Systematic Errors for Saccades to Remembered Targets: Evidence for a Dissociation Between Saccade Metrics and Activity in the Superior Colliculus

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Pronounced systematic errors are a consistent feature of saccades to remembered target locations. In an effort to determine their neural basis, we recorded from saccade-related burst neurons (SRBNs) in the superior colliculus and compared the discharges associated with saccades to visual and remembered targets. For all recorded SRBNs, the relationship between discharge rate and saccade metrics differed for saccades to visual and remembered targets; movement fields constructed from saccades to remembered targets were shifted relative to those for visual targets. The shifts of the remembered movement fields were consistent with the direction and magnitude of the systematic errors observed on memory trials. These findings suggest that the superior colliculus is not the source of the systematic errors observed on memory trials. Systematic errors are likely due to the addition or omission of signals downstream from the superior colliculus.

Superior colliculus  Saccades  Memory

INTRODUCTION

The behavioral studies presented in the preceding article (White, Sparks & Stanford, 1993) confirm the finding that monkeys make systematic errors when required to look to the remembered locations of visual targets (Gnadt, Bracewell & Andersen, 1991). Although the severity of the errors varies for individual monkeys, and under different experimental conditions, our results, as well as those of Gnadt et al. (1991), show that systematic errors are a consistent feature of saccades to remembered target locations. The neural basis for the errors is unknown. One hypothesis, proposed by Gnadt et al. (1991), is that the errors occur during a memory-dependent stage in the process of translating retinotopic signals into motor commands. Although plausible, there is little neurophysiological evidence to confirm or refute the notion that the systematic errors are due to a "memory-linked" spatial transformation.

The posterior parietal cortex, an area involved in the sensorimotor transforms required for making goal-directed saccades (Gnadt & Andersen, 1988), is a potential site for the origin of systematic errors (Gnadt et al., 1991). At present, however, this may be difficult to confirm by recording the activity of neurons in parietal cortex. Although it is known that some parietal neurons encode saccadic motor error and that others have changes in activity correlated with saccade onset (Lynch, Mountcastle, Talbot & Yin, 1977; Andersen, Essick & Siegel, 1987; Gnadt & Andersen, 1988; Barash, Bracewell, Fogassi, Gnadt & Andersen, 1991a, b), the relationship between parietal activity and saccade metrics has not been evaluated to the extent that it has for neurons in other structures with saccade-related activity. For example, in the superior colliculus (SC) and frontal eye fields (FEF), the relationships between neural activity and saccade metrics have been described in detail; neurons with saccade-related activity discharge maximally for movements of a particular amplitude and direction and less vigorously for saccades encompassing a large range of directions and amplitudes (Sparks, Holland & Guthrie, 1976; Ottes, Van Gisbergen & Eggermont, 1986; Bruce & Goldberg, 1985). In contrast, demonstrations of the relationship between neural activity and saccade metrics for parietal neurons have been limited to showing large differences in discharge rate in association with movements of grossly different metrics. Early studies reported activity in relation to movements to targets of a single eccentricity placed along either the horizontal or vertical meridian (Lynch et al., 1977). The most detailed study varied saccade direction in increments of 45 deg and examined just three amplitudes (Barash et al., 1991b). Because it is not known how the discharge of parietal neurons is related to small differences in saccade direction or amplitude for normometric,
visually-guided saccades, interpreting the changes in firing rate associated with the errors observed for saccades to remembered targets would be problematic. Considering even the largest errors observed on memory trials, the difference in metrics for visual and remembered saccades to the same target are small in relation to the resolution at which parietal neurons have been tested.

For the reason outlined above, an examination of saccade-related activity in the SC could provide important information regarding the neural basis of the systematic errors observed on memory trials. Saccade-related burst neurons (SRBNs) in the intermediate and deep layers of the SC generate a high-frequency burst approx. 20 msec before the onset of a saccade (Sparks, 1978). As noted above, the movement fields of collicular SRBNs have been examined with high resolution demonstrating that the discharge rate of a given SRBN is greatest preceding movements to the center of its movement field and declines monotonically as saccade metrics deviate from these values (Sparks et al., 1976; Ottes et al., 1986). Electrical stimulation and recording studies have demonstrated that SRBNs are arranged topographically according to their movement fields, an arrangement that gives rise to a motor map in which amplitude and direction are represented anatomically along the antero-posterior and medio-lateral dimensions of the SC (Robinson, 1972; Wurtz & Goldberg, 1972; Schiller & Stryker, 1972).

