Cerebellar Flocculus and Paraflocculus Purkinje Cell Activity During Circular Pursuit in Monkey

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INTRODUCTION

The floccular and parafloccular regions of the cerebellum play an important role in controlling smooth pursuit eye movements (Zee et al. 1981). Previous studies of single-neuron responses during smooth pursuit have concentrated on its role in controlling eye movements during one-dimensional (1D) ramp, step-ramp, sinusoidal, square, and trapezoidal target motions. Many of these studies have used target motions restricted to the horizontal axis (Lisberger and Fuchs 1978). Some have studied a combination of horizontal and vertical target motions (Lisberger et al. 1994; Stone and Lisberger 1990), whereas others also have included diagonal motions (Krauzlis and Lisberger 1996; Miles et al. 1980; Noda and Suzuki 1979).

The experiments described in this paper extend this work to two-dimensional (2D) target motions. One goal was to determine how neural responses during 2D pursuit relate to responses from the same cell during 1D pursuit. We were interested particularly in whether the smooth pursuit system satisfies component additivity. That is, does a neuron’s response during 2D tracking equal the summation of responses obtained during 1D component motions that combine to create the 2D motion? Establishing component additivity is important because it simplifies data collection and data analysis and facilitates modeling of the pursuit system. For example, it implies that the response of the pursuit system during a general 2D motion can be characterized by its responses during the horizontal and vertical components of that 2D motion.

Circular target motions were selected for study because they are simple 2D trajectories that are radially symmetric. This allowed direct comparisons of component additivity for both horizontal/vertical (0°/90°) and diagonal/diagonal (45°/135°) coordinate axes. Combinations of horizontal and vertical sinusoids produce clockwise (CW) rotation when horizontal motion leads vertical motion by 90° and counterclockwise (CCW) rotation when vertical motion leads horizontal motion by 90°. Similarly, combinations of sinusoids on diagonal/diagonal axes (45°/135°) with phase shifts of ±90° produce the same CW and CCW motions.

Interestingly, some neurons showed stronger modulations in firing rate for CW pursuit than for CCW pursuit. Similar preferences for CCW pursuit also were observed. These responses were more complex than one would expect based on simple extrapolations from responses during 1D pursuit. We had expected that each neuron would have a single preferred direction related to its direction of maximal velocity sensitivity.
and that responses during circular pursuit would be related to
the component of circular pursuit aligned with this preferred
velocity direction. This single-direction hypothesis predicts
that modulation amplitudes will be the same for CW and CCW
circular pursuit because both have component motions of equal
amplitude on any single axis.

Instead, response patterns were related to both the position
and velocity of the eye based on responses during circular
pursuit at a single frequency, responses during sinusoidal pur-
suit at several frequencies, and responses during fixation. It
was hypothesized that response complexity was produced by
interactions between influences related to eye position and eye
velocity acting in different directions. This idea was tested
quantitatively with a model that characterized the firing rate of
each neuron as a function of the 2D position and velocity of the
eye. The model provided a good fit for responses during
sinusoidal and circular pursuit as well as good estimates of
modulation differences during CW and CCW circular pursuit.

METHODS

Animals

Two adult male rhesus monkeys (Macaca mulatta; 4–8 kg) were
cared for and housed by the Northwestern University Center for
Experimental Animal Resources (CEAR) according to Principles of
Laboratory Animal Care (National Institutes of Health publica-
 tion No. 86-23, revised 1985). The monkeys were checked daily by a
certified veterinarian, and care was provided if necessary. Although
the monkeys did not receive water outside of the experimental room
on week days, they did obtain as much water as they were willing to
drink during each experimental session. On a typical day the monkeys
received from 500 to 900 ml of liquid during experimental tasks. This
is a large volume of water, and well within the normal range of liquid
intake for such a small animal. When neural recording failed, the
monkey still was allowed to perform the task until he received his
standard amount of water, or infrequently, was given supplemental
water to satiation. Free water was given on weekends. Supplemental
foods and toys were used to improve the well being of the monkeys.

Surgery

Sterile surgery was performed under deep anesthesia induced by
sodium thiopental (20 mg/kg iv) and maintained with halothane (1%)
administered via an endotracheal tube. An oval of skin was resected
and the underlying cranium scraped clean of periosteal tissue. A
stainless steel socket used to fix the head during the experiment was
positioned forward on the head so that a recording chamber could be
placed above the cerebellum after training was complete. An eye coil
was implanted under the conjunctiva of one eye (Judge et al. 1980;
Robinson 1963) with its connecting wires led under the skin to an
electrical plug positioned near the head fixation socket. The exposed
drainage, fixation socket, and eye-coil plug then were covered with a
smoothed layer of dental acrylic anchored with stainless steel screws
into the skull. A recording chamber was implanted in a later
surgery to reduce the chance of infection during a period of several
months when training and initial behavioral experiments were per-
established optimal behavioral parameters. A trephine hole 20
mm in diameter was made over the cerebellum that left the dura intact.
A stainless steel recording cylinder of 20 mm ID was placed over the
opening and held in place by dental acrylic. The chamber was filled
with sterile saline combined with a dilute antibiotic solution and
sealed with a sterile cap. For 1 wk after surgery, the monkey was
given daily doses of cephalolin (15 mg/kg im), and an antibiotic
salve was applied topically to prevent infection. Analgesia was main-
tained for 4 days by injections of buprenorphine HCl (0.01 mg/kg im)
and later with topical applications of lidocaine until the incision had
healed.

Apparatus

Eye position was monitored by a magnetic search coil system (CNC
Engineering). Horizontal eye position was monitored using phase
differences relative to a reference coil mounted 3 cm from the eye coil
based on a rotating electromagnetic field vector (Collewijn et al.
1975). Vertical eye position was based on amplitude changes in
induced eye-coil current (Robinson 1963); these were not corrected
for cosine error because eye motion was less than ±10°. Eye position
measurements were accurate to 15 min of arc for the range of eye
movements studied. The pursuit stimulus was a laser spot (0.7° diam,
luminance 92 cd/m²) back-projected onto a tongue screen that mea-
sured 60 by 60° located 40 cm from the monkey’s eyes. Spot motion
was controlled by a pair of servo-controlled mirror galvanometers
(General Scanning, Watertown, MA) that provided output signals
proportional to mirror position. Mirror and eye position signals to the
computers were amplified and filtered with 8-pole low-pass 500-Hz
Bessel filters. Galvanometer control signals from the computer were
amplified and filtered with 8-pole low-pass 100-Hz Bessel filters. One
computer was used to generate analogue waveforms (1,000 samples/s)
and to deliver juice rewards when the eye was within the ±2° target
window for a specified time. A second computer collected six chan-
nels of analogue data (1,000 samples/s): horizontal and vertical eye
position, horizontal and vertical target position, laser level, and reward
pulses. It also stored the time of individual neural events with an
accuracy of 0.1 ms.

