J Neurophysiol 108: 3161–3171, 2012.
First published September 26, 2012; doi:10.1152/jn.00344.2012.

Is saccade averaging determined by visual processing or movement planning?

Neha Bhutani,[1] Supriya Ray,[1] and Aditya Murthy[2]
[1]*National Brain Research Centre, Near NSG Campus, Haryana, India; and* [2]*Centre for Neuroscience, Indian Institute of Science, Karnataka, India*

Submitted 25 April 2012; accepted in final form 13 September 2012

Bhutani N, Ray S, Murthy A. Is saccade averaging determined by visual processing or movement planning? *J Neurophysiol* 108: 3161–3171, 2012. First published September 26, 2012; doi:10.1152/jn.00344.2012.—Saccadic averaging that causes subjects' gaze to land between the location of two targets when faced with simultaneously or sequentially presented stimuli has been often used as a probe to investigate the nature of computations that transform sensory representations into an oculomotor plan. Since saccadic movements involve at least two processing stages—a visual stage that selects a target and a movement stage that prepares the response—saccade averaging can either occur due to interference in visual processing or movement planning. By having human subjects perform two versions of a saccadic double-step task, in which the stimuli remained the same, but different instructions were provided (REDIRECT gaze to the later-appearing target vs. FOLLOW the sequence of targets in their order of appearance), we tested two alternative hypotheses. If saccade averaging were due to visual processing alone, the pattern of saccade averaging is expected to remain the same across task conditions. However, whereas subjects produced averaged saccades between two targets in the FOLLOW condition, they produced hypometric saccades in the direction of the initial target in the REDIRECT condition, suggesting that the interaction between competing movement plans produces saccade averaging.

double-step; hypometric saccade; midway saccade; sequential saccades; saliency map; priority map

WHEN SUBJECTS ARE FACED WITH two simultaneous or sequentially presented visual stimuli, subjects' gaze may land between the spatial locations of the two targets (Arai et al. 2004; Aslin and Shea 1987; Becker and Jürgens 1979; Chou et al. 1999; Coren and Hoenig 1972; Findlay 1982; Ottes et al. 1984, 1985), hence producing averaged saccades. Because making a saccadic eye movement involves at least two stages of processing—a visual (sensory) stage that selects a target and a movement-planning (motor) stage that prepares the response (Schall and Thompson 1999)—saccade averaging may be a consequence of interactions occurring either in the visual or the movement stage. Whereas numerous neurophysiological experiments have attempted to test whether saccade averaging involves sensory (Glimcher and Sparks 1993) or movement representations (Edelman and Keller 1998; Van Opstal and Van Gisbergen 1990), the conclusions drawn from them are limited. For example, inferences based on microstimulation experiments are hampered by our lack of understanding of what representations are being activated (Histed et al. 2009). Complicating this issue further is the evidence that subthreshold microstimulation of frontal eye fields (FEF), through feedback connections, can influence the activity of individual V4 neurons and affect attention directed at the stimulus sites (Armstrong et al. 2006; Moore and Fallah 2004). The interpretations of neurophysiological experiments are also hampered by the difficulty in clearly identifying cell types that only represent stimulus locations independent of saccade goals (Murthy et al. 2009; Sato and Schall 2003). In fact, the dominant cell types in the superior colliculus (SC) (Shen and Paré 2007) and FEF (Bruce and Goldberg 1985) are visuomovement, representing both stimulus locations and saccade goals. Compounding these issues is the problem that both stimulus location and saccade goals are typically inextricably linked and therefore hard to distinguish. Whereas the double-step paradigm resolves this issue by creating the necessary dissociation between the retinal location of the second target and the saccade vector necessary to acquire it, many visual neurons throughout the oculomotor system are sensitive to intended/actual eye position/displacement and appear to remap their receptive fields in accordance, making them difficult to distinguish from cells representing movement planning (Duhamel et al. 1992; Sparks and Barton 1993).

In this study, we used a behavioral readout to test whether saccade averaging involves sensory or movement computation by recording subjects on two different double-step saccade tasks (FOLLOW and REDIRECT) (Ray et al. 2004). Whereas the retinal information is the same in the two tasks, the instructions differ, hence requiring different movement planning. Thus any qualitative difference in the type of averaged saccades produced in the two tasks may be attributed to the difference in movement planning that these tasks entail.

METHODS

We have analyzed the data of the 14 subjects of Ray et al. (2004), who had performed both the tasks in two separate sessions. All subjects gave their informed consent in accordance with the Institutional Ethics Committee of National Brain Research Centre and the Declaration of Helsinki.

Task and Stimuli

We used two types of double-step tasks, called the FOLLOW and the REDIRECT tasks. Both tasks have been described in detail elsewhere (Ray et al. 2004). Briefly, in both tasks, each trial started with the appearance of a central fixation spot, which was a 1° white square presented on a dark background. Subjects were required to fix their gaze within a ±2.5° electronically drawn window centered at the fixation spot. Tasks consisted of two types of trials. The majority of the trials (60%) were no-step trials. The remaining 40% trials were step trials. On no-step trials, following fixation for a random duration that ranged from 300 to 800 ms, the fixation spot disappeared, and a green target (1° × 1°, 6.5 cd/m^2) appeared in one of the eight possible locations on an imaginary circle of radius 10° centered on the fixation

---

Address for reprint requests and other correspondence: A. Murthy, Centre for Neuroscience, Indian Institute of Science, Bangalore 560012, Karnataka, India (e-mail: aditya@cns.iisc.ernet.in).

spot. On step trials, the green target was followed by a red target (1° × 1°, 6.5 cd/m^2) after a random temporal delay, called the target step delay (TSD). We used 4 TSDs with means 49 ± 14, 99 ± 14, 149 ± 14, and 199 ± 14 ms. Both types of trials were pseudorandomly interleaved throughout each recording session. An angular separation of ≥90° was maintained between the initial target (IT) and the final target (FT) locations. Subjects were given prior verbal instructions and ~50 practice trials. On average, a total of 500 trials were completed for each subject. To avoid the contamination of data with nonspecific impairments due to excessive fatigue, breaks were interleaved regularly throughout the recording session, and the total duration of the recording session did not exceed 1 h. Each correct trial was followed by an auditory beep to provide feedback to subjects. All subjects were monetarily rewarded at the end of the recording session. Apart from monetary compensation for overall participation, extra reward was given based on the number of correct trials.

FOLLOW task. In this task (Fig. 1*A*), the targets remained on the screen throughout the trial. In no-step trials, the appearance of the target acted as a "GO" signal for the subject to make a saccade to the target. In step trials, the first green target was followed by a second red target after a random TSD. Subjects were instructed to visually follow the locations of two targets with sequential saccades, fixating the respective targets within an electronically drawn window of ±2.5° centered at the target.

REDIRECT task. In this task (Fig. 1*B*), as in the FOLLOW task, a no-step trial was scored as successful if followed by a brief fixation, subjects made a saccade to the target and maintained fixation within an electronically drawn window of ±2.5° centered at the target. On step trials, however, contrary to the FOLLOW task, subjects were instructed to saccade directly to the later-appearing red target. This behavior entailed cancellation of the initial plan to foveate the green target and instead redirect their gaze to later-appearing red target.

Recording Setup

Experiments were under computer control using TEMPO/VideoSYNC software (Reflective Computing, St. Louis, MO), which displayed visual stimuli and sampled and stored eye positions and other behavioral parameters. Eye position was sampled at 200 Hz with an infrared pupil tracker (ISCAN, Woburn, MA) that interfaced with the TEMPO software in real time. Before starting the recording session, each subject was made to look at five positions on the monitor—one at fixation in the center of the monitor and at least four (horizontal left, right; vertical up, down) target positions. The monitor (SONY Trinitron 500 GDM monitor, 21 in., 70 Hz refresh rate; 640 × 480 resolution) was placed 57 cm from the subject. While subjects fixated at the targets, we adjusted the horizontal and vertical gain parameters in real time such that the end-point of saccades would typically coincide with the center of the electronic windows centered on their respective target positions (but visible only to the experimenter). Since the electronic window (for fixation and target position) was displayed throughout the experiment, we could adjust the gains and recalibrate the fixation spot from time to time to compensate for drifts and slight changes in head positions. To facilitate calibration across trials, each trial began only after subjects' eye position was deemed to be within the limits set by the fixation window ±2.5°. In our experiment, targets were displayed at 10° of eccentricity, and the minimum angular separation between the two targets in a step trial was 90°. Thus the minimum spatial separation between two targets was at least 14°. Thus the error introduced as a consequence of our calibration procedure (±2.5°) and the typical accuracy of the tracker (~1°) were well within limits to be confident that trials were classified correctly.