The established relationships between collicular activity and saccade metrics greatly increases the probability of correlating changes in neural activity with the systematic errors observed on memory trials. For example, based upon the rationale outlined in the following paragraphs, it should be possible to determine whether the signals responsible for the systematic errors arise as a result of processing that occurs prior to, or subsequent to, that which occurs in the SC. This can be accomplished by comparing two movement fields obtained for the same SRBN, one movement field for saccades to visual goals, and the other for saccades to remembered targets. Because the SC occupies an intermediate position in the saccadic command chain, determining whether systematic errors are introduced above or below this level will provide valuable direction for attempts to understand its neural basis. Should the results indicate that the error signals arise above the level of the SC, attention should be directed toward the cortical and subcortical structures (e.g. frontal and parietal cortex, substantia nigra pars reticulata) that provide inputs to the SC. Should the opposite be found, attention should be directed toward other brainstem regions known to be involved in the generation of saccadic command signals. Figure 1 illustrates the rationale for comparing movement fields for saccades to visual and remembered targets.

Figure 1(A) is a schematic representation of the relationship between target location, the site of SRBN activity in the SC, and saccade metrics for a visually-guided saccade. The target (solid square, far left panel) appears on the horizontal meridian at an eccentricity of 10 deg. The flow diagram immediately to the right indicates that visual information, initially represented as a locus of activity on the retina, must be transformed into a representation suitable for extracting information about the change in eye position needed to foveate the image. The direction and amplitude of the change in eye position needed to direct gaze to the target, or motor error, is encoded by the locus of activity within the collicular motor map (see Sparks & Mays, 1990 for review). Thus, continuing to the right of Fig. 1(A), activity in the SC is centered about the intersection of the 10 deg isoamplitude and 0 deg isodirection lines, thereby specifying a purely horizontal (direction = 0 deg) movement of 10 deg. The trajectory of the leftward saccade (arrow) resulting from activity at this locus is diagrammed to the right (above). The high-frequency burst of a single SRBN recorded at site A is shown to precede movement onset (arrow) in the trace below. Finally, the far right panel of Fig. 1(A) shows the hypothetical movement field for a cell recorded at site A. The SRBN discharges for movements encompassing a range of amplitudes and directions, centered about an amplitude of 10 deg and a direction of 0 deg.

These same relationships are shown in Fig. 1(B, C) for saccades made to the remembered location of a visual target. Figure 1(B, C) shows how the relationship between discharge rate and saccade metrics would differ depending upon whether systematic errors are introduced above [Fig. 1(B)] or below [Fig. 1(C)] the level of the SC. Because the most pronounced component of the systematic errors observed on memory trials is an “upward bias”, in which saccades end above the actual target location, we will focus primarily on the vertical error component in these examples.

In Fig. 1(B, C), the target is presented on the horizontal meridian at an eccentricity of 10 deg (open circles). The scheme illustrated in Fig. 1(B) is consistent with the hypothesis that the signals responsible for the upward bias arise upstream from the SC, as might be the case if systematic errors resulted from a distorted memory-based representation of target location in parietal cortex. Accordingly, the SC, a recipient of the erroneous signal, specifies a movement that reflects the upward bias. Because the desired change in eye position includes an upward component, the collicular motor error signal originates at a more medial site (B) and the ensuing saccade ends above the actual target location. Because the motor error signal originates at site B, the activity of a SRBN at site A would be diminished or absent because the metrics of the movement would be near the limit or completely beyond its movement field. We would expect the movement field of a cell at A to be the same whether saccades are to visual [Fig. 1(A); right] or remembered [Fig. 1(B); right] targets.

In the scheme outlined in Fig. 1(B), the movement fields are the same for visual and memory trials because, in both cases, the activity of a SRBN always corresponds to the metrics of the actual movement, not the metrics of a movement to the true location of the target. This is
in contrast to the scheme outlined in Fig. 1(C) in which the upward bias is due to a signal introduced downstream from the SC. Here, because the memory of target location is accurate, the desired change in eye position is the same as for a visual trial [Fig. 1(A)]. Accordingly, the locus of collicular activity is at site A in order to specify a leftward saccade of 10 deg. Despite the fact that the collicular motor error signal specifies a purely horizontal saccade, the saccade ends above the target because the collicular command signal is combined with a vertical signal at a later stage. In this case, the mismatch is between the saccade metrics specified by the SC, and the metrics of the saccade actually executed. In contrast to the scheme of Fig. 1(B), the collicular activity specifies a movement to the actual location of the target, not the metrics of the movement that actually occurs.