Training, calibration, and behavioral paradigms

The monkeys were trained using positive reinforcement with fruit
and juice rewards. Training proceeded at a slow rate so that the
animals never were frustrated. Initially, larger error windows and
shorter fixation times produced reward delivery, but the monkeys
rapidly developed accurate pursuit behavior. The monkeys were
trained for several weeks before neural recording started until stable
and consistent performance was obtained. Laser-spot and eye-position
signals were calibrated each day both statically (horizontal, vertical,
and diagonal locations at 0, ±5, and ±10°) and dynamically (5 and
10° circles). This was done relative to lines on a moveable screen that
was in contact with the viewing screen during calibrations and then
moved away during the experiment. Calibration gain was very stable
and there were only slight changes in offset each day.

CIRCLES AND SINUSOIDS TASK. Neural responses were recorded
during smooth pursuit along six waveform trajectories (5°, 0.6 Hz):
CW and CCW circles, and sinusoids along four axes that provided
information about pursuit in eight directions (0–315° in steps of 45°).
Trials began when the monkey fixated a stationary target light at the
start of the trajectory for 1,000 ms. The monkey was required to track
error (error rate <5%) occurred during a waveform presentation, the
monkey did not receive a reward and the waveform was repeated.
Trajectories were selected randomly without replacement until all six
had been presented in two blocks of trials.

FIXATION TASK. Neural responses were recorded during fixation at
a center point and eight peripheral points 5° from the center in
directions ranging from 0 to 315° in steps of 45°. A trial began after
center fixation was maintained for 1,000 ms. The target then jumped
to one of the eight peripheral fixation points for 1,000 ms. The
monkey received a reward after each successful fixation defined as
maintenance of eye position within ±2° of the target during a 600-ms
The brain was cut in 50-
1.2 Hz) using a
modulation amplitude of 5°. Trial initiation, reward delivery, and trial
completion after five error-free cycles were as described earlier (CIR-
cles and sinusoids task). The frequency of each trial was selected
randomly without replacement until all six frequencies had been
presented in two blocks.

FREQUENCY TASK. Neurons were studied during horizontal and
vertical sinusoidal pursuit at six frequencies (0.2–1.2 Hz) using a
modulation amplitude of 5°. Trial initiation, reward delivery, and trial
completion after five error-free cycles were as described earlier (cir-
cles and sinusoids task). The frequency of each trial was selected
randomly without replacement until all six frequencies had been
presented in two blocks.

Physiological recording, localization of recording sites, and
euthanasia

On each day of recording, the head was attached to the primate
chair, and a sterile plastic insert with a grid of drilled holes (Crist et
al. 1988) was inserted into the recording chamber. A guide tube
preloaded with an electrode was inserted into one of the grid holes,
and the electrode was lowered with a microdrive to the region of
study. The microelectrodes were glass-coated platinum-iridium wires
(1–2 μm tip diameter, 1–2 MΩ impedance) optimized for extracellular
recording from Purkinje cells. Only stable single waveforms that
were clearly separable from background activity were selected for
further study. These initial decisions about waveform separation
were verified later by analyzing stored waveforms using spike-sorting dis-
plays and algorithms (DataWaves). All neurons selected for this report
showed clear separation in scatter plots of waveform parameters and
in overlaid waveform traces. Neurons were identified as Purkinje cells
based on a combination of factors including waveform shape, spike
width, the presence of complex spiking patterns, extended recording
times that generally exceeded 1 h, and maintained recording while
moving the electrode 50 μm. A single microelectrode penetration was
generally made each day. Recording times were limited to 3–5 h and
continued for 4–6 mo in each monkey.

A three-dimensional (3D) map of each recording site was con-
ducted during the course of the experiments that was later overlaid
on an anatomic reconstruction of the flocculus and paraflocculus.
Anterior-posterior and lateral-medial locations were measured relative
to the 1-mm spacing of the grid system that held the guide-tube/
electrode assembly. Depths relative to the bottom of the grid were
obtained from the microdrive scale. After the completion of recording,
the same grid was used to localize 12 marking lesions (30 μA direct
positive current for 30 s) that bracketed the recording sites of interest.
Gliosis was allowed to develop for 1 wk. The animals then were
sedated with ketamine hydrochloride (10 mg/kg im), killed by an
overdose of pentobarbital sodium (100 mg/kg iv), and perfused trans-
septed with ketamine hydrochloride (10 mg/kg im), killed by an
euthanasia

Gliosis was allowed to develop for 1 wk. The animals then were
positive current for 30 s) that bracketed the recording sites of interest.

RESULTS

Responses during circular pursuit

During circular and sinusoidal pursuit, a variety of responses were
observed for 69 neurons in two monkeys that showed
significant modulation in firing rate during circular pursuit (see
METHODS). A model that expressed firing rates in terms of
position and velocity sensitivities accounted for all these re-
ponses. We first describe the phenomena that motivated this
model with four examples. These neurons do not represent
distinct classes of neurons but instead illustrate the range of a
response continuum.

Responses from a “velocity/position” neuron (Fig. 1 ) were
explained by a dominant sensitivity to downward eye velocity
and a much weaker sensitivity to downward eye position.
Raster/histogram displays at the top of this figure show a strong
and consistent modulation in activity that was approximately
sinusoidal. Modulation amplitudes were strongest during ver-
tical pursuit, minimal during horizontal pursuit, and approxi-
mately equal during CW and CCW pursuit. The dependence on
downward eye velocity is apparent in the 2D plots at the
bottom of the figure. Firing increased in the direction of down-
ward eye velocity during both CW and CCW pursuit, as well
as during outward (centrifugal) pursuit along a center-to-down
trajectory and inward (centripetal) pursuit along an up-to-
center trajectory. A weak dependence on downward eye posi-
tion was indicated by activity during inward pursuit at down-
ward positions even though the target was moving with a slow
upward velocity.

The “position/velocity” neuron illustrated in Fig. 2 had
responses that were influenced by both eye position and eye
velocity. Raster/histogram plots indicated consistent variations
in firing rate that were similar in amplitude during circular
pursuit and showed a preference for horizontal pursuit. Inter-
estingly, the direction of maximal response was different for
CW compared with CCW pursuit. There was also a strong
preference for outward pursuit and a much weaker activation

period beginning 300 ms after the target had moved. A complete trial
consisted of five successful cycles of center to peripheral fixation.
Cycles were repeated if there were errors (error rate <5%). Fixation
points were selected randomly without replacement until all eight had
been presented in one or two blocks.
during inward pursuit. These responses can be explained by sensitivities to both leftward position and leftward velocity. Maximal responses to the top left in the 2D plot of CCW pursuit reflect position influences that were maximal along the left of the trajectory and velocity influences that were maximal along the upper part of the trajectory. A rotation of the maximal response during CW pursuit reflected a change in the point of maximal leftward velocity from upper to lower points on the trajectory. Similarly, a preference for outward pursuit was explained by the combined action of position and velocity influences that reinforced to the left and canceled to the right.

During inward pursuit, these two influences were always in opposite directions resulting in low firing rates in all directions.

This neuron’s sensitivity to eye position also was observed during fixation. Responses were recorded during fixation at a central point and at eight peripheral points in equally spaced directions. The raster/histogram plots in Fig. 3 show responses at leftward and rightward fixation points that produced the largest and smallest firing rates, respectively. The tuning function in the center shows average firing rates in these two fixation directions as well as the six other directions that were studied. It indicates that firing rate was maximal during left-
ward fixation, minimal during rightward fixation, and had intermediate values in other directions.