Data Analyses

All offline analyses were performed using custom-made programs written in MATLAB (MathWorks, Natick, MA). The analog eye

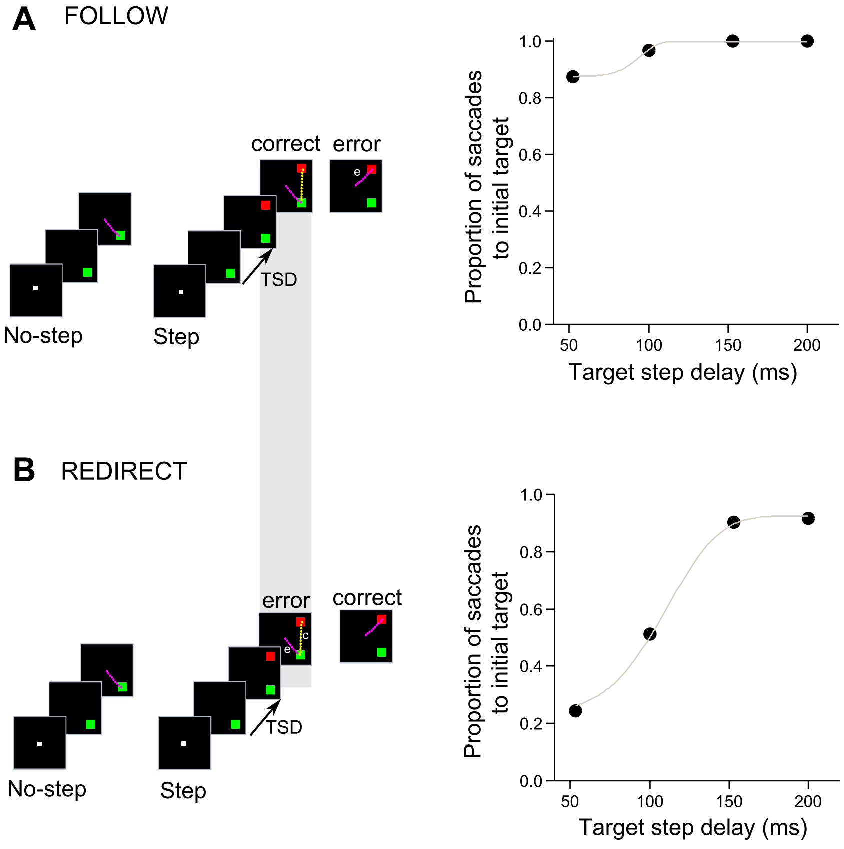


Fig. 1. Schematic showing the temporal events in the FOLLOW (*A*) and REDIRECT (*B*) tasks. The tasks consist of 2 types of trials: no-step and step trials. In no-step trials, only a single green target is presented. In step trials, a second red target is presented after a variable target step delay (TSD). The no-step trials are same in both of the tasks. Subjects make a saccade, shown in magenta, to the target. *A*: in FOLLOW step trials, subjects are instructed to make a sequential saccade, as shown in yellow, to the final target (FT) after the initial saccade (magenta) to the red target. The probability of compensation is thus not affected by the TSD. *B*: the no-step trials in the REDIRECT task are same as in the FOLLOW task. In step trials, subjects are instructed to cancel the planned saccade to the initial target (IT) and redirect their gaze to the later-appearing red target. In some step trials, an erroneous saccade ("e", magenta) to the IT is followed by a corrective saccade ("c", yellow) to the FT location, thus generating sequential saccades similar to the FOLLOW task. The increasing compensation function shows that at larger TSDs, the cancellation of the preprogrammed saccade becomes difficult, hence increasing the probability that the initial saccade will finish before the second target.

position data were smoothed from which blinks were removed. A velocity threshold of 30°/s was used to demarcate the initiation of saccades. The saccade detection algorithm was subsequently verified manually for every saccade. All blink-perturbed saccades were eliminated from analysis. Trials in which saccade latency was <80 ms (anticipatory saccades) were rejected. All statistical tests were done using SigmaStat or Statistics Toolbox in MATLAB. We used the Bonferroni test for all planned comparisons. Unless mentioned otherwise, results of averaged data are presented as mean ± SE. Analyses for the classification of midway and hypometric saccades were based on the end-point of the initial saccade. The direction of the end-point of the saccade was obtained by calculating the slope of the line segment joining the start and the end-point of the saccade.

Classification of midway saccades. With the use of no-step trials, we calculated the 95% confidence interval of the distribution of the direction of the end-point of correct saccades to corresponding targets (Fig. 2*A*). Step trials, in which subjects' eye traces landed between the ITs and the FTs but beyond the 95% confidence interval for the distribution of the end-point of no-step saccades to the two targets, were classified as midway saccades (Fig. 2*A*). Also shown is the second saccade directed at the second target after an initial saccade directed to the first target in a correct step trial.

Classification of hypometric saccades. From the no-step data, we obtained the means and the 95% confidence intervals for the direction and amplitude of correct saccades. An ellipse was drawn for which the center was defined by the means, and the two axes were defined by the confidence intervals for the direction and amplitude (Fig. 2*B*). The ellipse thus demarcated the distribution of saccade end-points of correct no-step saccades. Saccades toward the IT, whose directions were within the 95% confidence interval for the direction of correct no-step saccades but were terminated so that their amplitudes were less than the lower confidence bound of the amplitude spread, were classified as hypometric saccades (Fig. 2*B*). Also shown is the saccade directed toward the FT in a correct step trial. In some trials, hypometric saccades toward the IT were followed by a "corrective" saccade to the FT, which will be referred to as hypometric corrections. Figure 2*B* shows a typical hypometric saccade in a step trial. On average, 61.2 ± 3.6% of hypometric saccades were followed by a corrective saccade to the FT (Fig. 2*C*) after a short intersaccade interval (29.8 ± 4.4 ms), whereas on some trials, although a saccade was initiated to the IT location, subjects made a correction online, resulting in curved saccade trajectories directed to the FT without any intersaccdic interval (Fig. 2*C*).

Classification of curved saccades in the REDIRECT task. Saccade curvature was defined as the maximum perpendicular deviation from the straight line drawn from the start to the end of the saccade, normalized by the amplitude of the saccade (Smit and Van Gisbergen 1990). The analysis was done separately for different target locations. Those step trials were analyzed where saccades were made to the FT location. Inherent mean curvature for each target location was obtained by estimating the curvature for no-step saccades for individual subjects. The mean curvature (in no-step trials) was subtracted from the actual curvature value observed in step trials to estimate the "corrected curvature" index, similar to McPeek et al. (2003). Those saccades that had corrected curvature values beyond 0.75× SD from the mean corrected curvature were classified as curved saccades. To distinguish hypometric corrections from curved saccades to the FT, we plotted their velocity profiles. Figure 2*C* plots the velocity profile of a single curved saccade and hypometric correction. The hypometric correction clearly shows two peaks in the velocity profile separated by an intersaccade interval of 5 ms, whereas the curved saccade shows only a single peak in the velocity profile.

Those trials where subjects failed to correct the midway/hypometric saccade in the REDIRECT condition or saccades to the first target followed by another saccade to the second target in the FOLLOW task were not rewarded.