Because a signal introduced downstream from the SC alters the relationship between the metrics of the movement and the discharge of the SRBN, the movement fields for saccades to visual [Fig. 1(A)] and remembered [Fig. 1(C)] targets would not be the same. Instead, for all SRBNs, the movement fields recorded for movements to remembered targets should be shifted upward relative to those recorded for visually-guided saccades. A comparison of the movement fields in Fig. 1(A, C) illustrates this point for the hypothetical SRBN recorded at site A.

Figure 1(C) presents the possibility that systematic errors are due to the addition of erroneous vertical signals on memory trials. Errors could also result from the omission of signals on memory trials, signals that would normally be added downstream to the collicular command in order to produce accurate visually-guided saccades (see Discussion). The experiment we conducted was designed to determine if systematic errors are introduced upstream or downstream from the SC, not to distinguish between the addition or omission of signals.

FIGURE 1. Hypotheses for the introduction of systematic errors. (A) Schematic representing the relationship between target location, collicular activity, SRBN discharge, and saccade metrics for a visually-guided saccade. (B) Remembered saccade: upward bias introduced above the level of the SC due to a mismatch between perceived and remembered target locations. (C) Remembered saccade: upward bias introduced downstream to the SC. Discharge rate histograms for hypothetical SRBN at site A are based on interspike intervals of a SRBN (0403) recorded from the right SC of monkey 4781. Arrow represents time of saccade onset. Amount of time before and after saccade onset is 150 msec. Abbreviation: s-r trans, sensorimotor transformation.
50 msec before saccade onset to 30 msec after saccade onset. A velocity criterion was used to define saccade onset and offset. Saccade amplitude and direction were computed from the measurements of horizontal and vertical eye position.

RESULTS

Extracellular recordings of single SRBNs were obtained from the right SC of monkey 4781. For each neuron, the relationship between discharge rate and saccade metrics was examined for visually-guided saccades and for saccades to the remembered location of visual targets.

If the systematic errors observed on memory trials result from a combination (addition or omission) of signals that occurs downstream from the SC, the relationship between SRBN activity and saccade metrics should differ for visual and remembered saccades. Figure 2 illustrates the activity of three SRBNs that is consistent with this prediction. The left panel of Fig. 2(A) shows, for one neuron, the discharge associated with an accurate visually-guided saccade to a target (solid square) presented on the horizontal meridian at an eccentricity of 5 deg. The saccade was near the limit of the SRBN’s movement field and a moderately vigorous burst preceded saccade onset (arrowhead). This neuron did not discharge in association with an accurate saccade to a visual target presented above the horizontal meridian (middle panel) indicating that such a movement was beyond the boundary of its movement field. The right panel of Fig. 2(A) shows the activity of the cell associated with a saccade to the remembered location of a target (open circle). An accurate saccade would be in the movement field of the cell, but because of the upward bias, the movement was nearly identical to the one shown in the middle panel, a saccade that was not in the cell’s movement field. Nevertheless, the cell discharged vigorously. The profile of instantaneous discharge frequency was very similar to the discharge preceding an accurate movement to the target (left panel) and did not resemble the discharge associated with a visually-guided movement of similar trajectory (middle panel).

The SRBN shown in Fig. 2(B) also discharged in association with a saccade to a remembered location even though, judging from visual trials, the movement was not in its movement field. Again, the SRBN activity appeared appropriate for producing the trajectory of an accurate saccade, not the movement that actually occurred. The SRBN in Fig. 2(C) shows a vigorous discharge associated with an up and left movement to a visual target (left panel) and a very weak discharge associated with a purely leftward movement (middle) that was near the limit of its movement field. Unlike the previous examples [Fig. 2(A, B)], on the memory trial (right), the target location was such that an accurate movement would be beyond the limit of the cell’s movement field. In this case, the upward bias produced a saccade into the cell’s movement field. Though nearly identical to the visually-guided saccade associated with a strong discharge (left), the neuron did not discharge.

As in the previous examples, the activity seemed appropriate for specifying a movement to the true location of the target, in this case, a movement that was not in the movement field of the cell.

For each of the SRBNs shown in Fig. 2, the discharges observed were quite different on visual and memory trials, even for saccades of virtually identical trajectory. As detailed in Fig. 1, this would be expected if, on memory trials, an erroneous signal were added or a necessary signal omitted downstream from the SC. While Fig. 2 illustrates this point for a few individual trials, Fig. 3 shows that the entire movement field for memory trials was shifted in a manner consistent with the prediction outlined in Fig. 1(C) (right).

For each of six SRBNs, Fig. 3 plots the relationship between saccade metrics and discharge rate for both visual and memory trials. The coordinates of each square represent saccade amplitude (r) and direction (θ); the color of the square represents the relative discharge frequency associated with a movement of those metrics (red, maximum; violet, no response; white, not sampled).