Responses from a “CW” neuron were more complex (Fig. 4). One striking feature was a stronger modulation during CW pursuit and a weaker modulation during CCW pursuit. Another interesting finding was a tendency for directional preferences to be stronger during inward pursuit than for outward pursuit. This is opposite to what was observed for the position/velocity neuron in Fig. 2. These responses suggest that this neuron had position and velocity sensitivities that pointed in opposite directions: a leftward sensitivity for position and a rightward sensitivity for velocity. During inward motion, these two sensitivities combined to produce maximal responses during left-to-center motions. During outward motion, these two influences were in opposite directions, and their combined action produced similar responses in all directions. This combination of position and velocity influences also explained differences in CW compared with CCW pursuit, but these interactions are best visualized using a computer simulation that will be presented later.

Responses from a “CCW” neuron (Fig. 5) were even more complex. For CCW trajectories there were strong increases in activity during pursuit in the leftward (contralateral) positions with a somewhat weaker velocity preference for pursuit in the leftward direction. See Fig. 1 and the text for more detail.

Fig. 2. Position/velocity cell that fired maximally at leftward (contralateral) positions with a somewhat weaker velocity preference for pursuit in the leftward direction. See Fig. 1 and the text for more detail.
circular pursuit in one direction was quantified by fitting a cosine function

\[ R(t) = B + M \cos(2\pi ft + \phi) \]

to each neuron’s response during CW and CCW pursuit. Here \( B \) is the average firing rate, \( M \) is the modulation amplitude, \( f \) is the frequency of target rotation, and \( \phi \) is the phase relative to the start of target motion. Computed values of \( M \) during CW and CCW pursuit are shown in Fig. 6 for the entire population of 69 neurons. Differences in response modulation during CW versus CCW pursuit also were evaluated statistically using \( \chi^2 \) tests. Data from nine neurons that showed significant differences (\( P < 0.01 \)) are plotted as ○ in Fig. 6. It is clear that many neurons showed similar response modulations during CW versus CCW circular pursuit including those cells showing the strongest modulations during circular pursuit. However, others showed significant differences in response modulation for the two directions of rotation.

Component additivity

When two component motions \( A \) and \( B \) sum to create a composite motion \( A + B \), the pursuit system exhibits component additivity if its response during the composite motion equals the sum of its responses during the components tracked individually. For example, horizontal (\( h \)) and vertical (\( v \)) sinusoidal motions that are 90° out of phase sum to create a circular (\( c \)) motion. Component additivity implies that \( R_{h}(t) + R_{v}(t) = R_{c}(t) \), where \( R_{h}(t) \), \( R_{v}(t) \), and \( R_{c}(t) \) represent the firing rates along horizontal, vertical, and circle trajectories at time \( t \). Similarly, 45° diagonal (\( d_{45} \)) and 135° diagonal (\( d_{135} \)) sinusoidal motions sum to create a circular motion with \( R_{d_{45}}(t) + R_{d_{135}}(t) = R_{c}(t) \).

Component additivity was observed for all of the neurons studied. This is illustrated in Fig. 7 for the four neurons described in the preceding text. Each set of three traces in this figure depicts the modulation in firing rate relative to baseline during circular tracking (thick lines), summed horizontal and vertical sinusoidal tracking (medium lines), and summed tracking along 45 and 135° diagonals (thin lines). In each case, a good correspondence among the three traces indicates component additivity. In particular, additivity held for the CW and CCW neurons. \( \chi^2 \) tests indicated nonsignificant (\( P > 0.94 \)) differences in modulation profile during circular and summed component pursuit (CW vs. \( h + v \), CW vs. \( d_{45} + d_{135} \), CCW vs. \( h + v \), CCW vs. \( d_{45} + d_{135} \)) for all 69 neurons.

In Fig. 8, the modulation and phase during circular pursuit are compared with the modulation and phase of summed responses during pursuit along horizontal and vertical components (●) or along diagonal 45 and 135° components (◇). Each summation is based on standard rules for combining sinusoids of different amplitude and phase. The tendency for points to lie along the diagonal in each scatter plot indicates good component additivity across the population. Thus component modulations sum to create equal modulations during CW and CCW pursuit for some neurons and unequal modulations for others. This is true independent of any specific model. However, component additivity does suggest the use of a class of multilinear models that includes the model described in the following text.

Model of instantaneous firing rate during pursuit

A model was used to quantify the relationship between neural firing rate and the motion of the eye. This model tested the hypothesis that a neuron’s firing rate at time \( t \), \( R(t) \), is a multilinear function of the 2D position and velocity of the eye. The model equation had three mathematically equivalent forms

\[ R(t) = \beta + \rho_{h} P_{h}(t) + \rho_{v} P_{v}(t) + \nu_{h} V_{h}(t) + \nu_{v} V_{v}(t) \]  

\[ \theta = \beta + |\rho||P(t)| \cos(\theta_{\rho} - \theta_{\rho_{0}}) + |\rho||V(t)| \cos(\theta_{\nu} - \theta_{\nu_{0}}) \]

Because a neuron cannot have a negative firing rate, \( R(t) \) was set to zero if it took on a negative value.

The “component form” of the model (Eq. 2a) expressed firing rate in terms of eye motion relative to a specific 2D coordinate system. In this instance, a horizontal/vertical coordinate frame was used to specify the horizontal and vertical components of position \( \{P_{h}(t), P_{v}(t)\} \) and velocity \( \{V_{h}(t), V_{v}(t)\} \) at time \( t \), where \( \beta \), \( \rho_{h} \), \( \rho_{v} \), \( \nu_{h} \) and \( \nu_{v} \) were parameters estimated using multilinear regression techniques. This form of the model shows the very simple linear relationship between firing rate and increases in each component of eye motion. It also makes clear why the model satisfies component additivity:
components on different axes combine via simple addition. This equation does not suggest a preference for a particular coordinate frame. A similar model equation can be written for other coordinate systems including the diagonal/diagonal system associated with axes at 45 and 135°. Thus the eye motion data and the model could just as easily have been collected and modeled in a diagonal coordinate frame by suitable rotations of the galvanometer and reference-coil axes.

The “vector form” of the model (Eq. 2b) is the same equation expressed using vector notation with vectors in bold type. The top of Fig. 9 shows how the position vector, \( \mathbf{P}(t) = [P_h(t), P_v(t)] \), and the velocity vector, \( \mathbf{V}(t) = [V_h(t), V_v(t)] \), specify the position and velocity of the eye at time \( t \). Component parameters also were reexpressed as vectors so that \( \mathbf{r} = (r_h, r_v) \) and \( \mathbf{v} = (v_h, v_v) \) and multiplication was via the vector dot product \( (\mathbf{r} \cdot \mathbf{P} = r_h P_h + r_v P_v) \). Illustrations in Fig. 9, bottom, show the parameter vectors calculated for the CCW cell (Fig. 5) and their relationship to the position and velocity vectors (top).

The “polar-coordinate form” of the model (Eq. 2c) defines each vector by its length and direction. For example, \( \mathbf{r} \) is defined by its length \( |\mathbf{r}| = (r_h^2 + r_v^2)^{1/2} \) and its angle, \( \theta_r \), with respect to the axis of the polar frame. This form of the equation illustrates two important properties of the model. First, it shows that cosine tuning is a natural consequence of the model. Second, it indicates how position and velocity influence firing rate via vector projection.

