Is saccade averaging determined by visual processing or movement planning?

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ABSTRACT

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 versus FOLLOW the sequence of targets in their order of appearance), we tested two alternative hypotheses. If saccade averaging was due to visual processing alone, the pattern of saccade averaging is expected to remain the same across the task conditions. However, while 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.
INTRODUCTION

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; Ottes et al., 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. While 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 sub-threshold 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 Superior Colliculus (SC; Shen and Paré, 2007) and FEF (Bruce and Goldberg, 1985) are visuomovement, representing both stimulus location 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. While 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
teurons 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). While 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 fourteen 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 the 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 ±3° 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% of the trials were step trials. On no-step trials, following fixation for a random duration that ranged from 300-800 ms, the fixation spot disappeared and a green target (1° X 1°, 5.83 cd/m²) appeared in one of the six possible locations on an imaginary circle (except vertical up and down positions) of radius 12°, centered on the fixation spot. On the step trials, the green target was followed by a red target (1° X 1°; 6.5 cd/m²) after a random temporal delay called the Target Step Delay (TSD). We used four TSDs that occurred between 50 and 200 ms, and were accurate to the screen refresh rate. Both types of trials were pseudo-randomly interleaved throughout each recording session. An angular separation of ≥ 90° was maintained between the initial and the final target locations. Subjects were given prior verbal instructions and 50-100 practice trials. On an average a total of 500 trials were completed for each subject. In order to avoid the contamination of data with non-specific impairments due to excessive fatigue, breaks were regularly interleaved throughout the recording session, and the total duration of recording session did not exceed one hour. Each correct trial was followed by an auditory beep to provide a feedback to the subjects. All
subjects were monetarily rewarded at the end of the recording session. Apart from the monetary compensation for overall participation in each session, extra reward was given based on the number of correct trials.

FOLLOW task: In this task (Figure 1A) 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 target step delay. Subjects were instructed to visually follow the locations of two targets with sequential saccades, fixating the respective targets within an electronically drawn window of ±2.5º centered at the target.

REDIRECT task: In this task (Figure 1B), like 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 ±2.5º centered at the target. On the step trials, however, contrary to the FOLLOW task, subjects were instructed to saccade directly to the later appearing red target. This entailed cancellation of the initial plan to move towards the green target and redirect their gaze to the later appearing red target.

Recording set up: Experiments were under computer control using TEMPO/VIDEOSYNC software (Reflective Computing, St. Louis, USA) that displayed visual stimuli, sampled and stored eye positions and other behavioral parameters. Eye position was sampled at 200 Hz with an infrared pupil tracker (ISCAN, Boston, USA) that interfaced with the TEMPO software in real time. Before starting the recording session, each subject was made to look at 5 positions on the monitor; one at fixation in the centre of the monitor and at least 4 (horizontal left, right; vertical up, down) target positions. The monitor (SONY Trinitron 500
GDM monitor; 21 inch 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 coincides with the centre 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 ± 2.5º. In our experiment targets were displayed at either 12º of eccentricity and the minimum angular separation between the two targets in a step trial was 90º. Thus, the minimum spatial separation between two targets was at least 17º. Thus, the error introduced as a consequence of our calibration procedure (± 2.5º) and the typical accuracy of the tracker (~1º) was well within limits to be confident that trials were correctly classified.

**Data analyses:** All offline analyses were performed using custom made programs written in Matlab (Mathworks, USA). The analogue eye position data were smoothed from which blinks were removed. A velocity threshold of 30º/sec 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 Statistical toolbox in Matlab. We used Bonferroni test for all the planned comparisons. Unless mentioned otherwise, all the results of averaged data are presented as ‘mean ± s.e.m.’. All the 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: Using the no-step trials, we calculated the 95%
confidence interval of the distribution of the direction of end-point of correct saccades to
corresponding targets (figure 2A, left panel). In step trials, when subjects’ eye trace landed
between the initial and the final targets but beyond the 95% confidence interval for the
distribution of end-point of no-step saccades to the two targets were classified as midway
saccades (figure 2A, centre panel). Right panel shows the second saccade (red dots) directed
at the second target (pale red) after an initial saccade (green dots) directed to the first target
(pale green) in a correct step trial.