RESULTS

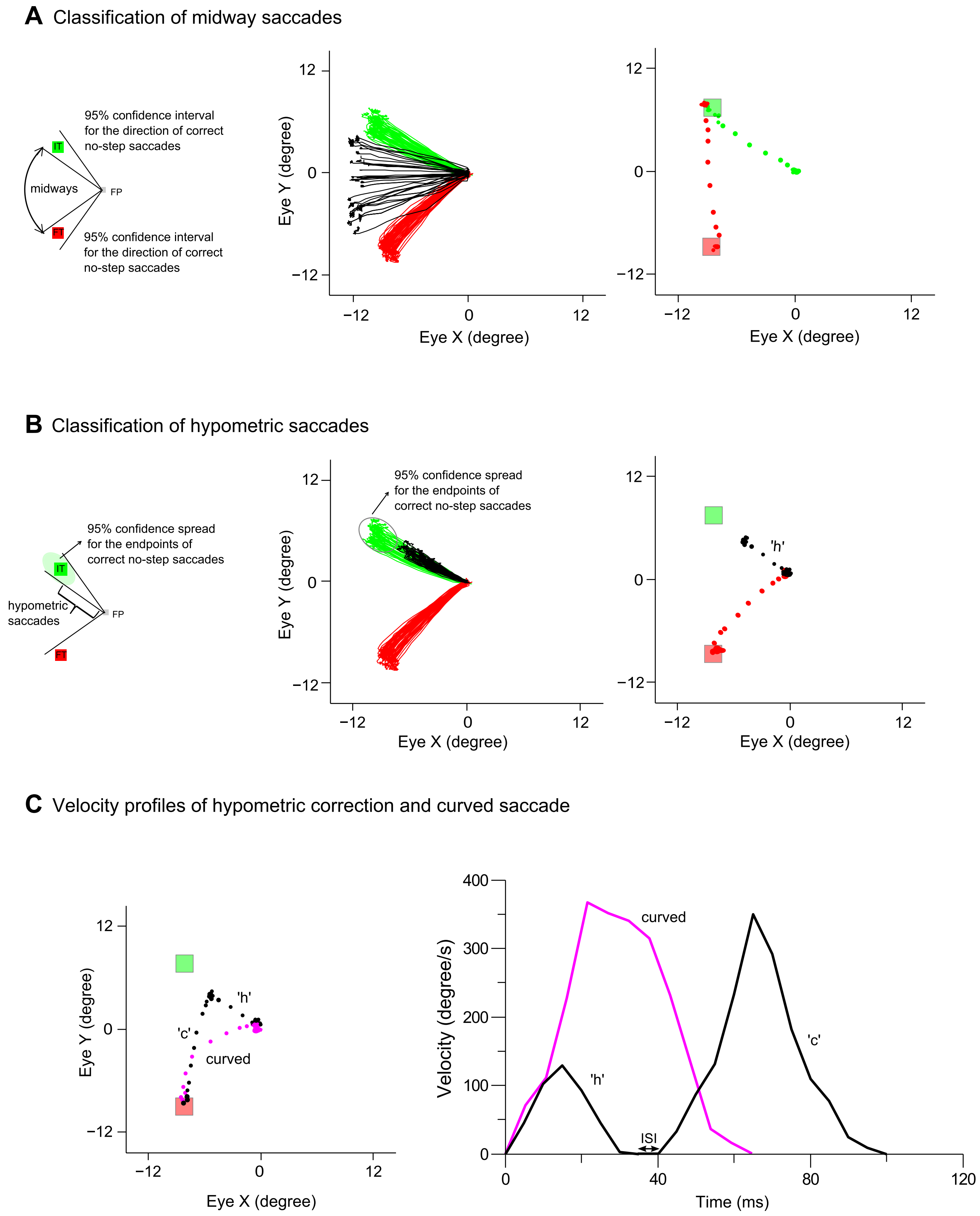
In the FOLLOW task (Fig. 1*A*), subjects were rewarded for making two sequential saccades. Trials in which subjects' eye trace landed directly at the location of the second target or in which subjects made a saccade only to the first target were not rewarded. In the REDIRECT task (Fig. 1*B*), subjects had to cancel the partially planned saccade to the first target and make a saccade directly to the second target. Thus although the retinal information in the two tasks was the same, the two tasks entailed different movement programs to be instantiated for successful performance. However, in many cases, subjects failed to cancel the saccade directed to the first target (error saccade in Fig. 1*B*). Such erroneous trials were then followed by a second corrective saccade (Fig. 1*B*) directed to the position of the second target. Thus sequential saccades produced in the REDIRECT task reflect error correction in contrast to the FOLLOW task, where it is part of the correct response.

The performance of subjects in both tasks was described using a compensation function, which plots the probability of making a saccade to the IT with TSD. Figure 1, *A* and *B*, depicts the performance of a representative subject in the FOLLOW and the REDIRECT tasks, respectively. In the FOLLOW task, since subjects are to make sequential saccades, this probability is not affected by the TSD, but in the REDIRECT task, where the subjects are required to cancel the initial preprogrammed saccade, the probability to saccade to the IT increases with the TSD. The increasing compensation function is expected because at larger TSDs, the cancellation of the preprogrammed saccade becomes difficult, hence increasing the probability that the initial saccade will finish before the second target. These differences in performance were quantified by fitting a cumulative Weibull function

$$W(t) = \gamma - (\gamma - \delta)\exp^{-\left(\frac{t}{\alpha}\right)^{\beta}}$$

where t is the TSD, α is the time at which the inhibition function reaches the sum of 63.2% of its maximum value γ and 36.8% of its minimum value δ, and β is the slope (Ray et al. 2009). Since the term $(\gamma - \delta)$ describes the increase in the probability of making a saccade directed at the first target, we used it as an index to describe the monotonic dependence of the data as a function of TSD and to quantify the degree of cancellation. Subjects had higher values of this index for the REDIRECT task compared with the FOLLOW task (Fig. 4*B* in Ray et al. 2004). The mean (±SE) index for the FOLLOW and REDIRECT task for these subjects was found at 0.29 (±0.03) and 0.59 (±0.04), respectively.

Figure 3 describes how two different cognitive contexts (instructions) give rise to different sets of predictions depending on whether saccade averaging were to involve sensory or movement-related processing. Figure 3*A* describes the sensory averaging hypothesis, which in its simplest form, would predict no difference between the REDIRECT and FOLLOW tasks since the retinal/sensory information is identical in both tasks. However, since the cognitive context in which the saccade sequences are generated is different between the two conditions, it is conceivable that differential amounts of visual attention, operating on sensory representations, may be allocated to the targets. For example, in the FOLLOW task, more attention is expected to be allocated to the IT location (Fig.



A Classification of midway saccades

B Classification of hypometric saccades

C Velocity profiles of hypometric correction and curved saccade

3*A*). In contrast, in the REDIRECT task, greater attention could be allocated to the FT (Fig. 3*B*). If averaging occurs in the sensory domain, which is modulated by such attentional allocation, then the end-points of averaged saccades may follow the locus of attention (Rizzolatti et al. 1987). Thus if attention were to operate differentially across the two tasks, the end-points of the averaged saccades are expected to lie closer to the IT in the FOLLOW task but closer to the FT locations in the REDIRECT task (Fig. 3*A*). In contrast, if saccade averaging is the result of computations specific to the movement-planning stage, a qualitatively different outcome is expected (Fig. 3*B*). This is a consequence of the different instructions given to subjects in both tasks. Whereas in the FOLLOW task, saccade averaging is expected as a collision between movement programs (Fig. 3*B*) directed at the ITs and FTs, saccade end-points are expected to occur accordingly between the first and second target positions as before. However, in the REDIRECT task (Fig. 2*B*), since subjects have to cancel the initial saccade plan and redirect the gaze to the second target, the behavior involves a movement plan (GO) that must interact with another movement plan, which cancels this plan. Such an interaction should produce hypometric saccades that are directed toward the first target (Ramakrishnan et al. 2010).

To test whether saccade averaging is sensitive to processing in sensory or movement representations, we classified averaged saccades into midway and hypometric saccades in the two tasks. Figure 4 plots the percentage of hypometric saccades vs. midway saccades for the 14 subjects in FOLLOW and REDIRECT tasks. In the FOLLOW task, subjects produced 19.65 ± 1.13% and 5.01 ± 0.82% midway and hypometric saccades, respectively. In the REDIRECT task, subjects generated 9.92 ± 1.25% and 24.77 ± 1.79% midways and hypometric saccades, respectively. We performed a two-way ANOVA with task type (FOLLOW/REDIRECT) and trial type (midway/hypometric saccades) as factors. There was a significant interaction between the task type and trial type ($P < 0.001$; F = 129.46). Further planned comparisons revealed that the extent of midway saccades was significantly more in the FOLLOW task than in the REDIRECT task (t = 5.31; $P < 0.001$). On the contrary, the percentage of hypometric saccades was significantly more in the REDIRECT compared with the FOLLOW task (t = 10.78; $P < 0.001$). Within each task, the percentage of midway saccades was significantly more than the percentage of hypometric saccades in the FOLLOW task (t = 7.99; $P < 0.001$), whereas in the REDIRECT task, the extent of hypometric saccades was significantly more than the midway saccades (t = 8.10; $P < 0.001$). This difference in the types of errors produced in the two tasks suggests that averaging is sensitive to the differences in the cognitive architecture demanded by the different tasks, since the retinal/sensory information in the FOLLOW and REDIRECT tasks is the same.