The vector \( \mathbf{r} \) was called the position sensitivity vector and its direction, \( \theta_r \), the preferred position direction. On the basis of Eq. 2b, the influence of position on firing rate at point \( \mathbf{P}(t) \) equals the vector dot product of \( \mathbf{r} \) and \( \mathbf{P}(t) \). Geometrically, this calculation corresponds to multiplying the length of \( \mathbf{P}(t) \) by the length of the projection of the vector \( \mathbf{r} \) onto the axis of \( \mathbf{P}(t) \).
This is illustrated in Fig. 9, bottom left, for the CCW cell. When $p$ is aligned with $P(t)$, its projection is maximal, when $p$ is perpendicular to $P(t)$, its projection is zero, and when $p$ and $P(t)$ point in opposite directions, its projection is negative. Equivalently (see Eq. 2c), the influence of position at $P(t)$ equals the length of $p$ times the length of $P(t)$ times the cosine of the angle between $p$ and $P(t)$.

For similar reasons, $v$ was called the velocity sensitivity vector and its direction, $\theta_v$, was called the preferred velocity direction. It determines the influence of velocity via projection as illustrated in Fig. 9, bottom right. In this instance, the influence of velocity was stronger than the influence of position. It is important to remember that the relative influences of position and velocity will change over time as the eye-position and eye-velocity vectors $P(t)$ and $V(t)$ change with respect to $p$ and $v$. Thus the influence of position will exceed that of velocity when $P(t)$ is more nearly aligned with $p$, and when $V(t)$ is less aligned with $v$.

Statistical evaluation of the model

Model parameters were fit using standard multilinear regression techniques (Draper and Smith 1981, Press et al. 1992). Examples of the model’s prediction of firing rate over time compared with actual firing levels are shown at the bottom of each panel in Figs. 1, 2, 4, and 5. For neurons studied in the circles and sinusoids task ($n = 69$), regression fits of Eq. 2 were always statistically significant ($R^2_{\text{tot}} = 43.5 \pm 19.5\%$, $P < 0.001$) and lack-of-fit tests were always nonsignificant ($P > 0.05$). Although small deviations from model fits were sometimes observed (Fig. 5), these trends were not systematic and did not suggest a need for transformations of the data.

Other models also were tested. These models will be iden-
ified by their use of position (\(P\)), velocity (\(V\)), and acceleration (\(A\)) terms. Standard statistical approaches were used to select the PV model (Eq. 2) as the most appropriate for explaining the data collected in the present experiments. This choice was based on a lack of change in total \(R^2\) values when acceleration terms were added to the PV model to create the PVA model (\(R^2_{Tot} = 43.5 \pm 19.4\%\)). The PVA model also produced small partial \(R^2\) values for acceleration (0.7 \(\pm\) 2.4%) compared with position (7.2 \(\pm\) 9.7%) and velocity (21.5 \(\pm\) 22.0%). In addition, position and velocity parameters (\(r_x, r_y, n_x, n_y\)) obtained for the PV model and the PVA model were not statistically different (\(P > 0.19, t < 1.5, \text{diff} < 0.06 \pm 0.35\)). The VA model (\(R^2_{Tot} = 38.4 \pm 19.0\%\)) produced smaller total \(R^2\) values than either the PV model or the PVA model for all 69 neurons and many (16/69) showed significant lack of fit. Other neurons (53/69) showed nonsignificant lack of fit based primarily on the velocity term in the VA model. This is supported by the relatively good performance of the V model (\(R^2_{Tot} = 34.4 \pm 19.4\%\)). The improved performance of the VA model over the V model resulted from a weak correlation between eye position and eye acceleration that caused inappropriate loading of ac-

![FIG. 6](http://jn.physiology.org/content/21/6/1884/F6)

**FIG. 6.** Comparisons between responses during CW versus CCW circular pursuit. Horizontal and vertical coordinates of each point are the modulation amplitudes, \(M_{CW}\) and \(M_{CCW}\), for CW and CCW circular pursuit. Diagonal line indicates equal modulation. Points above the diagonal indicate stronger modulation during CCW circular pursuit and points below it correspond to neurons with stronger modulation during CW pursuit. ○, cells with statistically different modulations (\(P < 0.05, \chi^2\) test) for the 2 pursuit directions; ●, cells with nonsignificant differences.

![FIG. 7](http://jn.physiology.org/content/21/6/1884/F7)

**FIG. 7.** Component additivity for CCW and CW pursuit indicated by the similarity of overlaid plots of firing rate modulation during circular pursuit (cir, thick line), the sum of modulations during horizontal and vertical pursuit (h + v, medium line), and the sum of modulations during 45 and 135° diagonal pursuit (d + d, thin line). Data come from the velocity/position, position/velocity, CW, and CCW cells described in Figs. 1, 2, 4, and 5. Left: modulations related to 1 cycle of CCW pursuit; right: modulations related to CW pursuit.

![FIG. 8](http://jn.physiology.org/content/21/6/1884/F8)

**FIG. 8.** Additivity tests for the entire population of 69 neurons. Point near a diagonal indicates component additivity because modulations during circular pursuit equaled the summed response during horizontal plus vertical (●) or 45 plus 135° diagonal (○) pursuit. Left: firing rate modulations in spikes/s; right: response phases in degrees.

![FIG. 9](http://jn.physiology.org/content/21/6/1884/F9)

**FIG. 9.** Examples of the vectors used in Eq. 2. Top: position and velocity vectors, \(P(t)\) and \(V(t)\), specify target motion at time \(t\) along a circular trajectory. Bottom left: how position sensitivity vector, \(\rho\), determines the influence of position via vector projection. Bottom right: how velocity sensitivity vector, \(\nu\), determines the influence of velocity.
celflation parameters when position terms were absent. This is demonstrated by the nearly identical performance of the PA model \( R^2_{\text{Tot}} = 23.8 \pm 15.3\% \) and the P model \( R^2_{\text{Tot}} = 23.5 \pm 15.3\% \) and the relatively reduced performance of the A model \( R^2_{\text{Tot}} = 19.8 \pm 15.0\% \).

Comparison with responses in the frequency task

More detailed evaluations of the model were conducted for 20 neurons studied in both the circles and sinusoids task and the frequency task. Again, fits of Eq. 2 based on the frequency task were significant \( (R^2_{\text{Tot}} = 34.4 \pm 11.2\%, P < 0.001) \) and lack-of-fit tests were nonsignificant \( (P > 0.05) \) for every neuron. Although this task allowed clearer distinctions among position, velocity, and acceleration influences, the PV model (Eq. 2) still produced the most parsimonious description of the data. The addition of an acceleration term in the PVA model produced little change in fit \( (R^2_{\text{Tot}} = 34.8 \pm 10.9\%) \) with small partial \( R^2 \) values for acceleration \( (0.7 \pm 0.8\%) \) compared with values for position \( (5.2 \pm 10.3\%) \) and velocity \( (11.3 \pm 10.1\%) \). Again, differences in position and velocity parameters obtained for the PV model and the PVA model were not statistically different \( (P > 0.83, t < 0.25, \text{diff} = 0.07 \pm 0.13) \).