Classification of hypometric saccades: From the no-step data, we obtained the means
and the 95% confidence interval for the direction and amplitude of correct saccades. An
ellipse (pale green) was drawn for which the centre was defined by the means and the two
axes were defined by the confidence intervals for the direction and amplitude (figure 2B left
panel). The ellipse thus demarcated the distribution of the saccade end-points of correct no-
step saccades. Saccades towards the initial target, 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 (figure 2B centre panel). Right panel shows the saccade
(red dots) directed towards the final target (pale red) in a correct step trial. In some trials,
hypometric saccades towards the initial target were followed by a 'corrective' saccade to the
final target, which will be referred to as hypometric corrections. The right panel in figure 2B
shows a typical hypometric saccade (black) in a step trial. On an average, 61.2 ± 3.6% of
hypometric saccades were followed by a corrective saccade to the final target (Figure 2C,
black) after a short intersaccade interval (29.8 ± 4.4 ms), whereas on some trials, although a
saccade was initiated to the initial target location, subjects made a correction online, resulting
in curved saccade trajectories directed to the final target, without any intersaccadic interval
(Figure 2C, magenta).

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 analysed where saccades were made to the final target 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 which had corrected curvature values beyond
0.75 times standard deviation from the mean corrected curvature were classified as curved
saccades. To distinguish hypometric corrections from curved saccades to the final target, we
plotted their velocity profiles. Figure 2C plots the velocity profile of a single curved saccade
(magenta) and hypometric correction (black). 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.

Figure 2 around here
RESULTS

In the FOLLOW task (figure 1A), subjects were rewarded for making two sequential saccades. Trials in which subjects’ eye trace landed directly at the location of the second target or subjects made a saccade only to the first target, were not rewarded. In the REDIRECT task (figure 1B), subjects had to cancel the partially planned saccade to the first target, and make a saccade directly to the second target. Thus, though 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 ‘e’ in figures 1B). Such erroneous trials were then followed by a second ‘corrective saccade’ (‘c’ in figure 1B) directed to the position of the second target. Thus, the sequential saccades produced in the REDIRECT task reflects 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 initial target with target step delay. The right columns of figure 1A and 1B depict 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 target step delay. But in the REDIRECT task, where the subjects are required to cancel the initial pre-programmed saccade, the probability to saccade to the initial target increases with the target step delay. The increasing compensation function is expected because at larger target step delays the cancellation of the pre-programmed 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:
where $t$ is the target step delay, $\alpha$ is the time at which the inhibition function reaches the sum of 63.2% of its maximum value $\gamma$ and 36.8% of its minimum value $\delta$, $\beta$ 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 as compared to the FOLLOW task (figure 4B in Ray et al., 2004). The mean ($\pm$ s.e.m.) index for the FOLLOW and REDIRECT task for these subjects was found 0.29 ($\pm$ 0.03) and 0.59 ($\pm$ 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 3A 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 is 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 initial target location (IT; figure 3A left panel). On the contrary, in the REDIRECT task, greater attention could be allocated to the final target (FT; figure 3B). If the averaging occurs in the sensory domain, which is modulated by such attentional allocation, the endpoints of the averaged saccades may follow the locus of attention (Rizzolatti et al., 1987). Thus, if attention were to operate differentially
across the two tasks, the endpoints of the averaged saccades are expected lie closer to the
initial target (IT) in the FOLLOW task, but closer to the final target (FT) locations in the
REDIRECT task (figure 3A right panel). In contrast, if saccade averaging is the result of
computations specific to the movement planning stage, a qualitatively different outcome is
expected (figure 3B). This is a consequence of the different instructions given to subjects in
both tasks. While in the FOLLOW task, saccade averaging is expected as a collision between
movement programs (depicted as GO1 and GO2 in figure 3B) directed at the initial and final
targets, saccade endpoints are expected to accordingly occur between the first and second
target positions like before. However, in the REDIRECT task (figure 2B right panel), 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 towards the first target (Ramakrishnan et al., 2010).