For each SRBN, the movement field for memory trials is shifted relative to that for visual trials. For example, on visual trials, the SRBN shown in Fig. 3(A) discharged maximally for downward saccades with amplitudes of between 5 and 7 deg. Note that this neuron did not fire in association with any movements of θ > +15 deg. In contrast, for memory trials, the maximum discharge occurred in association with movements above the horizontal meridian. Similar upward shifts are apparent for the remembered movement fields illustrated in Fig. 3(B, C, D). Each of these SRBNs discharged most vigorously for downward visually-guided saccades. However, for saccades to remembered target locations, high-frequency discharges occurred in association with movements above the horizontal meridian.

The shifts of the remembered movement fields are consistent with the corresponding patterns of error associated with saccades to remembered target locations. This point is most clearly illustrated by considering the movement fields shown in Fig. 3(E, F). As demonstrated in the preceding article (White et al., 1993), the magnitude of the vertical bias depends strongly on the vertical position of the target. Large errors occur for downward targets while smaller errors are observed for saccades to upward targets. This is clearly reflected in the movement field shifts shown in Fig. 3(E, F). For both, the lower boundary of the movement field shifts upward while the upper boundary remains relatively stable. This is most apparent when comparing the extent of the areas of maximum discharge (red). As a result, the remembered movement fields appear constricted in comparison to their visual counterparts.

Figure 4(A, B) shows the patterns of error associated with movements to remembered target locations while recording the SRBN activity depicted in Fig. 3(E, F), respectively. The location of the target (open symbol) and the average saccade end point for all movements
FIGURE 2. Relationship between discharge rate, target location, and saccade metrics for saccades to visual and remembered targets. (A) Saccade trajectories (above) and associated instantaneous firing frequency histograms (below) for three trials. Left: trajectory and associated discharge for an accurate, visually-guided saccade into the movement field of SRBN 0403. Middle: trajectory and discharge of SRBN 0403 for a saccade to the remembered location of a visual target. Right: trajectory and discharge for SRBN 0403 for an accurate, visually-guided saccade out of the movement field. Target locations are indicated by solid squares and open circles, respectively. Arrow on abscissa of each instantaneous frequency histogram indicates time of saccade onset. Time before and after saccade onset is 150 msec. Ordinate of histogram in units of spikes/sec.
corresponding to the presentation of the target (solid symbol) are shown. For clarity, data are presented for
only a subset of the targets used to plot the remembered movement field. For targets located along any given
radial, the distortion was primarily upward, and a
systematic relationship between error magnitude and
target position is apparent. The error was largest for
downward targets and smallest for upward targets. The

FIGURE 3. Movement fields for saccades to visual and remembered targets for six SRBNs. Color bar provides index of relative
discharge rate. In all cases, minimum discharge (dark violet) corresponds to complete absence of discharge. Movement fields
are plotted with an amplitude and direction resolution of 1 and 5 deg, respectively. Discharge rate (color) is an average for
all trials in which saccades were within $1 \times 5$ ($r \times \theta$) bin. White space indicates that discharge rate was not sampled in
association with a saccade of those metrics. (A) SRBN 0402. (B) SRBN 0513. (C) SRBN 0403. (D) SRBN 0422. (E) SRBN
0603. (F) SRBN 0425.
movement field shifts in Fig. 3(E, F) could be predicted from the pattern of errors shown in Fig. 4. For example, in Fig. 3(E), the shift of the lower boundary is consistent with the direction and magnitude of the error for movements to targets presented along the 180 deg radial [Fig. 4(A)]. Similarly, the stability of the upper boundary agrees with the observation that relatively small errors were observed for movements to the remembered location of targets presented in this region (θ = +30–45 deg). A similar correspondence between the pattern of errors and movement field shift may be seen by comparing Figs 3(F) and 4(B).

According to the hypothesis that the upward bias is due to a combination of signals downstream from the SC [Fig. 1(C)], activity of the collicular SRBNs specifies movements of similar metrics for visual and memory trials. The relationship between neural discharge and saccade metrics differs because of the addition or omission of signals on memory, but not visual, trials. If true, the relationship between neural discharge and the actual location of the target should be similar for visual and memory trials. Figure 5 demonstrates this point for each of the SRBNs shown in Fig. 3 by plotting discharge rate as a function of both saccade (left) and target (right) direction for both visual (open symbols) and memory trials (solid symbols). The activity profiles shown in each plot represent iso-amplitude slices through the corresponding visual and remembered movement fields of Fig. 3. For example, Fig. 5(A) plots discharge rate as a function of movement (left panel) and target (right panel) direction for saccades with amplitudes of 5–7 deg, a range that approximately bisects the movement field center.

