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Responses of Pigeon Vestibulocerebellar Neurons to Optokinetic Stimulation. II. The 3-Dimensional Reference Frame of Rotation Neurons in the Flocculus

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SUMMARY AND CONCLUSIONS

1. The complex spike activity of Purkinje cells in the flocculus in response to rotational flowfields was recorded extracellularly in anesthetized pigeons.

2. The optokinetic stimulus was produced by a rotating "planetarium projector." A light source was placed in the center of a tin cylinder, which was pierced with numerous small holes. A pen motor oscillated the cylinder about its long axis. This apparatus was placed above the bird's head and the resultant rotational flowfield was projected onto screens that surrounded the bird on all four sides. The axis of rotation of the planetarium could be oriented to any position in three-dimensional space.

3. Two types of responses were found: vertical axis (VA; n = 43) neurons responded best to visual rotation about the vertical axis, and H-135i neurons (n = 34) responded best to rotation about a horizontal axis. The preferred orientation of the horizontal axis was at ~135° ipsilateral azimuth. VA neurons were excited by rotation about the vertical axis producing forward (temporal to nasal) and backward motion in the ipsilateral and contralateral eyes, respectively, and were inhibited by rotation in the opposite direction. H-135i neurons in the left flocculus were excited by counterclockwise rotation about the 135° ipsilateral horizontal axis and were inhibited by clockwise motion. Thus, the VA and H-135i neurons, respectively, encode visual flowfields resulting from head rotations stimulating the ipsilateral horizontal and ipsilateral anterior semicircular canals.

4. Sixty-seven percent of VA and 80% of H-135i neurons had binocular receptive fields, although for most binocular cells the ipsilateral eye was dominant. Binocular stimulation resulted in a greater depth of modulation than did monocular stimulation of the dominant eye for 69% of the cells.

5. Monocular stimulation of the VA neurons revealed that the best axis for the contralateral eye was tilted back 11°, on average, to the best axis for ipsilateral stimulation. For the H-135i neurons, the best axes for monocular stimulation of the two eyes were approximately the same.

6. By stimulating circumscribed portions of the monocular receptive fields of the H-135i neurons with alternating upward and downward largefield motion, it was revealed that the contralateral receptive fields were bipartite. Upward motion was preferred in the anterior 45° of the contralateral field, and downward motion was preferred in the central 90° of the contralateral visual field. Stimulation of the ipsilateral field revealed that upward motion was preferred in both the anterior 45° and central 90°. Stimulation restricted to the posterior 45° of either visual field did not affect the cells' firing rates.

7. These results suggest that the three-dimensional reference frame of the optokinetic system for self-rotation in the flocculus is similar to those of the semicircular canals and eye muscles.

INTRODUCTION

In the accompanying paper (Wylie et al. 1993) it was shown that the complex spike (CS) activity of Purkinje cells in the pigeon vestibulocerebellum (VbC) exhibited direction selectivity in response to a moving largefield visual stimulus. Most neurons were binocular, preferred either the same or opposite directions of largefield motion in the two eyes, and thus responded best to largefield motion resulting from either translation or rotation, respectively. Four functional types were found: descent neurons preferred upward motion in both eyes; ascent neurons preferred downward motion in both eyes; roll neurons preferred upward and downward motion in the ipsilateral and contralateral eyes, respectively; and yaw neurons preferred forward and backward motion in the ipsilateral and contralateral eyes, respectively. The translation cells (descent and ascent) were found in the medial VbC (ventral uvula and nodulus) and rotation cells (roll and yaw) were found in the lateral VbC (flocculus).