To test whether attention might also play a role in the generation of midway saccades, we plotted the spread of the end-point of midway saccades in the REDIRECT and the FOLLOW task. For this analysis, we used only those trials where the angular separation between the two targets was equal to 90°, since there was a greater extent of midway saccades for the 90° angular separation compared with 135° and 180 °. To pool the data across different target locations, we rotated the target locations and the accompanying saccade vector so that the first and second targets were at 0° and 90°, respectively. Furthermore, midway trials were classified based on the extent of time allowed for parallel programming of the two saccades, called the reprocessing time (RPT). The RPT is the time between the first saccade and the appearance of the second target and reflects the time allowed for the processing of the second saccade while the first is still underway (Becker and Jürgens 1979). Typically, shorter TSDs are associated with longer RPTs and vice versa. The RPTs were binned into uniform intervals of 50 ms, and the corresponding values of the direction of end-points of midway saccades were averaged to calculate their mean (and SE) for each subject. The direction of the end-point of midway saccades vs. RPT for the REDIRECT and the FOLLOW task is shown in Fig. 5*A*. A two-way balanced ANOVA revealed a significant shift in the scatter toward the FT with increasing RPT ($P < 0.001$; F = 53.82). Furthermore, comparisons for individual subjects revealed that all subjects showed a significant trend in scatter with increasing RPT ($P < 0.001$). In addition, although we observed an overall shift in the scatter of end-points toward the second target in the REDIRECT task (46.34° ± 2.64° in the REDIRECT task vs. 43.82° ± 2.14° in the FOLLOW task), this shift was not significant for the two tasks ($P > 0.05$) in 11/14 subjects. Most importantly, we did not see any significant change in the scatter of the midway saccade end-points across the two tasks ($P = 0.107$; F = 2.63) across the population, suggesting that the extent of midway saccades was not affected by visual attention but was instead sensitive to the extent of overlap in movement planning.

To further test the role of attention, we plotted the percentage of midway saccades as a function of RPT (Fig. 5*B*) for the two tasks (FOLLOW and REDIRECT). A balanced two-way ANOVA with RPT and task as two factors revealed a significant effect of RPT ($P < 0.001$; F = 8.27) and the task ($P = 0.002$; F = 12.67) on the percentage of midway saccades. Subjects produced a significantly greater frequency of midway saccades in the FOLLOW compared with the REDIRECT task ($P = 0.002$). Thus even though differential allocation of visual attention at the second target can explain the shift in the scatter of midway saccade end-points toward FT in the REDIRECT task, in and of itself, it cannot explain the greater frequency of midway saccades in the FOLLOW task. We propose instead that the

Fig. 2. *A*: classification of midway saccades in step trials. Initial saccades in step trials, which landed between (i.e., beyond the 95% confidence interval of the spread of the end-points of corresponding no-step saccades) the IT and the FT were midway saccades (*left panel*). FP is the fixation point. *Center panel*: the first (green), second (red), and midway (black) saccades in step trials. *Right panel*: the first (green) and second (red) saccade directed at the initial (pale green) and final (pale red) targets in a correct step trial in the FOLLOW task. *B*: classification of hypometric saccades in step trials. The ellipse defines the 95% confidence interval for the spread of the end-points of correct no-step saccades. *Left panel*: saccades directed toward the IT in step trials, which fell short of entering the region defined by the confidence ellipse, were hypometric saccades. *Center panel*: correct (red), incorrect (green), and hypometric saccades (black). *Right panel*: a correct saccade (red) and a hypometric saccade ("h"; black) to the FT (pale red) and IT (pale green) in a step trial. *C*, *left panel*: a curved saccade (magenta) and a hypometric correction (black) in a step trial. *Right panel*: velocity profile of a curved saccade (magenta) and hypometric correction (black) for an individual trial. The intersaccade interval (ISI) is the time delay between the start of the corrective saccade and the end of the hypometric saccade.

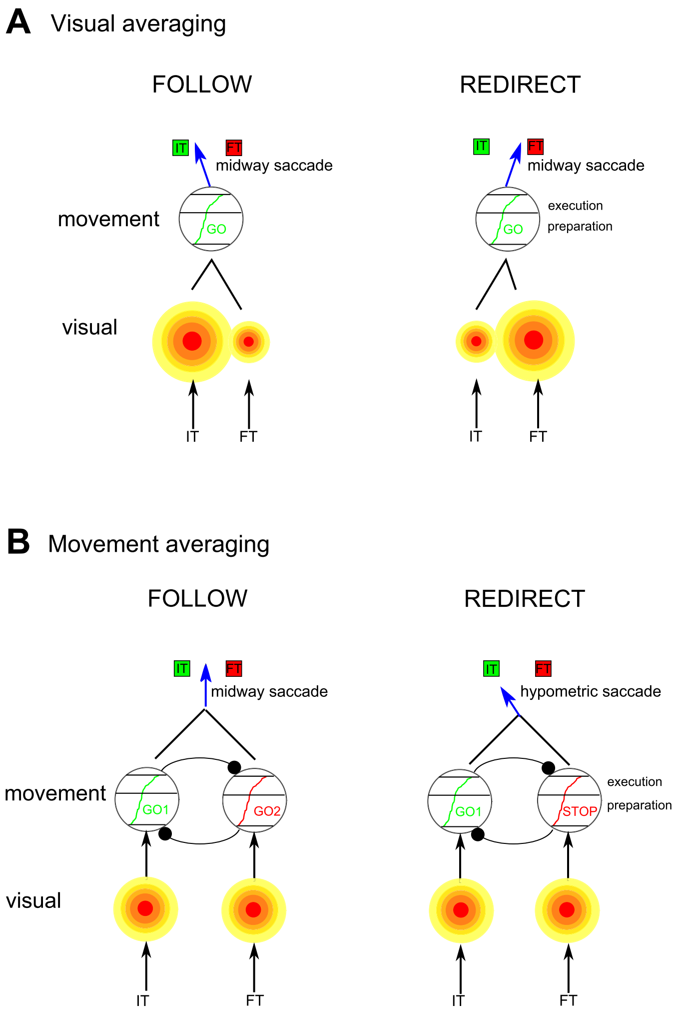


Fig. 3. Schematic showing the predictions of visual (*A*) and movement (*B*) averaging in the FOLLOW and the REDIRECT tasks. *A*: since the 2 targets are presented sequentially, greater attention may be allocated to the IT location in the FOLLOW task, hence generating greater activity of the ensemble of cells centered at the IT location. A weighted visual averaging of the ensemble of cells centered at IT and FT would activate a population of cells whose center is located close to the IT. An input from the visual cell to the movement-related cells leads to generation of the averaged saccade whose end-point is located near the IT. In the REDIRECT task, since greater attention is expected to be allocated to the FT, the end-point of the averaged saccade is expected to be located close to the FT. *B*: in the FOLLOW task, the 2 movement plans for saccades toward IT and FT (GO1 and GO2, respectively) interact to produce a saccade that lands between the IT and FT. In the REDIRECT task, an interaction of the movement plan with another plan to abort the planned movement would produce a hypometric saccade toward the IT.

greater percentage of midway saccades in the FOLLOW task compared with the REDIRECT task is a consequence of different movement plans adopted in the two tasks (see DISCUSSION).

We also tested whether the greater preponderance of midway saccades in the FOLLOW task was due to differences in reaction times. However, the first saccade latencies in the two tasks were not significantly different (two-way ANOVA, $P = 0.965$; $F = 0.0019$), and the mean first saccade latencies in the FOLLOW and the REDIRECT tasks were 213 ± 1.8 ms and 211.7 ± 1.9 ms, respectively. Furthermore, latencies associated with the second saccade were significantly shorter in the REDIRECT task (310.5 ± 3.8 ms), which yielded fewer midway saccades, compared with the FOLLOW task (366.4 ± 2.8 ms; two-way ANOVA, $P < 0.001$; $F = 139.82$), which yielded more midway saccades. Most importantly, in the FOLLOW task, the mean (±SE) latency of these midway saccades (211 ± 1 ms) was comparable with that of target-directed saccades (213 ± 2 ms; two-tailed paired *t*-test: $t = -1.74$; $P = 0.105$). Furthermore, a Kolmogorov-Smirnov test revealed no significant difference in the distribution of saccade latencies directed to the IT and midway saccades for all 14 subjects (mean, $P = 0.470$; minimum, $P = 0.069$). We also did not observe any significant difference in the proportion of midway saccades as a function of initial saccade latency for the FOLLOW (one-way ANOVA, $P = 0.068$; $F = 2.16$) and the REDIRECT (one-way ANOVA, $P = 0.214$; $F = 1.46$) tasks. Thus the greater frequencies of midway saccades in the FOLLOW task are not a consequence of speed-accuracy tradeoffs.