In each case, the upward shift of the remembered movement field is evident as a leftward shift in the activity profile for saccades to remembered targets (solid symbols) relative to that for saccades to visual targets (open symbols). In contrast, when plotted as a function of target direction (right panel), the activity profiles for visual and memory trials are in register. For example, in Fig. 5(A, B, D) (left), the movement directions corresponding to maximum discharge for visual and memory trials are quite different, but little difference is apparent for target direction. Plotted against movement direction, the activity/direction profiles in Fig. 5(E, F) reflect the constriction of the corresponding remembered movement fields [Fig. 3(E, F)]. When plotted against target position, the activity profiles for remembered saccades expand to closely approximate those for visual trials.

Estimates of maximum discharge rate ($R_g$), the direction corresponding to maximum discharge ($D_g$), and the breadth of direction tuning ($T_g$), were obtained for each activity profile by fitting the data with the Gaussian function

$$f(\Theta) = R_g e^{-1/2(\Theta - D_g)^2/T_g^2}$$

where $f(\Theta)$ is discharge rate as a function of either movement or target direction (\(\Theta\)). The solid lines in Fig. 5 illustrate the least squares approximation to the data.
FIGURE 5. Discharge rate in relation to movement direction [left panels of (A–F)] and target direction [right panels of (A–F)] for saccades to visual and remembered targets. Activity profiles shown in (A–F) correspond to SRBNs represented in Fig. 3(A–F). Open symbols, visual trials; solid symbols, memory trials; solid line, Gaussian function fit by method of least squares. (See text; parameter estimates in Table 1.)
points. The corresponding parameter estimates, along with values estimated for six additional single units, are presented in Table 1.

The direction tuning of SRBNs is well described by a Gaussian formula; correlation coefficients ($r$: predicted vs observed) indicate that a high proportion of the variance in discharge rate is accounted for on both visual and memory trials. In addition to the parameter estimates, Table 1 shows the differences (bold type) between these estimates for visual and memory trials when plotted against both movement (left) and target (right) direction. Substantial differences in $D_g$ for visual and memory trials plotted against movement direction are in agreement with the apparently upward shifts of remembered activity profiles. (Directions above and below the horizontal meridian are denoted by positive and negative values, respectively. Differences are visual relative to memory; thus for example, “−25.1” is read “visual 25 deg down with respect to memory”.) Plotted against target position, the difference is reduced to −2.7 deg (visual: 3.4 ± 21.9 deg; memory: 6.1 ± 21.8 deg; mean ± SD). Though it approaches significance at the level of $P = 0.01 (t = 2.7, d.f. = 10, P < 0.02), this difference is small. On average, plots against target direction accounted for 92% of the shift between visual and remembered activity profiles.

The similarity in direction tuning when visual and remembered activity is plotted against target direction is consistent with the idea that collicular signals specify saccades of similar metrics on visual and memory trials. Further support for this claim was obtained by fitting each remembered activity profile with a Gaussian function having only $R_g$ as a free parameter. Both $D_g$ and $T_g$ were constrained to values estimated by least squares fit to the corresponding visual activity profiles. Thus, only absolute discharge level ($R_g$), which, on average, tended to be higher for visual trials, remained a free parameter. The results are summarized in Table 2 which shows correlation coefficients for the unconstrained and constrained fits to the remembered activity profiles. As expected, when plotted against movement direction, a fit of the “visual” Gaussian to the remembered activity profile accounts for relatively little of the variance in
DISSOCIATION BETWEEN SC ACTIVITY AND SACCADe METRICS

TABLE 2. Fit of “visual” Gaussian to “remembered” activity

<table>
<thead>
<tr>
<th>Unit</th>
<th>Movement direction</th>
<th>Target direction</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Constrained r = 0.35 ± 0.20</td>
<td>Unconstrained r = 0.83 ± 0.06</td>
</tr>
<tr>
<td>0402</td>
<td>0.24</td>
<td>0.70</td>
</tr>
<tr>
<td>0513</td>
<td>0.28</td>
<td>0.83</td>
</tr>
<tr>
<td>0403</td>
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</tr>
<tr>
<td>0502b</td>
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<td>0.72</td>
</tr>
<tr>
<td>Mean ± SD 0.35 ± 0.20</td>
<td>0.83 ± 0.06</td>
<td>0.83 ± 0.07</td>
</tr>
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</table>

discharge frequency (constrained $r = 0.35 ± 0.20$; unconstrained $r = 0.83 ± 0.06$; mean ± SD). In contrast, plotted against target direction, the “visual” Gaussian predicts the remembered activity profiles nearly as well as does a Gaussian fit with $D_g$ and $T_g$ as free parameters (constrained $r = 0.83 ± 0.07$; unconstrained $r = 0.87 ± 0.05$; mean ± SD).