To test whether the 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 versus
midway saccades for the fourteen subjects in FOLLOW (dark grey squares) and REDIRECT
(light grey squares) tasks. In the FOLLOW task, subjects produced $19.65 \pm 1.13\%$ and $5.01 \pm
0.82\%$ of midway and hypometric saccades, respectively. In the REDIRECT task, subjects
generated $9.92 \pm 1.25\%$ and $24.77 \pm 1.79\%$ of 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 to 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 extent of 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 $90^\circ$ since there were a greater extent of midway saccades for the $90^\circ$ angular separation as compared to $135^\circ$ and $180^\circ$. 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 $0^\circ$ and $90^\circ$, respectively. Further, the 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 
(s.e.m.) for each subject. The direction of end-point of midway saccades versus reprocessing 
time, for the REDIRECT (light grey) and the FOLLOW task (dark grey), are shown in Figure 
5A. A two-way balanced ANOVA revealed a significant shift in the scatter towards the final 
target with increasing RPT (p < 0.001; F = 53.82). Further, comparisons for the individual 
subjects revealed that all subjects showed a significant trend in the scatter with increasing 
RPT (p < 0.001). In addition, although we observed an overall shift in the scatter of end-
points towards the second target in the REDIRECT task (46.34 ° ± 2.64 ° in the REDIRECT 
task versus 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 the movement planning.

To further test the role of attention, we plotted the percentage of midway saccades as 
a function of reprocessing time (Figure 5B) for the two tasks (FOLLOW-dark grey; 
REDIRECT-light grey). 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 significantly greater frequency of 
midway saccades in the FOLLOW as compared to 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 the final target in the REDIRECT task, in 
and of itself cannot explain the greater frequency of midway saccades in the FOLLOW task. 
We propose instead that the greater percentage of midway saccades in the FOLLOW task as 
compared to 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 were 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) that yielded fewer midway saccades, as compared to the FOLLOW task (366.4 ± 2.8 ms; two-way ANOVA $p < 0.001; F = 139.82$) that yielded more midway saccades. Most importantly, in the FOLLOW task the mean (± s.e.m.) latency of these midway saccades (211 ± 1 ms) were comparable to 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 initial target and midway saccades for all the fourteen subjects (mean $p = 0.470; \text{min } p = 0.069$). 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 suggest that the processing of goal directed saccades involve 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 to 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 the saccades.

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, 1999). 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, 1999; 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 less than 30° (Ottes et al. 1985; Chou et al. 1999). 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 proximity grouping per se. In addition, averaging saccades generated from such putative proximity grouping in general, have shorter latencies than target-directed saccades (Chou et al., 1999; Coeffe and O'Regan, 1987; Findlay 1981a, 1997; Jacobs, 1987; Ottes et al., 1984, 1985; Walker et al., 1997). In contrast, in our study the latencies of these midway saccades were comparable to target-directed saccades suggesting that longer midway saccade latencies were not insufficient for the 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, that decide where a saccade should occur (target selection), independent of whether and when a saccade will occur (saccade planning), which is represented by visuo-movement 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; McPeek and Keller, 2002b; 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 the 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 (Moore and Armstrong, 2003; Moore and Fallah, 2002; Carello and Krauzlis, 2004; Lovejoy and Krauzlis, 2010). In our task even though the allocation of attention was not explicitly measured, 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 don’t 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 REDIRECT task were not significantly different compared to 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 (figure 5A).

**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 (Lee et al., 1999, Fecteau et al., 2004; Moore and Armstrong, 2003). The output of such process is thought to be a distributed representation of neurons within the lateral intraparietal cortex (LIP), 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 may, through additional input from areas such as prefrontal cortex (PFC), 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 which select the target regardless of the direction of the saccade (type I visual neurons in Sato and Schall, 2003) and the other which select 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 location of behaviorally relevant locations independent of physical target location. In addition, unlike neurons that mediate visual selection, the activity of neurons representing the priority are good predictors 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., 2004; 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 (Stanton et al., 1988; Scudder et
al., 1996a) 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 to as a consequence of oculomotor system
attempting cancelling the initial saccade (Ramakrishnan et al 2010; Corneil et al., 1999).
Support for this view derives from prior studies showing that saccade averaging is known to
occur in cases where in some aspect of the movement plan (like amplitude, direction etc.) is
known in advance (Coeffe 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 that suggests that the collision is either at the output or downstream to
the SC, which is thought to also 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. Further, 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, that 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), 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
target step delays): a GO1 process that prepares the saccade to the initial target; and GO2
process that instantiates saccade preparation to the final target. 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 towards their respective target directions.
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 that can explain midway saccades in the FOLLOW task, fails to explain midway saccades and even hypometric saccades in the REDIRECT task. This prediction is in congruent with the past work (Camalier et al., 2007; Kapoor and Murthy, 2008; Ramakrishnan et al., 2012) where it was shown that GO-GO model fails to fit the reaction times of the compensated and non-compensated saccades in REDIRECT double-step and search-step tasks.