Studies of the rabbit VbC have found CS activity of Purkinje cells related to rotation but not translation flowfields in the nodulus and flocculus (Graf et al. 1988; Kano et al. 1990a; Kusunoki et al. 1990). Subsequently, it was demonstrated that the rotation neurons are organized in vestibular coordinates (Graf et al. 1988; Kano et al. 1990b). That is, VbC neurons respond best to visual flow resulting from a head rotation maximally stimulating one pair of semicircular canals. This was demonstrated by Graf et al. (1988), who stimulated VbC neurons in the rabbit with rotational flowfields produced by a "planetarium projector." Graf et al. (1988) described three types of neurons: vertical axis neurons, anterior axis neurons, and posterior axis neurons. The CS activity of vertical axis (VA) neurons in the rabbit VbC was modulated by flowfields that would result from a head rotation maximally exciting the ipsilateral horizontal canal. Like the yaw cells in the pigeon VbC (Wylie and Frost 1991; Wylie et al. 1993), VA neurons responded best to forward and backward in the ipsilateral and contralateral eyes, respectively. The CS activity of anterior axis and posterior axis neurons was modulated by flowfields that would result from a head rotation maximally exciting the ipsilateral anterior canal. Kano et al. (1990a) and Kusunoki et al. (1990) also recorded from the rabbit VbC and, using a tangent screen largefield stimulus, described roll purkinje cells (U/D cells). As we described in the pigeon VbC (Wylie and Frost, 1991; Wylie et al. 1993), the CS activity of U/D

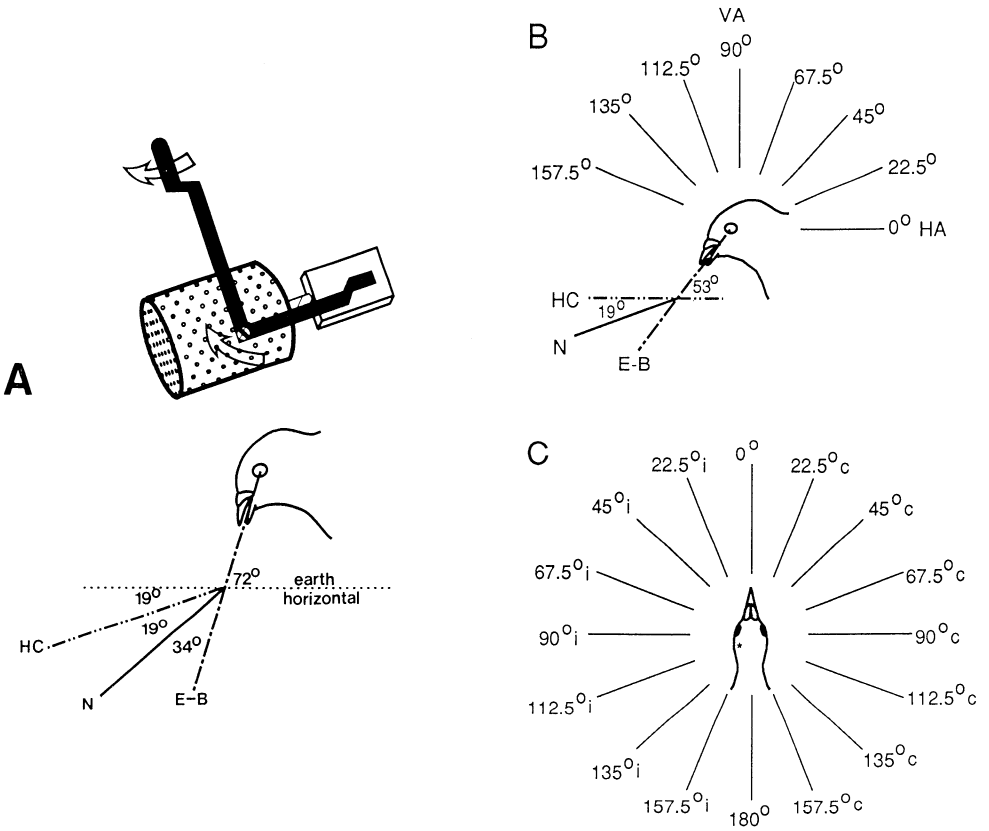


FIG. 1. Orientation of planetarium projector relative to pigeon in stereotaxic coordinates. *A*: with bird's head in stereotaxic apparatus, eye-bill axis (E-B) is 72° down from Earth horizontal, and normal visual horizontal (N) is 38° down from Earth horizontal (Erichsen et al. 1989). Arrows indicate axes of rotation of planetarium. Line representing plane of horizontal canal (HC) is approximately in agreement with value reported by Nalbach et al. (1990). HC is referred to as horizontal axis (HA) and 0° throughout text. *B* and *C*: coordinate systems used for elevation tuning curves and azimuth tuning curves, respectively. VA, vertical axis. *, side of recording site.