The VA model \( R^2_{\text{Tot}} = 29.4 \pm 8.5\% \), PA model \( R^2_{\text{Tot}} = 21.1 \pm 10.3\% \), P model \( R^2_{\text{Tot}} = 17.8 \pm 10.7\% \), V model \( R^2_{\text{Tot}} = 24.2 \pm 9.1\% \), and A model \( R^2_{\text{Tot}} = 13.1 \pm 5.8\% \) were associated with reduced performance. These model fits were based on a combination of data collected at several frequencies. To test the stability of the model in estimating position and velocity sensitivities across frequencies, regressions were recomputed at each frequency used in the frequency task. Figure 10 shows results from the 20 neurons studied. Here each line represents data from one neuron, and the flatness of each line indicates the near constancy of position and velocity sensitivities at frequencies from 0.2 to 1.0 Hz. These values were also very similar to the final point in each line that represents the “combined” sensitivity based on data at all frequencies. Analysis of variance tests confirmed that average parameter values at each frequency were not statistically different \( (P > 0.95, F(4, 95) < 0.17) \) and that there were no systematic errors in estimating sensitivities at different frequencies. These results also argue against the presence of strong acceleration influences that would have increased more rapidly with frequency than either position or velocity influences and resulted in systematic deviations from flatness in these curves.

To test the generality of the model in fitting data from different tasks, model parameters computed for the circles and sinusoids task were compared with parameters based on the frequency task. The constancy of position and velocity sensitivities is illustrated in Fig. 11 for three neurons studied first in the circles and sinusoids task, later in the fixation task (see next section) and then in the frequency task. For these three neurons, differences in position direction (black tuning functions) were 9, 6, and 28° for the two pursuit tasks, whereas differences in preferred velocity direction (gray tuning functions) were only 9, 8, and 11°.

Figure 12, A and B, shows parameter comparisons for all 20 neurons studied in the circles and sinusoids and frequency tasks. Although there is some variability, points tend to lie near diagonals that represent parameter equality. Population statistical tests indicated that parameters differences were not statistically different for position magnitude \( (P = 0.96, t = 0.05, \text{diff} = 0.0 \pm 2.2) \), position direction \( (P = 0.38, t = -0.90, \text{diff} = -7.6 \pm 32.8) \), velocity magnitude \( (P = 0.58, t = 0.57, \text{diff} = 5.8\%) \), position direction \( (P = 0.41, t = 0.41, \text{diff} = 5.8\%) \), velocity direction \( (P = 0.06, t = 2.2, \text{diff} = 9.1\%) \), and the relatively reduced performance of the A model \( (R^2_{\text{Tot}} = 19.8 \pm 15.0\%) \).
Fig. 12. Comparisons of model (Eq. 2) parameters obtained for the circles and sinusoids (Cir) task, the fixation (Fix) task, and the frequency (Freq) task. Points near each diagonal indicate similar parameters for the 2 tasks being compared. Magnitude refers to the modulation in spikes/s in the preferred position \( \left(M_{\text{pos}} = M|\rho| \right) \) or velocity \( \left(C, |M_{\text{vel}}| = 2\pi M|v| \right) \) direction during sinusoidal motion \( (M = 5^\circ, f = 0.6 \text{ Hz}) \). Angle refers to the direction of a neuron’s preferred position \( (\angle \rho) \) or velocity \( (\angle v) \) direction in degrees. Here, \( 360^\circ \) was added to some small angles to facilitate comparisons at the \( 0^\circ/360^\circ \) transition. Some parameters did not reach levels of statistical significance in regression fits. Nonsignificant magnitudes are plotted in A and C, but nonsignificant angles have been set to 0 and appear along the axes of B and D.

Comparison with responses in the fixation task

For 51 neurons studied in the circles and sinusoids task, the dependence of firing rate on eye position was independently evaluated in the fixation task. Figure 3 shows the position dependence of the position/velocity neuron during changes in fixation. Comparisons between model fits and average firing rate histograms are shown at the bottom of the right and left panels. For the population of neurons studied, regression fits of fixation task data were always statistically significant \( (R^2 = 18.2 \pm 16.2\%, P < 0.001) \) without significant lack of fit \( (P > 0.05) \). Nonlinearities corresponding to slow declines (“slides”) in firing rate during long periods of fixation were not required for good fits. This may result from a relatively shorter fixation time than used by others.

Correspondences and differences in the position sensitivities measured for pursuit and fixation tasks are illustrated in Fig. 11 for three neurons each studied in all three tasks. The neuron in Fig. 11A had similar preferred position directions of 118, 117, and \( 124^\circ \) in the three tasks. Figure 11B shows a neuron with similar position preferences of 259 and \( 250^\circ \) for the two pursuit tasks but a different preference of \( 221^\circ \) for the fixation task. Data from the CW cell (Fig. 11C) showed similar preferred position directions of 184 and \( 212^\circ \) during the pursuit tasks but showed a large change to \( 112^\circ \) during the fixation task. Some of this change can be attributed to a decline in tuning amplitude during the fixation task. Results from the entire population of neurons studied (Fig.

12, C and D) confirm that parameters obtained for the fixation task and the circles and sinusoids task were similar for some neurons and somewhat different for others. Across the entire population of neurons, parameter differences were not significantly different for either position magnitude \( (P = 0.50, t = 0.68, \text{diff} = 0.4 \pm 4.2) \) or position direction \( (P = 0.75, t = -0.32, \text{diff} = -3.1 \pm 58.7) \). However, the standard deviations of these differences \( (4.2 \text{ spikes/s and } 58.7^\circ) \) were about twice as large as those obtained in comparisons of frequency-task and circles-and-sinusoids-task parameters \( (2.2 \text{ spikes/s and } 32.8^\circ) \). In particular, some neurons showed a statistically significant position dependence exclusively during the circles and sinusoids task \( (n = 9) \), whereas others showed a position dependence exclusively during the fixation task \( (n = 3) \). Non-significant direction parameters have been set to zero and plotted on the axes of Fig. 12D.

Directional tuning function for position, velocity, and pursuit

Directional tuning functions for position, velocity, and pursuit were derived from the model by integrating firing rate along a sinusoidal trajectory from screen center to the end of target motion in a particular direction. These tuning functions take a relatively simple form during sinusoidal pursuit. The position tuning function, \( T_{\text{pos}}(\theta) \), gives the change in firing rate due to position in direction \( \theta \) by

\[
T_{\text{pos}}(\theta) = |M_{\text{pos}}| \cos (\theta - \theta_p)
\]

where \( M_{\text{pos}} = Mp \) is a vector that points in the preferred position direction, \( \theta_p \), with length equal to the modulation in firing rate in that direction for motions of modulation amplitude, \( M \). Similarly, the velocity tuning function, \( T_{\text{vel}}(\theta) \), describes the change in firing rate due to velocity by

\[
T_{\text{vel}}(\theta) = |M_{\text{vel}}| \cos (\theta - \theta_v)
\]

where \( M_{\text{vel}} = 2\pi Mv \) is a vector in the preferred velocity direction, \( \theta_v \), with length equal to the increase in firing rate in that direction. Finally, the pursuit tuning function, \( T_{\text{pur}}(\theta) \), describes the total change in firing rate from baseline during pursuit due to both position and velocity by

\[
T_{\text{pur}}(\theta) = T_{\text{pos}}(\theta) + T_{\text{vel}}(\theta) = |M_{\text{pur}}| \cos (\theta - \theta_{\text{pur}})
\]

Here \( M_{\text{pur}} = M_{\text{pos}} + M_{\text{vel}} \) is a vector pointing in the preferred pursuit direction, \( \theta_{\text{pur}} \), with length equal to the change in firing rate in that direction.