We propose that performance in the REDIRECT task, similar to previous studies (Camelier et al., 2007; Kapoor and Murthy, 2008; Ramakrishnan et al., 2010; Ramakrishnan et al., 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, a saccade towards the initial target can be executed; whereas if the STOP process wins the race then the first saccade can be cancelled 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 REDIRECT tasks.

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 Camelier et al. (2007) and more recently by Ramakrishnan et al. (2012). In contrast with another closely related scheme, the GO1-STOP-GO2 model, that 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 the GO1, GO2 and STOP processes (Camelier et al., 2007). The GO1-GO2+STOP model could account for midway saccades up to a maximum of about 10%, which is what is observed in our data set and compatible with past reports in the literature (Camalier et al., 2007; Arai and Keller, 2005). 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, in comparison to 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 were 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 Figure 1A) as well.
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FIGURE LEGENDS

**Figure 1.** Schematic showing the temporal events in the FOLLOW (A), REDIRECT (B) tasks. The tasks consist of two types of trials: no-step and step trials. In no-step trials, only a single green target is presented. In the step trials, a second red target is presented after a variable target step delay (TSD). The no-step trials are same in both 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 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 and redirect their gaze to the later appearing red target. In some step trials, an erroneous saccade ('e'; magenta) to the initial target is followed by a corrective saccade ('c'; yellow) to the final target location, thus generating sequential saccades similar to the FOLLOW task. The increasing compensation function shows that at larger TSDs, the cancellation of the pre-programmed saccade becomes difficult, hence increasing the probability that the initial saccade will finish before the second target.

**Figure 2.** (A.) Classification of midways saccades in step trials. Initial saccades in the step trials, which landed between the spatial positions (i.e., beyond the 95 % confidence interval of the spread of the end-points of corresponding no-step saccades) of the initial target (IT) and the final target (FT) were called midway saccades (left panel). Centre panel shows the first (green), second (red) and midway (black) saccades in step trials. Right panel shows 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 the correct no-step saccades. (left panel). Saccades directed towards the first target in step trials, but fell short of entering the region defined by the confidence ellipse, were called hypometric saccades. Centre panel shows correct (green), incorrect on-target (red), and hypometric saccades (black). Right panel shows a correct saccade (red) and a hypometric saccade (black) to the final (pale red) and initial targets (pale green) in a step trial. (C.) Left panel shows a curved saccade (magenta) and a hypometric correction (black) in a step trial. Velocity profile of a curved saccade (magenta), 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.

Figure 3. Schematic showing the predictions of visual (A) and movement (B) averaging in the FOLLOW and the REDIRECT tasks. (A) Since the two targets are presented sequentially, greater attention may be allocated to the initial target location in the FOLLOW task, hence, generating greater activity of the ensemble of cells centered at the initial target location (IT). A weighted visual averaging of the ensemble of cells centered at IT (initial target) and FT (final target) 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 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 two movement plans for the saccades towards 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 towards the IT.
Figure 4. The frequency of generation of hypometric and midway saccades are contrasted for individual subjects in the FOLLOW and REDIRECT tasks. All but one subject generated more hypometric saccades in the REDIRECT task than in the FOLLOW task. In contrast, all subject generated more midway saccades in the FOLLOW task than in the REDIRECT task.

Figure 5. (A) Distribution of the extent of scatter of end-points of midway saccades in step trials with 90° angular separation between the targets as a function of reprocessing times (RPT) for the FOLLOW (dark grey) and REDIRECT (light grey) tasks. Target locations were normalized such that the location of initial target (IT) was always at 0° and the final target (FT) at 90° to pool the data. IT and the FT on the y-axis denote the 0° and 90° target locations. (B) Distribution of the proportion of midway saccades as a function of reprocessing times (RPT) for the FOLLOW (dark grey) and REDIRECT (light) tasks. Error bars denote the standard errors of the corresponding mean.
A. Classification of midway saccades

B. Classification of hypometric saccades

C. Velocity profiles of hypometric correction and curved saccade

Figure 2
A. Visual averaging

B. Movement averaging

Figure 3
Figure 5