cells neurons responded best to upward and downward motion in the ipsilateral and contralateral eyes, respectively. However, in a subsequent study, by stimulating circumscribed parts of the visual field, Kano et al. (1990b) showed that the U/D cells were organized in vestibular coordinates. It was revealed that these cells had bipartite receptive fields in both eyes: upward motion was preferred in the anterior 135° of the ipsilateral hemifield and anterior 45° of the contralateral hemifield, and downward motion was preferred in the posterior 45° of the ipsilateral hemifield and posterior 135° of the contralateral hemifield. The best natural visual stimulus for this receptive field organization is the flowfield resulting from a head rotation maximally stimulating the ipsilateral anterior canal. Thus the U/D cells described by Kano et al. (1990a) and Kusunoki et al. (1990) are equivalent to the anterior axis and/or posterior axis neurons described by Graf et al. (1988). Some neurons in the medial terminal nucleus (MTN; Simpson et al. 1988a), visual tegmental relay zone (VTRZ; Simpson et al. 1988a), and inferior olive (IO; Leonard et al. 1988) are also organized in vestibular coordinates (see also Simpson et al. 1989a,b).

In the previous study (Wylie et al. 1993), the optokinetic stimulus consisted of largefield random dot patterns restricted to the central portion of each visual field, and the anterior and posterior quadrants of each hemifield were not stimulated. Thus it is possible that the roll cells described in the pigeon flocculus have bipartite receptive fields and are organized in vestibular coordinates as in the rabbit VbC (Graf et al. 1988; Kano et al. 1990b). In this study a "planetarium projector" was used to determine whether the roll cells in the pigeon VbC are organized in vestibular coordinates.

This research was part of a Ph.D. dissertation by Douglas R. Wylie.

METHODS

Recordings were obtained from the left flocculus of 20 adult pigeons (*Columba livia*) obtained from a local supplier. Surgical, extracellular recording, and histological procedures were as reported in the companion paper (Wylie et al. 1993).

Stimulus presentation

A "planetarium projector" modeled after that used by Simpson and colleagues (Graf et al. 1988; Leonard et al. 1988; Simpson et al. 1981, 1988a,b, 1989a,b) was constructed to present rotational flowfields. This consisted of a tin cylinder measuring 9.5 cm long and 6.6 cm in diameter. Holes were pierced in the tin cylinder and a 6.5-V incandescent flashlight bulb was positioned in its center. The resultant wholefield stimulus covered the entire visual field with the exception of a circular area at the back of the can, measuring 60° in diameter. The holes subtended 1.5–2.5° to the animal, and there were 25 holes within each circular area 50° across. An additional planetarium was constructed with a sphere 9 cm in