Examples of pursuit tuning functions for the four example neurons (Figs. 1, 2, 4, and 5) are illustrated in Fig. 13. In all instances there was a close correspondence between model predictions (dashed lines) and empirical measurements (solid lines) of pursuit tuning. Model and empirical preferred pursuit directions were highly correlated \( (r = 0.98, \text{slope} = 1.00, \text{intercept} = -3.7^\circ) \) and not significantly different \( (P > 0.25, t = 1.1, \text{diff} = 3.2 \pm 23.2) \) for the 69 neurons studied. Also shown are the \( M_{\text{pos}} \) (thin white arrow), \( M_{\text{vel}} \) (thin dark arrow), and \( M_{\text{pur}} \) (thick dark arrow) vectors that define these functions. As expected, tuning functions for the velocity/position neuron (Fig. 1) indicate a dominant role for velocity and a weaker influence from position. Pursuit tuning was therefore similar to velocity tuning. Position had a slightly stronger influence for the position/velocity neuron (Fig. 2), but velocity influences...
were almost as strong. Pursuit tuning for this neuron reflected
the combined influence of position and velocity. \( M_{\text{pos}} \), \( M_{\text{vel}} \),
and \( M_{\text{pur}} \) vectors for both of these neurons were in close
alignment. The CW (Fig. 4) and the CCW neurons (Fig. 5) had
position and velocity sensitivity vectors with different pre-
ferred directions. For these neurons, the pursuit-tuning vector
\( M_{\text{pur}} \) was obtained by taking the vector sum of \( M_{\text{pos}} \) and \( M_{\text{vel}} \).

Distributions of preferred position, velocity, and pursuit
directions (Fig. 14, right) indicate the existence of preferred-
direction vectors in all quadrants with a slight preference for
ipsilateral (0°) and down (270°) directions, particularly for
velocity. Comparisons among preferred position, velocity,
and pursuit directions (Fig. 14, left) indicate a close correspondence
among preferred directions for pursuit, position, and velocity for
some neurons, and clear differences for other neurons
particularly for position and velocity.

Figure 15 quantifies the relative strengths of position and
velocity influences for all 69 neurons using two measures. Left
compares position and velocity partial \( R^2 \) values based on
regression fits of Eq. 2. Average partial \( R^2 \) values were 11.9 ±
14.7% for position and 21.4 ± 21.9% for velocity. Right
compares the position and velocity modulation amplitudes
during circular pursuit. The average position modulation am-
plitude (\( |M_{\text{pos}}| \)) was 6.7 ± 6.8 spikes/s and the average velocity
modulation amplitude (\( |M_{\text{vel}}| \)) was 11.9 ± 13.1 spikes/s. A
comparison of these two averages indicates that 36% of the
average firing rate can be attributed to the influence of position
and the remaining 64% to velocity. Both show that both
position and velocity played significant roles in determining

**FIG. 13.** Tuning functions for the velocity/position,
position/velocity, CW, and CCW cells de-
scribed in Figs. 1, 2, 4, and 5. Left: computed
(dashed lines) and observed (thick lines) pursuit
tuning functions are in good agreement. Right: \( M_{\text{pos}} \)
(small open arrowhead) and \( M_{\text{vel}} \) (small filled arrow-
head) sum to create \( M_{\text{pur}} \) (large filled arrowhead with
thicker line). They define a parallelogram with area
related to the difference in modulation during CW
vs. CCW circular pursuit.

**FIG. 14.** Left: scatter plots comparing preferred directions for position and
velocity, position and pursuit, and velocity and pursuit. Right: distributions of
\( M_{\text{pos}} \), \( M_{\text{vel}} \), and \( M_{\text{pur}} \) the preferred tuning vectors for position, velocity, and
pursuit.

**FIG. 15.** Scatter plots showing the relative influence of eye position vs. eye
velocity in determining responses during circular pursuit. Left: percentage
partial \( R^2 \) values for position vs. velocity. Right: modulation amplitudes during
circular pursuit due to position (\( |M_{\text{pos}}| \)) and velocity (\( |M_{\text{vel}}| \)).
firing rate during circular pursuit although velocity had a stronger influence.

These values are based on pursuit at 0.6 Hz along trajectories with modulation amplitudes of 5°, values associated with the mid- to upper-range of accurate pursuit behavior. It should be emphasized that the relative influence of position and velocity depend on the velocity, amplitude, and frequency of target motion. The model predicts that the ratio of modulations during sinusoidal or circular pursuit due to position and velocity will be

\[ \frac{|M_{pos}|}{|M_{vel}|} = \frac{\rho}{2 \pi \sqrt{|\rho|}} \] (6)

As expected, this equation indicates that the relative roles played by position and velocity are related to the lengths of \( \rho \) and \( \nu \), the position and velocity sensitivity vectors of the neuron. In addition, the influence of position will tend to be dominate at lower frequencies when velocities are lower, and the influence of velocity will tend to dominate at higher frequencies when velocities are higher.

Model description of rotation direction preferences

Figure 16 shows computer simulations that provide an intuitive explanation of how the model combined position and velocity influences to produce responses during circular pursuit. Responses from the velocity/position cell (Fig. 1) were produced by a dominant sensitivity to downward eye velocity that caused the neuron to fire at leftward locations during CCW pursuit and at rightward locations during CW pursuit. A weak sensitivity to downward eye position caused responses during circular pursuit to rotate slightly toward downward locations.

The position/velocity cell (Fig. 2) had more complicated firing patterns. Although its position and velocity sensitivities were aligned, interactions between them were stronger because they were nearly equal in amplitude. Its position sensitivity caused firing increases at leftward locations for both rotation directions. In contrast, its velocity sensitivity increased firing rates along the upper trajectory during CCW pursuit and the lower trajectory during CW motion. Their combination resulted in a shift in the point of maximal modulation so that increases were maximal along the top left part of the CCW trajectory and along the bottom right part of the CW trajectory. Even so, modulation amplitudes were again similar during CCW and CW pursuit because position and velocity influences overlapped in a similar fashion during the two directions of circular pursuit.

The CW cell (Fig. 4) showed interactions between position and velocity input that produced stronger modulations in firing rate during CW rotation and weaker modulations during CCW rotation. Position and velocity responses tended to reinforce during CW pursuit and to cancel during CCW pursuit. This cell did not show the largest differences in CW and CCW pursuit because its position and velocity sensitivities were in almost opposite directions.