DISCUSSION

Converging evidence from psychophysical and neurophysiological experiments suggests that the processing of goal-directed saccades involves at least three distinct representations. The first representation involves a stage that reflects sensory encoding of stimuli. These sensory representations are thought to feed forward to areas where bottom-up stimulus salience is computed (Gottlieb et al. 1998; Itti and Koch 2000, 2001; Li 2002; Thompson and Bichot 2005). The interaction of bottom-up salience with top-down processing is thought to instantiate an intermediate representation of movement goals, generating a priority map (Awh et al. 2012; Bisley and Goldberg 2010; Fecteau and Munoz 2006). Finally, the movement goals generate motor representations to move the eyes. In this study, we addressed a long-standing issue concerning the nature of representations where such saccade averaging might occur between the sensory encoding of stimuli and the execution of eye movements. We provided evidence that type of averaged saccades changed qualitatively based on the types of instructions given to the subjects. We observed a higher extent of midway saccades in the FOLLOW task and hypometric saccades in the REDIRECT task, providing evidence in favor of the hypothesis that the averaging of saccades occurs due to an interaction between movement-planning stages of saccades.

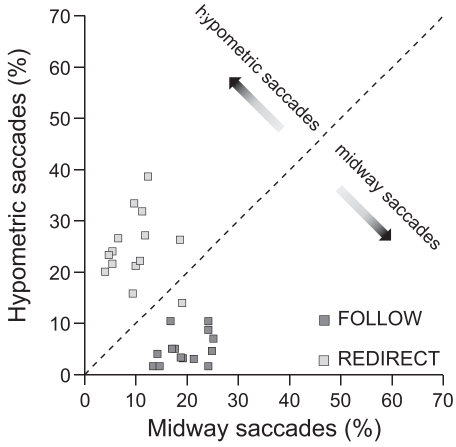


Fig. 4. The frequency of generation of hypometric and midway saccades is contrasted for individual subjects in the FOLLOW and REDIRECT tasks. All but 1 subject generated more hypometric saccades in the REDIRECT task than in the FOLLOW task. In contrast, all subjects generated more midway saccades in the FOLLOW task than in the REDIRECT task.

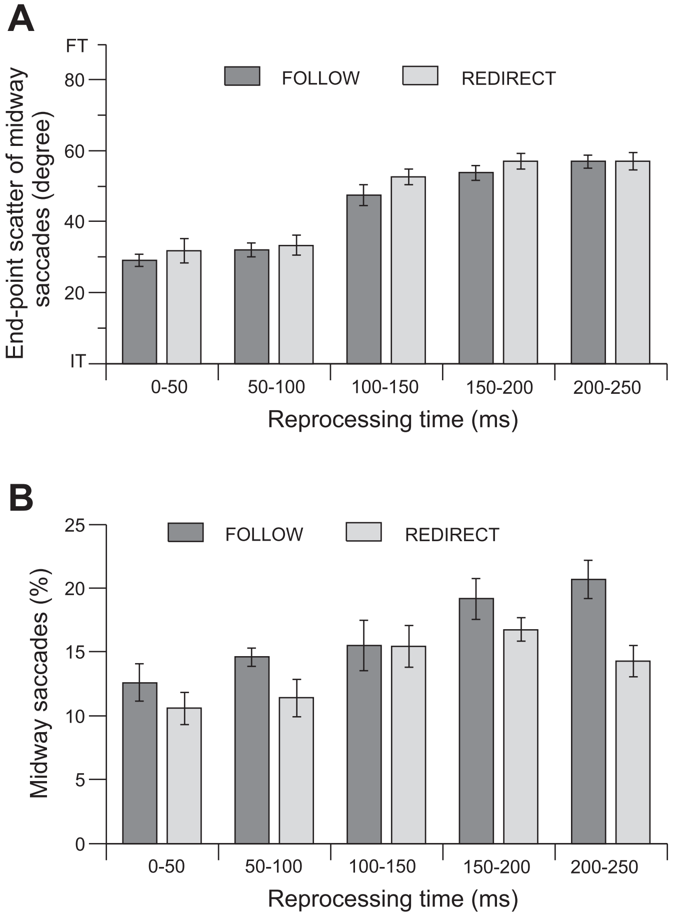


Fig. 5. *A*: distribution of the end-points of midway saccades in step trials with 90° angular separation between the targets as a function of reprocessing times (RPTs) for the FOLLOW (dark gray) and REDIRECT (light gray) tasks. Target locations were normalized such that the location of IT was always at 0° and the FT at 90° to pool the data. IT and FT on the *y*-axis denote the 0° and 90° target locations. *B*: distribution of the proportion of midway saccades as a function of RPTs for the FOLLOW (dark gray) and REDIRECT (light gray) tasks. Error bars denote the SEs of the corresponding mean.

Averaging as a Consequence of Sensory Processing

Gestalt laws of grouping (Westheimer 1938) provide an organizing principle that explains saccade averaging as a consequence of visual processing (Compton and Logan 1993; Palmer 1992). In such a framework, stimulus items that are located close together are more likely to be grouped together by proximity grouping (Compton and Logan 1993; Kowler et al. 1995; Palmer 1992; Van Oefflen and Vos 1982). Many of these perceptual organization processes occur early in the visual processing stream (Driver et al. 2001) and are therefore expected to occur prior to visual selection and movement planning. Such visual computations have been identified in previous oculomotor studies where the frequency of averaged saccades was found to be markedly greater for targets separated by $<30^\circ$ (Chou et al. 1999; Ottes et al. 1985). However, in our study, the two stimuli were presented at very wide angular separations (≥90°). Thus the occurrence of averaged saccades in our experiment cannot be completely accounted for by a proximity grouping per se. In addition, averaging saccades generated from such a putative proximity grouping in general have shorter latencies than target-directed saccades (Chou et al. 1999; Coëffé and O'Regan 1987; Findlay 1981a, 1997; Ottes et al. 1984, 1985; Walker et al. 1997). In contrast, in our study, the latencies of these midway saccades were comparable with target-directed saccades, suggesting that longer midway saccade latencies were not insufficient for perceptual selection of the saccade goal and hence, were not the possible cause for their production (Chou et al. 1999; Sharika et al. 2008). The relatively larger number of averaged saccades observed in the FOLLOW task at large target eccentricities may be a consequence of the instructions given to subjects who were encouraged to generate successive saccades "as quickly as possible" to the locations of the targets in the order they appeared, facilitating the parallel preparation of saccades in the sequence.

Averaging as a Consequence of Visual Selection

The flexibility that characterizes primate behavior cannot be explained without a distinction between visual and movement-related processes in the brain. In congruence with such intuition, there is now general agreement that neurons in the oculomotor system can be classified into those that have predominantly visual properties representing a salience map of the potential targets, deciding where a saccade should occur (target selection), independent of whether and when a saccade will occur (saccade planning), which is represented by visuomovement and movement-related neurons (Bruce and Goldberg 1985; DiCarlo and Maunsell 2005; Helminski and Segraves 2003; Horwitz et al. 2004; Mays and Sparks 1980; McPeek and Keller 2002a, b; Murthy et al. 2001, 2009; Sato and Schall 2003; Sato et al. 2003; Segraves and Goldberg 1987; Thompson et al. 1996, 1997; Umeno and Goldberg 1997, 2001). Indeed, the double-step task has often been used as a paradigm to dissociate neurons coding for stimuli in retinal coordinates, presumably reflecting sensory processing, from neurons coding for stimuli in spatial or oculocentric coordinates, presumably for movement preparation (Bracewell et al. 1996; Guthrie et al. 1983; Mazzoni et al. 1996). In this study, we recorded subjects on two different double-step saccade tasks (FOLLOW and REDIRECT) (Ray et al. 2004). Since the retinal information was the same in the two tasks, qualitative and quantitative difference in averaging between the two tasks is unlikely to be a consequence of visual selection per se, which is expected to occur in retinocentric coordinates (Golomb et al. 2008).