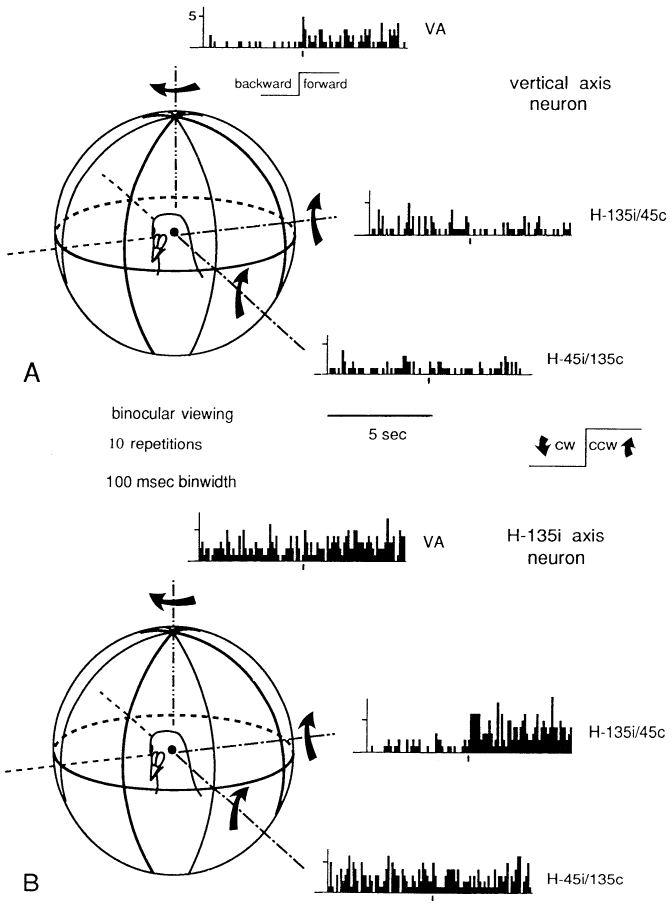


FIG. 2. Peristimulus time histograms (PSTHs) of complex spike (CS) activity of a vertical axis (VA) neuron (*A*) and an H-135i axis neuron (*B*) in response to rotation of planetarium about the 3 canal axes. Ordinate mark, 5 spikes/bin. Large arrows indicate direction of motion for 2nd half of sweep. VA, vertical axis. Note that VA neuron responded best to rotation about vertical axis, and rotation about horizontal axes is less effective. H-135i neuron responded best to rotation about H-135°i/45°c axes, but not to rotation about VA or H-45°i/135°c axes.

diameter. Because the cylinder proved easier to use, and the neurons responded well to each, the cylinder was more often used. The wholefield pattern was projected onto a series of four white screens that surrounded the bird on all four sides at a distance of ~57 cm. (This, however, proved unnecessary; the neurons were as well modulated when the pattern was projected onto the walls of the room).

The shaft of a pen motor (model G320; General Scanning) was attached to the tin can along its longitudinal axis. This assembly was fastened to gimbals such that rotation could occur about any axis in three-dimensional space. The planetarium was suspended above the bird's head as indicated in Fig. 1, which also shows the coordinate system referred to throughout the text. With the bird in stereotaxic coordinates the normal visual horizontal is oriented 38° downward (Erichsen et al. 1989). With the head in this position, we designated the plane of the horizontal canal to be pitched forward ~19° from the Earth horizontal because this was in close agreement with the preferred directions of neurons preferring horizontal (backward) motion in the pigeon nucleus of the basal optic root (nBOR) (Wylie and Frost 1990). This is close to what others have observed to be the orientation of the horizontal canal (Nalbach et al. 1990, 17°; Baldo 1990, 27°; or Erichsen et al. 1989, 23–33°).

The pen motor was driven by a function generator (model 184; Wavetek). Typically a triangular wave was used at a frequency of 0.1 Hz, producing wholefield motion of uniform velocity, with the direction of rotation changing every 5 s. The peak-to-trough amplitude was ~6°; thus the velocity was ~1.2°/s.

The window discriminator produced standardized square-wave pulses, each representing a single spike time, which were stored in a 286 personal computer (Zenith) to produce peristimulus time histograms (PSTHs). Data collection was triggered by the function generator at the peak of the waveform and proceeded for one period.

Once a cell was isolated, a qualitative assessment its preferred axis was made. Elevation and azimuth tuning curves were then determined by varying the orientation of the axis of rotation in 22.5° steps (less frequently, 45° steps were used). Typically, PSTHs were cumulated over 10 sweeps. When possible this was done both for each eye separately (monocular) and with binocular stimulation.