The CCW cell (Fig. 5) showed larger differences between CW and CCW pursuit than the CW cell because its preferences for position and velocity were nearly perpendicular. The influence of eye position produced maximal firing to the right during both CW and CCW pursuit. In contrast, the influence of eye velocity generated maximal increases to the right during CCW pursuit and to the left during CW pursuit. When summed, these two influences strongly reinforced each other during CCW pursuit and nearly cancelled each other during CW pursuit.

The modulations during CW and CCW pursuit predicted by Eq. 2 are

\[ M_{CW} = (|M_{pos}|^2 + |M_{vel}|^2 + 2|M_{pos}||M_{vel}|| \sin (\theta_p - \theta_v)|)^{1/2} \] (7)

\[ M_{CCW} = (|M_{pos}|^2 + |M_{vel}|^2 - 2|M_{pos}||M_{vel}|| \sin (\theta_p - \theta_v)|)^{1/2} \] (8)

where \( M_{CW} \) and \( M_{CCW} \) are the modulation amplitudes during CW and CCW pursuit. The dual roles of amplitude and direction become more apparent when Eqs. 7 and 8 are squared and then subtracted so that

\[ \frac{|M_{pos}|}{|M_{vel}|} = \frac{\rho}{2 \pi \sqrt{|\rho|}} \]

FIG. 16. Graphic explanation of how the model explains CW vs. CCW modulation differences for the velocity/position, position/velocity, CW, and CCW cells described in the text. In each panel, the total response during circular pursuit (left) equals responses due to position (middle) and velocity (right) influences. Curved arrows indicate the direction of circular pursuit for all 3 plots. Straight arrows indicate the direction of position and velocity sensitivities. The radius of each small circle represents firing rates above (open circles) and below (filled circles) zero at points along the eye trajectory. Firing rates due to position and velocity are each added to half the baseline level so that their sum produces the full baseline level for the total response. Contra-lateral is to the left and ipsilateral is to the right.
when \( \mathbf{p} \) and \( \mathbf{v} \) are orthogonal \( (\theta_p - \theta_v = \pm 90^\circ, \text{Fig. 13D}) \); modulation differences then decline as the angle between \( \mathbf{p} \) and \( \mathbf{v} \) increases (Fig. 13C) and then return to zero when \( \mathbf{p} \) and \( \mathbf{v} \) point in opposite directions \( (\theta_p - \theta_v = 180^\circ) \). Specific conditions must occur for modulation to be completely eliminated in one rotation direction: \( \mathbf{M}_{\text{pos}} \) and \( \mathbf{M}_{\text{vel}} \) must be equal in length and orthogonal (Fig. 13D). Figure 17 quantifies these ideas for the entire population of 69 neurons. It indicates that predictions of the model based on Eq. 9 are in good agreement with the differences in modulation observed experimentally. This plot also shows the relatively wide and continuous distribution of rotation preferences across the population of neurons studied.

### Anatomic location of neurons

The anatomic locations of the 69 neurons studied are shown in Fig. 18. We found responsive neurons in four regions: the flocculus, the ventral paraflocculus, the lobulus petrosus, and the dorsal paraflocculus (Larsell 1970). The posterolateral fissure was used to mark the division between the flocculus and the ventral paraflocculus and the lobulus petrosus was used to indicate the transition from ventral paraflocculus to dorsal paraflocculus. Most of the neurons were localized to the flocculus and the ventral paraflocculus with a smaller number found within the base of the lobulus petrosus adjacent to the ventral paraflocculus and within the dorsal paraflocculus. There was no obvious correspondence between a neuron’s directional properties and its anatomic location, although there was a tendency for neurons with similar response properties to be in adjacent locations. For example, a clear line of horizontal sites is shown in Fig. 18A.
DISCUSSION

Purkinje cells in the flocculus and paraflocculus showed a variety of responses during circular pursuit. Some showed relatively simple responses that were maximal for a particular direction of pursuit and showed similar amplitudes of modulation during CW compared with CCW pursuit. Others showed more complicated responses including preferences for a particular direction of circular pursuit or preferences for either inward or outward target motion. A simple model accounted for all the responses that were observed. It expressed firing rate as a multi-linear function of eye position and eye velocity sensitivities that sometimes pointed in different directions.

Component additivity

Component additivity was observed for all neurons studied. That is, neural modulation during circular pursuit equaled the sum of modulations for circle components. This suggests that the pursuit system can be characterized by its responses along only two axes. Possible choices include the horizontal/vertical and diagonal/diagonal axis pairs used in the present study. The results also demonstrate that it is not generally possible to evaluate a neuron’s response on only one axis even if the axis is a diagonal axis because many neurons had position and velocity sensitivity vectors that were not aligned. For sinusoidal motions, this implies that the phase of a neuron’s response can differ with spatial direction as well as its gain.

Theoretically, component additivity is compatible with the hypothesis that the pursuit system satisfies approximate spatial linearity, at least for the ranges of position and velocity values that were studied. This allowed modeling of the relationship between neural firing rate and eye motion using a relatively simple class of multilinear functions. Whether spatial linearity holds for a larger range of values will require additional experimentation. Linearity clearly will fail for very large values of target position and velocity, but it is also possible that pursuit behavior will break down at the point where linearity fails. Such a breakdown in pursuit performance was observed in the present studies. This suggests that Purkinje cell firing rates may be modeled adequately by a multilinear system for a “normal” range of velocities that allow accurate pursuit behavior with minimal saccadic intrusion. Pursuit behavior also shows good linearity for this range of target velocities during circular pursuit (Collewijn and Tamminga 1984; Deno et al. 1995; Kettner et al. 1996; Leung and Kettner 1997) although velocity gain declines and saccade frequency increases at higher velocities.

Model of neural firing rate that allows 2D interactions between position and velocity influences

Complex interactions between position and velocity influences with different spatial directions were simulated using a model that expressed the instantaneous neural firing rate in terms of the instantaneous position and velocity of the eye. The model quantified position and velocity influences during pursuit with two sensitivity vectors. A position sensitivity vector pointed in the preferred position direction of the neuron and had a magnitude equal to its position sensitivity in that direction. A velocity sensitivity vector had a magnitude equal the velocity sensitivity of the neuron in its preferred velocity direction. This approach represents an extension to 2D motions of 1D analyses of pursuit and ocular following in the flocculus and paraflocculus (De Zeeuw et al. 1995; Gomi et al. 1998; Lisberger and Fuchs 1978; Lisberger et al. 1994; Miles et al. 1980; Shidara et al. 1993; Stone and Lisberger 1990; Zhang et al. 1995), the vestibular nucleus (McFarland and Fuchs 1992; Scudder and Fuchs 1992; Stahl and Simpson 1995b; Tomlinson and Robinson 1984), and the abducens nucleus (Fuchs et al. 1988; Keller 1973; Stahl and Simpson 1995a).

The model produced good estimates of the instantaneous firing rate of each neuron during circular pursuit as well as during sinusoidal pursuit at several frequencies using a single set of baseline, position, and velocity sensitivity parameters. As expected, neurons with aligned position and velocity sensitivity vectors had simpler responses and showed similar modulations during CW and CCW circular pursuit. In contrast, neurons with nonaligned position and velocity sensitivity vectors of comparable amplitude showed responses that were more complicated including preferences for either CW or CCW pursuit. A natural consequence of the model is that position and velocity influences act via vector projection. This property produces cosine tuning for position, velocity, and pursuit.

