizontal and vertical components of saccades are thought to be frequency encoded (Leigh & Zee, 2015), with larger and faster saccades accompanied by greater neural activity. For example, an instruction to make a saccade to the left of a target array could enhance the activity of PPRF neurons mediating the leftward component of saccades.

However, Edelman et al. (2007) showed that an object-centered effect on saccades was dependent upon not only the spatial instruction but on the spatial extent of the visual stimulus, with the effect greater for a larger object than a smaller object. This visual dependence indicates the effect was influenced directly by target presence, and is thus likely to be mediated by areas in which a visual response is present. This suggests that a locus of the effect was more likely to be at the SC or upstream of it in the oculomotor pathways, namely in frontal or parietal cortex, rather than downstream in the brainstem, such as in the PPRF or mesencephalic reticular formation, where more purely motor-related signals are found (Leigh & Zee, 2015).

The SC and saccade-related areas upstream of the SC not only carry visual signals, but also code for saccades spatially. In particular, the SC and the FEF code for saccades in terms of a spatial map, where saccades of a particular vector are preceded by neural activity in a circumscribed spatial region of the SC or FEF, with visual locations close to the fovea being represented by larger amounts of the neural map than locations further away (Leigh & Zee, 2015). Interactions between neurons in such a spatial map may produce the asymmetry observed presently with the polar amplitude instructions, with the near instruction having a much larger effect than the far instruction. These differences suggest the effects of polar magnitude instructions are also mediated by modulated visual activity on a spatial map, and thus are mediated by the SC or areas upstream.

Conclusion

These data provide further evidence that the visuomotor system can rely on cognitive commands in some, but not all, object-centered reference frames to influence the vector of ESs while demonstrating that the these effects are innate to the human saccadic system and evolve to full effect over several hundred milliseconds.

Keywords: saccade, human, express, gap, cognition, object-centered, preparatory set

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Corresponding author: Jay A. Edelman.
Email: jedelman@ccny.cuny.edu.
Address: Department of Biology, The City College of New York, New York, NY, USA.

References

Capaday, C., Forget, R., Fraser, R., & Lamarre, Y. (1991). Evidence for a contribution of the motor cortex to the long-latency stretch reflex of the human thumb. *Journal of Physiology*, *440*, 243–255.

Comtois, R. (2003). *Vision Shell PPC* [Software libraries]. Cambridge, MA: Raynald Comtois.

Coren, S., & Hoenig, P. (1972). Effect of non-target stimuli upon length of voluntary saccades. *Perceptual and Motor Skills*, *34*, 499–508.

Dafoe, J. M., Armstrong, I. T., & Munoz, D. P. (2007). The influence of stimulus direction and eccentricity on pro- and anti-saccades in humans. *Experimental Brain Research*, *179*(4), 563–570, doi:10.1007/s00221-006-0817-8.

Edelman, J. A., & Keller, E. L. (1996). Activity of visuomotor burst neurons in the superior colliculus accompanying express saccades. *Journal of Neurophysiology*, *76*, 908–926.

Edelman, J. A., Kristjansson, A., & Nakayama, K. (2007). The influence of object-relative visuomotor set on express saccades. *Journal of Vision*, *7*(6):12, 1–13, doi:10.1167/7.6.12. [PubMed] [Article]

Evarts, E. V., & Tanji, J. (1974). Gating of motor cortex reflexes by prior instruction. *Brain Research*, *71*(2–3), 479–494.

Findlay, J. M. (1982). Global visual processing for saccadic eye movements. *Vision Research*, *22*, 1033–1045.

Fischer, B., & Boch, R. (1981). Enhanced activation of neurons in prelunate cortex before visually guided saccades of trained rhesus monkeys. *Experimental Brain Research*, *44*, 129–137.

Fischer, B., & Boch, R. (1983). Saccadic eye movements after extremely short reaction times in the monkey. *Brain Research*, *260*, 21–26.

Fischer, B., & Ramsperger, E. (1984). Human express-saccades: Extremely short reaction times of goal directed eye movements. *Experimental Brain Research*, *57*, 191–195.

Fischer, M. H., Deubel, H., Wohlschlager, A., & Schneider, W. X. (1999). Visuomotor mental rotation of saccade direction. *Experimental Brain Research*, *127*(2), 224–232.

Goldring, J., & Fischer, B. (1997). Reaction times of vertical prosaccades and antisaccades in gap and overlap tasks. *Experimental Brain Research*, *113*(1), 88–103.

He, P. Y., & Kowler, E. (1989). The role of location probability in the programming of saccades: Implications for "center-of-gravity" tendencies. *Vision Research*, *29*, 1165–1181.

Horak, F. B., Diener, H. C., & Nashner, L. M. (1989). Influence of central set on human postural responses. *Journal of Neurophysiology*, *62*(4), 841–853.

Kristjansson, A., Mackeben, M., & Nakayama, K. (2001). Rapid, object-based learning in the deployment of transient attention. *Perception*, *30*(11), 1375–1387.

Leigh, R. J., & Zee, D. S. (2015). *The neurology of eye movements* (5th ed.). New York: Oxford University Press.

Olson, C. R. (2003). Brain representation of object-centered space in monkeys and humans. *Annual Review of Neuroscience*, *26*, 331–354, doi:10.1146/annurev.neuro.26.041002.131405.

Previc, F. H. (1998). The neuropsychology of 3-D space. *Psychological Bulletin*, *124*(2), 123–164, doi:10.1037/0033-2909.124.2.123.

Rolfs, M., Knapen, T., & Cavanagh, P. (2010). Global saccadic adaptation. *Vision Research*, *50*(18), 1882–1890, doi:10.1016/j.visres.2010.06.010.

Saslow, M. (1967). Effects of components of displacement-step stimuli upon latency for saccadic eye movements. *Journal of the Optical Society of America*, *57*, 1024–1029.

Weber, H., Latanov, A., & Fischer, B. (1993). Context dependent amplitude modulations of express and regular saccades in man and monkey. *Experimental Brain Research*, *93*(2), 335–344.

Wolpaw, J. R. (1997). The complex structure of a simple memory. *Trends in Neurosciences*, *20*(12), 588–594.