A number of studies have provided evidence for a relation between visual selection and covert spatial attention in oculomotor structures such as FEF and SC (Carello and Krauzlis 2004; Lovejoy and Krauzlis 2010; Moore and Armstrong 2003; Moore and Fallah 2004). In our task, even though the allocation of attention was not measured explicitly, spatial attention might have differed between the two tasks as a consequence of the behavioral relevance of the targets. This difference in the allocation of spatial attention could in principle explain differences in the pattern of saccade averaging. For two reasons, we do not believe that this can account for the observed results. First, allocation of attention is expected to occur at the two target locations and by itself cannot explain the greater number of hypometric saccades in the REDIRECT task. Second, and more importantly, differential allocation of attention is expected to change the relative end-points of the midway saccades. Since the end-point of midway saccades in the REDI-

RECT task were not significantly different compared with the FOLLOW task, we suggest that visual selection and attention cannot account for saccade averaging. Nevertheless, one cannot completely ignore the influence of visual attention on the generation of averaged saccades in our study since we did observe a trend of saccades landing closer to the second behaviorally relevant target in the REDIRECT condition (Fig. 5*A*).

Averaging as a Consequence of Goal Selection

In addition to computing salience of a target through a bottom-up process, target selection can be modulated by the top-down knowledge of the task demands (Fecteau et al. 2004; Lee et al. 1999; Moore and Armstrong 2003). The output of such a process is thought to be a distributed representation of neurons within the lateral intraparietal cortex, the FEF, and the SC, instantiating a so-called priority map [reviewed in Fecteau and Munoz (2006)]. Although a priori, the same cells that exhibit visual selection can, through additional input from areas such as prefrontal cortex, come to represent the selection of the saccade target, studies in the FEF have shown that there are two types of visual neurons in the FEF: one that selects the target regardless of the direction of the saccade [type I visual neurons in Sato and Schall (2003)] and the other that selects the saccade end-point independent of the location of the target [type II visual neurons in Sato and Schall (2003)]. Thus a priority map is thought to represent the behaviorally relevant locations independent of physical target positions. In addition, unlike neurons that mediate visual selection, the activity of neurons representing the priority is a good predictor of saccadic reaction time (Gottlieb et al. 1998; McPeek and Keller 2004; Sato and Schall 2003). Thus these neurons are expected to represent the movement goal consisting of both where and when a saccade should occur (Hafed and Krauzlis 2008; Khan et al. 2010; Krauzlis et al. 2004; Quaia et al. 2010). In this context, although hypometric saccades might be considered a manifestation of online control occurring at the level of the brain stem by the omnipause neurons, the activation of these neurons, in turn, may derive from upstream representations (Scudder et al. 1996; Stanton et al. 1988) that form the priority map representation of movement goals or vectors. Thus we propose that hypometric saccades may represent a form of averaging between the movement goal to the first target and a goal to refixate, as a consequence of the oculomotor system attempting to cancel the initial saccade (Corneil et al. 1999; Ramakrishnan et al. 2010). Support for this view derives from prior studies showing that saccade averaging is known to occur in cases where some aspect of the movement plan (such as amplitude, direction, etc.) is known in advance (Coëffé and O'Regan 1987; Findlay 1981b; Viviani and Swensson 1982; Zambarbieri et al. 1987) so as to allow some prior movement planning. Also, in microstimulation studies of the FEF (Schiller et al. 1979) and SC (Robinson and Fuchs 1969; Schiller and Sandell 1983), an electrically evoked saccade at different times during the preparation of an oculomotor command toward a selected target results in averaging saccades that are thought to reflect the weighted sum of the movement preparations toward the two potential targets.

This study is also compatible with the notion of the so-called downstream hypothesis of saccade averaging, which suggests that the collision is either at the output or downstream to the SC, also thought to be part of the priority map. In support of this idea, Edelman and Keller (1998) and Van Opstal and Van Gisbergen (1990) have previously shown the simultaneous activation of two neuron ensembles representing the two target locations in the SC while the monkeys made regular latency averaging saccades [but see Glimcher and Sparks (1993)]. Moreover, the discharge pattern was found to be broad enough so that the information from the two target configurations could be incorporated to decode the intermediate goal for the averaging saccades. Furthermore, Port and Wurtz (2003) and McPeek et al. (2003) have also shown that sequential/simultaneous activity in different SC neurons can result in curved/averaged saccades. Recently, Katnani and Gandhi (2011), using dual microstimulation in the SC, provided additional evidence supporting the downstream hypothesis. Their model overestimated the amplitudes of the averaged saccades if the estimation of the location of the goal for the averaged saccade was computed upstream of the SC, as proposed in Glimcher and Sparks (1993).

Accumulator Models for Double-Step Saccade Performance

Accumulator models, which posit movement planning as an accumulation of visual/sensory information into a movement plan, provide an elegant description of saccadic reaction-time distributions and neurophysiological activity in a variety of oculomotor areas (Bogacz 2007; Carpenter and Williams 1995; Ditterich 2006; Ratcliff and Rouder 1998; Ratcliff et al. 1999; Smith 2000; Usher and McClelland 2001). Such models can be naturally extended to explain behavior in the FOLLOW task (Ray et al. 2012). Here, performance can be described by the sequential yet concurrent activation of two movement plans (particularly at smaller TSDs): a GO1 process, which prepares the saccade to the IT, and a GO2 process, which instantiates saccade preparation to the FT. Instances where the activity in the GO2 accumulator can influence that in the GO1 or vice versa can produce saccades that are an average of the two single saccade vectors toward their respective targets. Such a model, however, does not provide an explanation of how hypometric saccades can be generated in the REDIRECT task unless we assume that the second GO process automatically activates a foveal signal that attempts to inhibit the first saccade. This being the case, it is not evident why such an automatic response should not occur in the FOLLOW task, where hypometric saccades are not typically observed. However, in our tasks, the fixation point disappeared with the visual stimulus presentation, preventing direct activation of a foveal stop/inhibitory signal. Thus a GO–GO model, which can explain midway saccades in the FOLLOW task, fails to explain midway saccades and even hypometric saccades in the REDIRECT task. This prediction is incongruent with past work (Camalier et al. 2007; Kapoor and Murthy 2008; Ramakrishnan et al. 2012), where it was shown that a GO–GO model fails to fit the reaction times of the compensated and noncompensated saccades in REDIRECT double-step and search-step tasks.

We propose that performance in the REDIRECT task, similar to previous studies (Camalier et al. 2007; Kapoor and Murthy 2008; Ramakrishnan et al. 2010, 2012), can be best explained as a race between a GO (associated with the first saccade) and an independent STOP process (to cancel the saccade). If the GO process reaches the threshold, then a saccade toward the IT can be executed, whereas if the STOP process wins the race, then the first saccade can be canceled successfully. An interaction of the GO and the STOP process beyond saccade planning can result in the generation of the hypometric saccades [see Ramakrishnan et al. (2010)]. Thus the GO–STOP architecture can explain the occurrence of relative predominance of hypometric over midway saccades in the REDIRECT task.

The presence of some midway saccades in the REDIRECT task provides indirect evidence for a variant of the GO–STOP architecture, called the GO1–GO2 + STOP model, proposed by Camalier et al. (2007) and more recently by Ramakrishnan et al. (2012). In contrast with another closely related scheme—the GO1–STOP–GO2 model, which also accounts for REDIRECT behavior—the GO1–GO2 + STOP model permits concurrent activation of all three processes. Such architecture allows for the interaction of GO1 and GO2, as in the FOLLOW task, predicting the occurrence of midway saccades in the REDIRECT task. However, because the shorter STOP process is expected to cancel the GO1 process before it can interact with the GO2 process, the interaction between GO1 and GO2 processes is expected to be infrequent. Such intuition has been simulated in a computer model based on experimentally estimated durations of GO1, GO2, and STOP processes (Camalier et al. 2007). The GO1–GO2 + STOP model could account for midway saccades up to a maximum of ~10%, which is what is observed in our data set and compatible with past reports in the literature (Arai and Keller 2005; Camalier et al. 2007). The presence of hypometric saccades in the FOLLOW task, however, is not readily explained by a simple GO–GO model. The relatively smaller percentage of such hypometric saccades (5.01 ± 0.82%) in the FOLLOW task compared with their counterparts in the REDIRECT task (19.91 ± 2.71%) may be explained by a prepotent tendency of subjects to cancel a planned saccade when a new target appears at very short TSDs, since 78.73 ± 2.80% of total hypometric saccades was produced at the shortest TSD. This tendency is also captured by the compensation functions that tend to show a dip in the percentage of sequential saccades made at the shortest TSD (see Fig. 1*A*) as well.