Well characterized movement fields for visual and remembered saccades were obtained for a total of 12 well isolated SRBNs. For each, the remembered movement field was shifted in a manner consistent with the behavioral bias. The small size of our sample reflects the difficulty of maintaining isolation long enough to fully characterize two movement fields, rather than a failure to encounter neurons that demonstrated the movement field shift. We did not encounter any units that provided evidence to the contrary. Data from an additional sample ($N = 11$) of partially studied single units and multunit recordings were consistent with the results illustrated.

DISCUSSION

Neurons in the intermediate and deep layers of the SC are critical components of the neural circuitry that initiates and controls saccadic eye movements (see Sparks, 1986; Sparks & Mays, 1990 for recent reviews). Of particular relevance to the present study is the question of how information about the direction, amplitude, and velocity of saccades is encoded by collicular neurons. There is little disagreement about three critical points. First, the discharge of collicular neurons provides a signal that specifies the change in eye position needed to acquire an eccentric target, not a signal for moving the eye to a particular position in the orbit. Second, because collicular neurons have large movement fields, a large population of neurons will be active before each saccade. Third, the location of the active population of collicular neurons within the topographical map of movement fields encodes information about saccadic motor error.

The goal of the present experiment was to determine whether the signals responsible for the systematic errors observed when saccades are directed to remembered target locations are introduced above or below the level of the SC. The experimental rationale, as outlined in Fig. 1, rests upon the assumption that the SC participates in the formation of saccadic motor error signals for remembered, as well as, visually-guided saccades. If this assumption is valid, the comparison of visual and remembered movement fields provides a straightforward test of the two alternative hypotheses detailed in Fig. 1(B, C). If the signals responsible for the systematic errors of remembered saccades originate at a stage of processing above the level of SC [Fig. 1(B)], the correspondence between saccade metrics and the locus of collicular activity will be the same for visually-guided and remembered saccades; in either case, there is agreement between the site of collicular activity and the metrics of the ensuing saccade. While this hypothesis predicts that the relationship between SRBN discharge and saccade metrics will be the same for saccades to visual or remembered goals, our data indicate that this is not the case. For every SRBN we encountered, the relationship between discharge frequency and saccade metrics was different for visually-guided and remembered saccades. This was particularly evident in the types of trials illustrated in Fig. 2. Similar rates of discharge were associated with visual and remembered saccades of different metrics; dissimilar discharge rates were associated with visual and remembered saccades of very similar trajectory.

The data we obtained are those predicted by the hypothesis that the signals responsible for the systematic errors occurring on memory trials arise at a point in the saccadic command chain that is between the SC and the motoneurons—i.e. below the level of the SC [Fig. 1(C)]. If signals were added or omitted downstream from the SC on memory, but not visual trials, the relationship between neural discharge and saccade metrics for remembered and visually-guided saccades would differ. Further, if the hypothetical signals correspond to the upward bias, the remembered movement field should be shifted relative to the visual movement field in a manner that is consistent with the pattern of errors observed on
memory trials. Our comparison of visual and memory trials confirms this prediction.

The most parsimonious explanation for our results is that the systematic errors observed on memory trials are due to the introduction of signals below the level of the SC. As noted above, this interpretation assumes that, as for visually-guided saccades, information about the metrics of saccades to remembered targets is extracted from the locus of collicular activity. It seems likely that the SC participates in coding the metrics of saccades to remembered targets. Data from this study indicate that, as is true for visually-guided saccades, there is a close temporal coupling between the discharge of a SRBN and the onset of a saccade to a remembered target location (see Fig. 2). Moreover, the existence of the collicular quasispecial (QV) cell, a cell type that maintains a signal of motor error long after a target has been extinguished (Mays & Sparks, 1980), indicates that the SC is capable of storing, or gaining access to, information about the recent history of target locations.

Anatomical data are also consistent with the presumptive role of the SC in generating saccades to remembered target locations. The SC receives direct projections from cortical and subcortical structures that are thought to be involved in the programming of remembered saccades, including parietal cortex (Lynch, Graybiel & Lobeck, 1985; Fries, 1984; Seleen & Goldman-Rakic, 1988; Gnadt & Andersen, 1988), dorsolateral prefrontal cortex (Seleen & Goldman-Rakic, 1988; Funahashi, Bruce & Goldman-Rakic, 1989), the FEF (Leichnetz, Spencer, Hardy & Astruc, 1981; Bruce & Goldberg, 1985) and the substantia nigra pars reticulata (Jayaraman, Batton, & Carpenter, 1977; Hikosaka & Wurtz, 1983a, b).