Position and velocity influences in flocculus and paraflocculus

Our analyses indicate that the firing rates of most flocculus and paraflocculus Purkinje cells are correlated with both the position and velocity of the eye. Velocity played a somewhat stronger role (64%) than position (36%) in determining firing rate modulation during circular pursuit but did not play an exclusive role. Preferred position directions tended to be uniformly distributed throughout the 2D directional space as also reported by Noda and Suzuki (1979). Preferred velocity directions were concentrated in the ipsilateral and downward directions in agreement with previous studies (e.g., Krauzlis and Lisberger 1996; Lisberger and Fuchs 1978; Lisberger et al. 1994; Miles et al. 1980; Stone and Lisberger 1990).

Interestingly, position and velocity influences sometimes pointed in different directions. Zhang et al. (1995) also observed differences between the ON direction of eye position and the direction of eye velocity sensitivity in the vestibular nuclei of squirrel monkeys. Studies of neural responses during a variety of other motor behaviors also have observed different responses for different spatial directions of motion. These studies used optokinetic (Gomi et al. 1998; Shidara et al. 1993; Zhang et al. 1995), head rotation (Angelaki 1991; Baker et al. 1984; Schor and Angelaki 1992), and arm movement (Georgopoulos and Massey 1985; Kittner et al. 1988) paradigms.

For motion of constant amplitude, the model indicates that the relative influence of velocity versus position will be stronger during higher velocity pursuit and weaker during lower velocity pursuit. A tendency for position influences to dominate at lower velocities and velocity influences to dominate at higher velocities was previously reported by Noda and Warabi (1982). This idea also may account for the emphasis placed on velocity control in other reports. The peak velocity used for most stimuli in the present study was lower (19°/s) than peak velocities used by Lisberger and Fuchs (1978, 51°/s), Miles et al. (1980, 25°/s), Stone and Lisberger (1990, 31°/s), and Krauz-
lis and Lisberger (1996, 31°/s). These studies also tended to focus on “gaze velocity” Purkinje cells that may turn out to be more sensitive to eye velocity.

Some reports (Lisberger and Fuchs 1978; Lisberger et al. 1994; Miles et al. 1980; Stone and Lisberger 1990) show broad distributions of response phase for individual neurons. Although these distributions peak near eye velocity, many neurons have phases that either lead or lag eye velocity by as much as 90°. Phase lags are compatible with a combination of position and velocity coding, whereas phase leads generally have been associated with the combined influence of velocity and acceleration. However, at the target accelerations used in the present experiments, acceleration had only a weak influence on firing rate. In these paradigms, phase leads were produced instead by position and velocity influences that acted in different directions. This does not rule out a role for acceleration influences in other paradigms that require larger eye accelerations or that study pursuit initiation.

**Position and velocity influences in pursuit behavior**

Behavioral experiments indicate that accurate pursuit is generated using a combination of position and velocity control. Early experiments by Rashbass (1961) clearly established the role of target velocity in controlling pursuit using a step-ramp paradigm. Lisberger and Pavelko (1989) later varied step size while keeping ramp velocity constant and showed that initial target position also influenced pursuit albeit 20 ms after movement initiation. Other experiments have demonstrated that smooth eye movements are elicited by stabilized retinal-position errors created using off-fovea photoflash afterimages (Kommerell and Taumer 1972) or eye-motion feedback (Pola and Wyatt 1980). Subsequent experiments (Morris and Lisberger 1987) have demonstrated that both retinal-position and retinal-velocity errors produce changes in eye motion when the eye is pursuing a target immediately before image stabilization. Flocculus and paraflocculus sensitivities to both eye position and eye velocity are compatible with a role in generating this position/velocity control.

There is also evidence for differences in the control of fixation and pursuit. Robinson et al. (1986) stated that “fixation is not pursuit at zero velocity” based on the occurrence of oscillations after a step to constant velocity pursuit and the absence of oscillations after a similar step back to zero velocity (see also Luebke and Robinson 1988). Others have shown that target oscillations (Goldreich et al. 1992) and target perturbations (Schwartz and Lisberger 1994) have a smaller effect during fixation than during pursuit. Morris and Lisberger (1987) have demonstrated that stabilized retinal-position error plays a reduced role when the eye is fixating a target and a stronger role when the eye is pursuing a target. Interestingly, Krauzlis and Miles (1996) report that the behavioral context can also influence transitions to fixation. Offset oscillations were not observed on blocks of trials where the target always stopped but did occur when the target only sometimes stopped or changed direction or speed. These differences in fixation and pursuit may reflect the combined influence of different neural systems. Recently neural responses in the superior colliculus have been related to tracking errors during pursuit eye movements in addition to its responses related to saccades (Krauzlis et al. 1997). This suggests its possible role in pursuit eye movements in addition to those regions more commonly associated with pursuit. The present experiments suggest that some neurons in the flocculus and paraflocculus have different sensitivities to static position during fixation and dynamic position during pursuit. These differences may reflect a partial separation in the control of fixation and pursuit within these brain regions.

**Coordination of position and velocity signals during complex motor control**

At the level of the motoneuron, a combination of position and velocity signals acting in different directions generally are required to produce smooth eye motion. The only time position and velocity influences are aligned is during radial motions away from the origin (e.g., rightward motion to a rightward location). During radial motions toward the origin (e.g., leftward motion to a rightward location) position and velocity signals point in opposite directions. The position and velocity control signals required for circular motion are always at right angles to each other while they vary continuously in time. For example, during CW pursuit a combination of downward velocity and rightward position signals must grade smoothly into signals reflecting a combination of leftward velocity and downward position. These signals are reminiscent of our recordings in the flocculus and paraflocculus during pursuit: position and velocity influences are aligned for some neurons, nearly opposite for others, and approximately orthogonal for still others. Other position/velocity combinations are required for more complicated motions in 2D space.

All models of the pursuit system acknowledge the need to provide a coordinated combination of position, velocity, and acceleration signals to motoneurons. That said, most modeling approaches (e.g., Deno et al. 1989, 1995; Kettner et al. 1997; Krauzlis and Lisberger 1989, 1994; Krauzlis and Miles 1996; Robinson et al. 1986; Young 1971) have simplified the control problem by focusing on eye velocity and acceleration and assuming that position information is obtained by integration. This is mathematically defensible because a “perfect integrator” can compute current eye position from an initial eye position and a velocity history. Whether “neural integration” actually is used by the brain systems that control pursuit is an empiric question that has been discussed extensively (Fukushima et al. 1992; Robinson 1989). The presence of position and velocity signals in the flocculus and paraflocculus suggest that these regions could be involved in neural integration during pursuit.

It is also possible that the flocculus and paraflocculus directly generate the position and velocity signals that are used to control eye motion without the need for an independent neural integrator. This might be useful for the control of very slow eye movements where the neural integration of weakly modulated velocity signals could produce large errors. Under these conditions, position control becomes more appropriate than velocity control. The direct calculation of position information by the pursuit system also would increase its processing speed by eliminating any additional time required to perform neural integration. These signals could be combined downstream with signals from other systems to produce accurate pursuit over a wide range of velocities.
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