ACKNOWLEDGMENTS

We thank Sheldon Hoffmann (Reflective Computing) for software support. Present address of S. Ray: SUNY College of Optometry, New York.

GRANTS

Support for this work was provided by grants from the Department of Biotechnology (DBT), Government of India, and the National Brain Research Centre. N. Bhutani was supported by a fellowship from the University Grants Commission (UGC), Government of India. S. Ray was supported by a fellowship from the Council for Scientific and Industrial Research (CSIR), Government of India.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

Author contributions: N.B. and A.M. conception and design of research; S.R. performed experiments; N.B. analyzed data; N.B. interpreted results of experiments; N.B. prepared figures; N.B. and A.M. drafted manuscript; N.B., S.R., and A.M. edited and revised manuscript; A.M. approved final version of manuscript.

REFERENCES

Arai K, Keller EL. A model of the saccade generating system that accounts for trajectory variations produced by competing visual stimuli. *Biol Cybern* 92: 21–37, 2005.

Arai K, McPeek RM, Keller EL. Properties of saccadic responses in monkey when multiple visual stimuli are presented. *J Neurophysiol* 91: 890–900, 2004.

Armstrong KM, Fitzgerald JK, Moore T. Changes in visual receptive fields with microstimulation of frontal cortex. *Neuron* 50: 791–798, 2006.

Aslin RN, Shea SL. The amplitude and angle of saccades to double-step target displacements. *Vision Res* 27: 1925–1942, 1987.

Awh E, Belopolsky AV, Theeuwes J. Top-down versus bottom-up attentional control: a failed theoretical dichotomy. *Trends Cogn Sci* 16: 437–443, 2012.

Becker W, Jürgens R. An analysis of the saccadic system by means of a double-step stimuli. *Vision Res* 19: 967–983, 1979.

Bisley JW, Goldberg ME. Attention, intention and priority in the parietal lobe. *Annu Rev Neurosci* 33: 1–21, 2010.

Bogacz R. Optimal decision making theories: linking neurobiology with behavior. *Trends Cogn Sci* 11: 118–125, 2007.

Bracewell RM, Mazzoni P, Barash S, Andersen RA. Motor intention activity in the macaque's lateral intraparietal area. II. Changes of motor plan. *J Neurophysiol* 76: 1457–1464, 1996.

Bruce CJ, Goldberg ME. Primate frontal eye fields. I. Single neurons discharging before saccades. *J Neurophysiol* 53: 603–635, 1985.

Camalier CR, Gotler A, Murthy A, Thompson KG, Logan GD, Palmeri TJ, Schall JD. Dynamics of saccade target selection: race model analysis of double step and search step saccade production in human and macaque. *Vision Res* 47: 2187–2211, 2007.

Carello CD, Krauzlis RJ. Manipulating intent: evidence for a causal role of the superior colliculus in target selection. *Neuron* 43: 575–583, 2004.

Carpenter RHS, Williams MLL. Neural computation of log likelihood in control of saccadic eye movements. *Nature* 377: 59–62, 1995.

Chou I, Sommer MA, Schiller PH. Express averaging saccades in monkeys. *Vision Res* 39: 4200–4216, 1999.

Coëffé C, O'Regan JK. Reducing the influence of non-target stimuli on saccade accuracy: predictability and latency effects. *Vision Res* 27: 227–240, 1987.

Compton BJ, Logan GD. Evaluating a computational model of perceptual grouping and proximity. *Percept Psychophys* 50: 403–421, 1993.

Coren S, Hoenig P. Effect of non-target stimuli upon length of voluntary saccades. *Percept Mot Skills* 34: 499–508, 1972.

Corneil BD, Hing CA, Bautista DV, Munoz DP. Human eye-head gaze shifts in a distractor task. I. Truncated gaze shifts. *J Neurophysiol* 82: 1390–1405, 1999.

DiCarlo JJ, Maunsell JH. Using neuronal latency to determine sensory-motor pathways in reaction time tasks. *J Neurophysiol* 93: 2974–2986, 2005.

Ditterich J. Stochastic models of decision about motion direction: behavior and physiology. *Neural Netw* 19: 981–1012, 2006.

Driver J, Davis G, Russell C, Turatto M, Freeman E. Segmentation, attention and phenomenal visual objects. *Cognition* 80: 61–95, 2001.

Duhamel JR, Colby CL, Goldberg ME. The updating of the representation in visual pace in parietal cortex by intended eye movements. *Science* 255: 90–92, 1992.

Edelman JA, Keller EL. Dependence on target configuration of saccade-related activity in the primate superior colliculus. *J Neurophysiol* 80: 1407–1426, 1998.

Fecteau JH, Bell AH, Munoz DP. Neural correlates of the automatic and goal-driven biases in orienting spatial attention. *J Neurophysiol* 92: 1728–1737, 2004.

Fecteau JH, Munoz DP. Salience, relevance and firing: a priority map for target selection. *Trends Cogn Sci* 10: 382–390, 2006.

Findlay JM. Global processing of saccadic eye movements. *Vision Res* 22: 1033–1045, 1982.

Findlay JM. Local and global influences on saccadic eye movements. In: *Eye Movements, Cognition and Visual Perception*, edited by Fisher DF, Monty RA, Senders JW. Hillsdale, NJ: Lawrence Erlbaum, 1981a, p. 171–179.

Findlay JM. Saccade target selection during visual search. *Vision Res* 37: 617–631, 1997.

Findlay JM. Spatial and temporal factors in the predictive generation of saccadic eye movements. *Vision Res* 21: 347–354, 1981b.

Glimcher PW, Sparks DL. Representation of averaging saccades in the superior colliculus of the monkey. *Exp Brain Res* 95: 429–435, 1993.

Golomb JD, Chun MM, Mazer JA. The native coordinate system of spatial attention is retinotopic. *J Neurosci* 28: 10654–10662, 2008.

Gottlieb JP, Kusunoki M, Goldberg ME. The representation of visual salience in monkey parietal cortex. *Nature* 391: 481–484, 1998.

Guthrie BL, Porter JD, Sparks DL. Corollary discharge provides accurate eye position information to the oculomotor system. *Science* 221: 1193–1195, 1983.

Hafed ZM, Krauzlis RJ. Goal representations dominate superior colliculus activity during extrafoveal tracking. *J Neurosci* 28: 9426–9439, 2008.

Helminski JO, Segraves MA. Macaque frontal eye field input to saccade-related neurons in the superior colliculus. *J Neurophysiol* 90: 1046–1062, 2003.

Histed MH, Bonin V, Reid C. Direct activation of sparse, distributed populations of cortical neurons by electrical microstimulation. *Neuron* 63: 508–522, 2009.

Horwitz GD, Batista AP, Newsome WT. Directional selective visual responses in macaque superior colliculus induced by behavioural training. *Neurosci Lett* 366: 315–319, 2004.

Itti L, Koch C. A saliency-based search mechanism for overt and covert shifts of attention. *Vision Res* 40: 1489–1506, 2000.

Itti L, Koch C. Computational modeling of visual attention. *Nat Rev Neurosci* 2: 194–203, 2001.

Kapoor V, Murthy A. Covert inhibition potentiates online control in a double-step task. *J Vis* 8: 1–16, 2008.

Katnani HA, Gandhi NJ. Order of operations for decoding superior colliculus activity for saccade generation. *J Neurophysiol* 106: 1250–1259, 2011.

Khan AZ, Heinen SJ, McPeek RM. Attentional cueing at the saccade goal, not at the target location, facilitates saccades. *J Neurosci* 30: 5481–5488, 2010.

Kowler E, Anderson A, Dosher B, Blaser E. The role of attention in programming of saccades. *Vision Res* 35: 1897–1916, 1995.

Krauzlis RJ, Liston D, Carello CD. Target selection and the superior colliculus: goals, choices and hypotheses. *Vision Res* 44: 1445–1451, 2004.

Lee DK, Itti L, Koch C, Braun J. Attention activates winner-take-all competition among visual filters. *Nat Neurosci* 2: 375–381, 1999.

Li Z. A saliency map in primary visual cortex. *Trends Cogn Sci* 6: 9–16, 2002.

Lovejoy RP, Krauzlis RJ. Inactivation of primate superior colliculus impairs covert selection of signals for perceptual judgements. *Nat Neurosci* 13: 261–266, 2010.