Of particular relevance is the projection from parietal cortex to the SC since parietal cortex is one site where systematic errors might arise (Gnadt et al., 1991). The intermediate and deep layers of the SC receive a heavy projection from the lateral bank of the intraparietal sulcus (LIP) (Lynch et al., 1985), an area of posterior parietal cortex known to contain neurons that discharge during memory intervals and prior to saccade onset (Bracewell, Barash & Andersen, 1990; Barash et al., 1991a, b). As a recipient of the information conveyed by these parietal neurons, the SC should reflect any memory-linked distortion were it to arise at this upstream site [see Fig. 1(B)]. The fact that the collicular SRBNs appear to convey a signal that specifies an accurate saccade, not one that would end above the target, argues against the possibility that the signals responsible for the upward bias arise in parietal cortex. While this same reasoning can be used to argue that the signals responsible for the systematic errors do not arise along any pathway that originates upstream to the SC, this possibility cannot be ruled out entirely. Erroneous signals arising in parietal cortex or FEF could influence saccade metrics via an extracollicular pathway. Parietal cortex projects to the frontal eye fields (FEF) (Andersen, Asanuma & Cowan, 1985), which in turn, project to oculomotor control circuits in the pons and medulla (Leichnetz, 1980; Leichnetz et al., 1981). Here these signals might be combined with collicular command signals to produce systematic errors. Although possible, this scheme seems less likely because it would require that upstream sites send an accurate signal to the SC, but an inaccurate signal to the pons and medulla.

Our finding that the relationship between discharge rate and saccade metrics differs for visual and memory trials has implications for all studies that attempt to relate neural activity to the metrics of saccades. These results underscore the possibility that the metrics of any given saccade might reflect the somewhat independent contributions of more than one oculomotor region, which, under different circumstances (e.g. visual vs memory trial), differ in their relative weight. Clearly, the farther from the periphery, the greater is the need to consider this possibility. Thus, for example, the observed relationships between saccade-related activity and the metrics of saccades to remembered target locations for sites antecedent to the SC, including, parietal cortex (Andersen et al., 1987; Bracewell et al., 1990; Gnadt et al., 1991; Barash et al., 1991a, b), FEF (Bruce & Goldberg, 1985), and dorsolateral prefrontal cortex (Funahashi et al., 1989), should be considered in the context of these findings. As is true for the SC, it cannot be assumed that, in every circumstance, the saccade-related activity of neurons in these regions specifies the metrics of the movement that actually occurs.

In addition to displaying systematic errors in end position, saccades to remembered target locations display more variability (Gnadt et al., 1991; White et al., 1993). Though not shown, this was consistently true in this study. With regard to systematic errors, our findings indicate that the SC is not the source; activity in the SC specifies saccades of similar direction and amplitude on visual and memory trials. Although the relationship of SRBN activity to variable error is less clear, we did find that, for repeated movements of the same direction and amplitude, discharge rate varied to a greater extent on memory trials. Consistent with this, Gaussian fits to the plots of SRBN activity against movement direction [Fig. 5(A–F), left panels] for memory trials yielded consistently lower correlation coefficients than did those for visual trials (see Table 1). Unlike the differences in direction tuning, differences in the variability of discharge rate on visual and memory trials persist when activity is plotted against target direction [Fig. 5(A–F), right panels]. By the same reasoning outlined in Fig. 5, it seems that this difference between SRBN activity on visual and memory trials is not due to the introduction of signals downstream from the SC. As suggested by White et al. (1993), variation in collicular output could be a source of variable error on memory trials. Variability in the relationship between collicular activity and saccade metrics might reflect memory-dependent spatial errors that arise at sites upstream to the SC (e.g. parietal cortex).

These findings also have implications for studies that attempt to relate neural activity to saccadic velocity. For example, Rohrer, White and Sparks (1987) compared visually-guided and remembered saccades of similar
metrics to determine if SRBN discharge rate was related to saccadic velocity. Their observation that SRBNs discharged at lower rates in association with the lower velocity remembered saccades supported the hypothesis that activity in the SC specifies saccadic velocity in addition to direction and amplitude. However, this interpretation needs to be reconsidered in the context of our findings. In their experiment, vigorous SRBN activity was evoked by eliciting visually-guided movements towards the center of a given cell's movement field. In order to obtain matched movements on memory trials, it was necessary to present targets at more downward locations (to compensate for the upward bias). Based on our findings, we would expect discharge rate to be reduced, not in relation to lower velocity, but because SRBN activity on memory trials specified a saccade to the target, which, unlike the corresponding visual trial, was not to the center of the movement field.

Other studies do provide strong evidence for a relationship between collicular activity and saccade velocity. For example, pharmacological deactivation of the SC leads to dramatic reductions in saccadic velocity (Hikosaka & Wurtz, 1985, 1986; Lee, Rohrer & Sparks, 1988). While it may be that saccadic velocity is encoded in the temporal discharge pattern of collicular SRBNs, because of the dissociation between collicular activity and saccade metrics, it is not possible to address this issue by comparing the discharge of a single cell on visual and memory trials. While plots of SRBN activity against target direction (Fig. 5, right panels) avoid the confound of comparing visual and remembered saccades of matched metrics, interpreting differences in discharge rate on visual and memory trials remains problematic since it is not possible to know the extent to which a velocity difference is due to the differential contributions of signals downstream from the SC.

The idea that signals are introduced downstream from the SC seems plausible considering that the neural signals observed in the SC are quite different from the innervation signals required for saccadic rotations of the eye. In discussing the transformations required to convert collicular signals to those needed by the premotor neuron pools, Sparks and Mays (1990) consider the addition of signals necessitated by kinematic constraints, in particular, those dictated by Donders' and Listing's laws; the need for signals that permit the velocity of horizontal and vertical saccades to be matched with overall saccade direction and amplitude; and the addition of signals to compensate for the presaccadic position of the eye in the orbit. Systematic errors on memory trials could result from the incorrect addition or omission of one or more of these signals. Additionally, it should be noted that, while some brain regions subserve specific oculomotor subsystems, ultimately, signals from the saccadic, pursuit, optokinetic, and vestibular systems combine and share a common final pathway which, at the very least, includes the motoneurons and extraocular muscles. Thus, the systematic errors observed for remembered saccades need not originate at a site that normally contributes to the programming of saccades.

Based upon the known innervation requirements of the oculomotor plant, it is possible to make inferences regarding the nature of the signals producing systematic errors. In their simplest form, all models of the oculomotor plant recognize two innervation requirements for producing saccadic eye movements: a pulse of activity, which moves the eye at high velocity by overcoming the viscous drag of the orbital tissues; and a step of innervation which, by opposing the elastic restoring forces of the extraocular muscles, holds the eye in its new position (see Robinson, 1981; Fuchs, Kaneko & Scudder, 1985 for reviews). Neural correlates of the pulse and step have been observed: burst neurons in the pons and medulla provide the pulse of high-frequency activity that encodes eye velocity, and tonic neurons, believed to arise via neural integration of the pulse, discharge with a rate proportional to eye position (see Fuchs et al., 1985 for review). Downstream, motoneurons generate both a pulse and a step of activity (Robinson, 1970; Fuchs & Luschei, 1970, 1971).

The signals responsible for the systematic errors appear to satisfy both of the primary innervation requirements of the plant since saccades to remembered targets do not show evidence of a pulse-step mismatch. For example, in the case of the upward bias, augmentation of the vertical velocity signal (pulse) alone would produce a saccade that ends above the target, but, due to the failure to augment the position signal (step), the eye would immediately drift downward and come to rest near the actual target location. Augmentation of the step but not the pulse would result in an accurate saccade followed by an upward drift. Visual inspection of the remembered saccades shown in Fig. 2 suggest that neither of these is observed. For example, in Fig. 2(A), far right, the velocity of the vertical component is clearly saccadic as evidenced by the straight trajectory of the obliquely directed saccade. Thus, the vertical bias is not due to a slow upward drift (step too large). Although not apparent from these plots, downward drift toward the true target location (pulse too large) was never observed. It seems most likely then, that systematic errors are introduced at a stage prior to the computation of the saccadic velocity command and its subsequent integration to form a signal of eye position.

Finally, it may be most intuitive to think of the upward bias as being due to the addition of erroneous vertical signals on memory trials. However, as we have stated, systematic errors could also be due to the omission of signals on memory trials, signals that would normally be added to produce accurate visually-guided saccades. As noted above, signals, such as those dictated by kinematic constraints (see May & Sparks, 1990 for review), are thought to be added below the level of the SC in order to produce normometric saccades to visual targets. The results of this study do not distinguish between the addition or omission of signals on memory trials; they do indicate that, whether by addition or
omission, systematic errors are due to a modification that occurs below the level of the SC.

REFERENCES


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