Mays LE, Sparks DL. Saccades are spatially, not retinocentrically coded. *Science* 208: 1163–1165, 1980.

Mazzoni P, Bracewell RM, Barash S, Andersen RA. Motor intention activity in the macaque's lateral intraparietal area. I. Dissociation of motor plan from sensory memory. *J Neurophysiol* 76: 1439–1456, 1996.

McPeek RM, Han JH, Keller EL. Competition between saccade goals in the superior colliculus produces saccade curvature. *J Neurophysiol* 89: 2577–2590, 2003.

McPeek RM, Keller EL. Deficits in saccade target selection after inactivation of superior colliculus. *Nat Neurosci* 7: 757–763, 2004.

McPeek RM, Keller EL. Saccade target selection in the superior colliculus during a visual search task. *J Neurophysiol* 88: 2019–2034, 2002a.

McPeek RM, Keller EL. Superior colliculus activity related to concurrent processing of saccade goals in a visual search task. *J Neurophysiol* 87: 1805–1815, 2002b.

Moore T, Armstrong KM. Selective gating of visual signals by microstimulation of frontal cortex. *Nature* 421: 370–373, 2003.

Moore T, Fallah M. Microstimulation of the frontal eye fields and its effects on covert spatial attention. *J Neurophysiol* 91: 152–162, 2004.

Murthy A, Ray S, Shorter SM, Schall JD, Thompson KG. Neural control of visual search by frontal eye field: effects of unexpected target displacement on visual selection and saccade preparation. *J Neurophysiol* 101: 2485–2507, 2009.

Murthy A, Thompson KG, Schall JD. Dynamic dissociation of visual selection from saccade programming. *J Neurophysiol* 86: 2634–2637, 2001.

Ottes FP, Van Gisbergen JA, Eggermont JJ. Latency dependence of colour-based target vs. nontarget discrimination by the saccadic system. *Vision Res* 25: 849–862, 1985.

Ottes FP, Van Gisbergen JA, Eggermont JJ. Metrics of saccade responses to visual double stimuli: two different modes. *Vision Res* 24: 1169–1179, 1984.

Palmer SE. Common region: a new principle of perceptual grouping. *Cogn Psychol* 24: 436–447, 1992.

Port NL, Wurtz RH. Sequential activity of simultaneously recorded neurons in the superior colliculus during curved saccades. *J Neurophysiol* 90: 1887–1903, 2003.

Quaia C, Joiner WM, Fitzgibbon EJ, Optican LM, Smith MA. Eye movement sequence generation in humans: motor or goal updating? *J Vis* 10: pii: 28, 2010.

Ramakrishnan A, Chokandre S, Murthy A. Voluntary control of multisaccade gaze shifts during movement preparation and execution. *J Neurophysiol* 103: 2400–2416, 2010.

Ramakrishnan A, Sureshbabu R, Murthy A. Understanding how the brain changes its mind: microstimulation in the macaque frontal eye field reveals how saccade plans are changed. *J Neurosci* 32: 4457–4472, 2012.

Ratcliff R, Rouder J. Modeling response times for two-choice decisions. *Psychol Sci* 9: 347–356, 1998.

Ratcliff R, Van Zandt T, McKoon G. Connectionist and diffusion models of reaction time. *Psychol Rev* 106: 261–300, 1999.

Ray S, Bhutani N, Murthy A. Mutual inhibition and capacity sharing during parallel preparation of serial eye movements. *J Vis* 12: 17, 2012.

Ray S, Pouget P, Schall JD. Functional distinction between visuomovement and movement neurons in macaque frontal eye field during saccade countermanding. *J Neurophysiol* 102: 3091–3100, 2009.

Ray S, Schall JD, Murthy A. Programming of double-step saccade sequences: modulation by cognitive control. *Vision Res* 44: 2707–2718, 2004.

Rizzolatti G, Riggio L, Dascola I, Umiltá C. Reorienting attention across the horizontal and vertical meridians: evidence in favour of a premotor theory of attention. *Neuropsychologia* 25: 19–29, 1987.

Robinson DA, Fuchs AF. Eye movements evoked by stimulation of frontal eye fields. *J Neurophysiol* 32: 637–648, 1969.

Sato TR, Schall JD. Effects of stimulus-response compatibility on neural selection in frontal eye field. *Neuron* 38: 637–648, 2003.

Sato TR, Watanbe K, Thompson KG, Schall JD. Effect of target-distractor similarity on FEF visual selection in the absence of the target. *Exp Brain Res* 151: 356–363, 2003.

Schall JD, Thompson KG. Neural selection and control of visually guided eye movements. *Annu Rev Neurosci* 22: 241–259, 1999.

Schiller PH, Sandell JH. Interactions between visually and electrically elicited saccades before and after superior colliculus and frontal eye field ablations in the rhesus monkey. *Exp Brain Res* 49: 381–392, 1983.

Schiller PH, True SD, Cornway JL. Paired stimulation of the frontal eye fields and superior colliculus of the rhesus monkey. *Brain Res* 179: 162–164, 1979.

Scudder CA, Moschovakis AK, Karabelas AB, Highstein SM. Anatomy and physiology of saccadic long-lead burst neurons recorded in the alert squirrel monkey. I. Descending projections from the mesencephalon. *J Neurophysiol* 76: 332–352, 1996.

Segraves MA, Goldberg ME. Functional properties of corticotectal neurons in the frontal eye field. *J Neurophysiol* 58: 1387–1419, 1987.

Sharika KM, Ramakrishnan A, Murthy A. Control of predictive error correction during a saccadic double-step task. *J Neurophysiol* 100: 2757–2770, 2008.

Shen K, Paré M. Neuronal activity in superior colliculus signals both stimulus identity and saccade goals during visual conjunction search. *J Vis* 23: 1–13, 2007.

Smit AC, Van Gisbergen JAM. An analysis of curvature of fast and slow human saccades. *Exp Brain Res* 81: 335–345, 1990.

Smith PL. Stochastic dynamic models of response time and accuracy: a foundational primer. *J Math Psychol* 44: 408–463, 2000.

Sparks DL, Barton EJ. Neural control of saccadic eye movements. *Curr Opin Neurobiol* 3: 966–972, 1993.

Stanton GB, Golberg ME, Bruce CJ. Frontal eye field efferents in the macaque monkey: II. Topography of terminal fields in midbrain and pons. *J Comp Neurol* 271: 493–506, 1988.

Thompson KG, Bichot NP. A visual salience map in the primate frontal eye field. *Prog Brain Res* 147: 251–262, 2005.

Thompson KG, Bichot NP, Schall JD. Dissociation of visual discrimination from saccade programming in macaque frontal eye field. *J Neurophysiol* 77: 1046–1050, 1997.

Thompson KG, Hanes DP, Bichot NP, Schall JD. Perceptual and motor processing stages in the activity of macaque frontal eye field neurons during visual search. *J Neurophysiol* 76: 4040–4055, 1996.

Umeno MM, Goldberg ME. Spatial processing in the monkey frontal eye field. I. Predictive visual responses. *J Neurophysiol* 78: 1373–1383, 1997.

Umeno MM, Goldberg ME. Spatial processing in the monkey frontal eye field. II. Memory responses. *J Neurophysiol* 86: 2344–2352, 2001.

Usher M, McClelland JL. The time course of perceptual choice: the leaky, competing accumulator model. *Psychol Rev* 108: 550–592, 2001.

Van Oefflen MP, Vos PG. Configurational effects on the enumeration of dots: counting groups. *Mem Cognit* 10: 396–404, 1982.

Van Opstal AJ, Van Gisbergen JAM. Role of monkey superior colliculus in saccade averaging. *Exp Brain Res* 79: 143–149, 1990.

Viviani P, Swensson R. Saccadic eye movements to peripherally discriminated visual targets. *J Exp Psychol Hum Percept Perform* 8: 113–126, 1982.

Walker R, Deubel H, Schneider WX, Findlay JM. Effect of remote distractors on saccade programming: evidence for an extended fixation zone. *J Neurophysiol* 78: 1108–1119, 1997.

Westheimer M. A source book of Gestalt psychology (1938). In: *Laws of Organization in Perceptual Forms*. London: Routledge & Kegan Paul, 1923.

Zambarbieri D, Schmid R, Ventre J. Saccadic eye movements to predictable visual and auditory targets. In: *Eye Movements: from Physiology to Cognition*, edited by O'Regan JK and Levy-Schoen A. Amsterdam: Elsevier, 1987, p. 131–140.