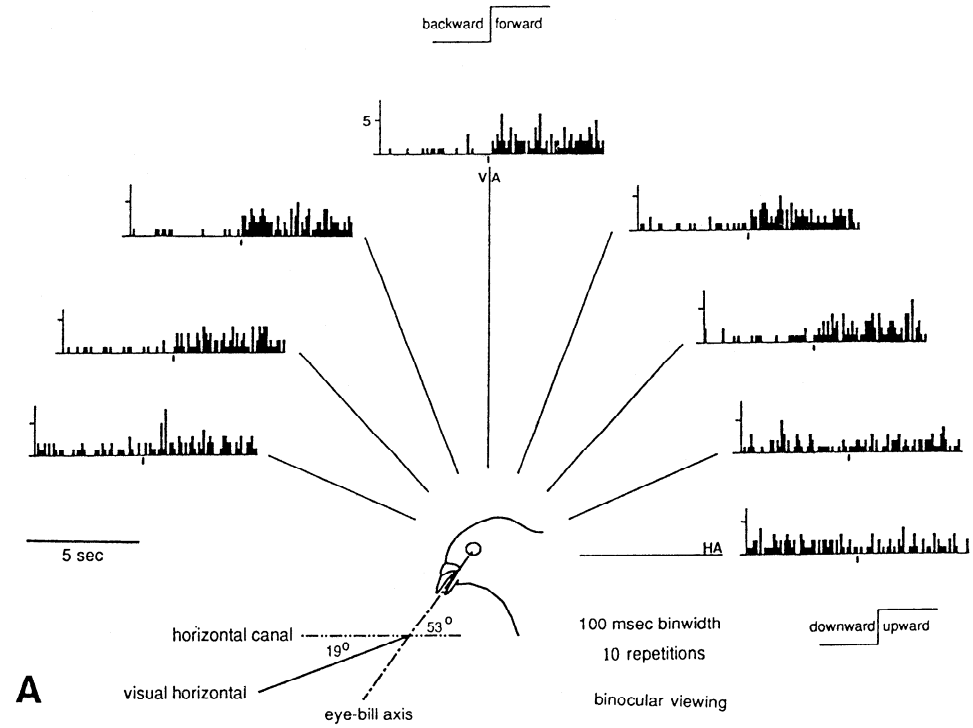
RESULTS

Rotation of the planetarium projector resulted in modulation of the CS activity of Purkinje cells in the flocculus. Cells with both monocular and binocular receptive fields showed maximum depth of modulation to either rotation about the vertical axis (VA neurons) or rotation about the horizontal 135°i/45°c axis (H-135i neurons). The VA and H-135i neurons correspond to the yaw and roll cells we have previously described (Wylie and Frost 1991; Wylie et al. 1993). This new nomenclature has been adopted because roll implies rotation about the longitudinal body axis. As in our previous study, with this preparation simple spike (SS) activity generally was not modulated by the stimulus. CS activity showed broad tuning but, at axes orthogonal to the best axis, little or no modulation occurred (the "null" axes). The responses of typical VA and H-135i neurons to visual rotation about the axes of the three semicircular canals are shown in Fig. 2.

For the H-135i neurons depicted in Fig. 2 and all subsequent figures, clockwise/counterclockwise (cw/ccw) directions of rotation of the visual flowfield are expressed with respect to the exposed eye. For example, a head rotation about the left H-135° axis, in the direction that tilts the head forward and down toward the left side, generally produces upward visual motion in the visual field in the vertical plane anterior to this axis, and downward motion in the vertical plane posterior to this axis. With respect to the pigeon's left eye, this appears as counterclockwise motion about the H-135° axis in the left hemifield. With respect to the pigeon's right eye, this appears as clockwise motion about the H-45° axis in the right hemifield.

VA neurons

Recordings were made from 43 VA neurons. These neurons increased their firing to contraversive (counterclockwise) rotation about the vertical axis. This rotation produced forward motion in the ipsilateral hemifield and backward motion in the contralateral hemifield. Rotation in the opposite direction resulted in strong inhibition. Generally, rotation about an axis orthogonal to this (i.e., horizontal axes) resulted in much less or no modulation of CS activity. For 21 neurons, elevation tuning curves were obtained by varying the inclination of the axis of the planetarium in 22.5° steps within the saggittal plane (i.e., the azimuth was



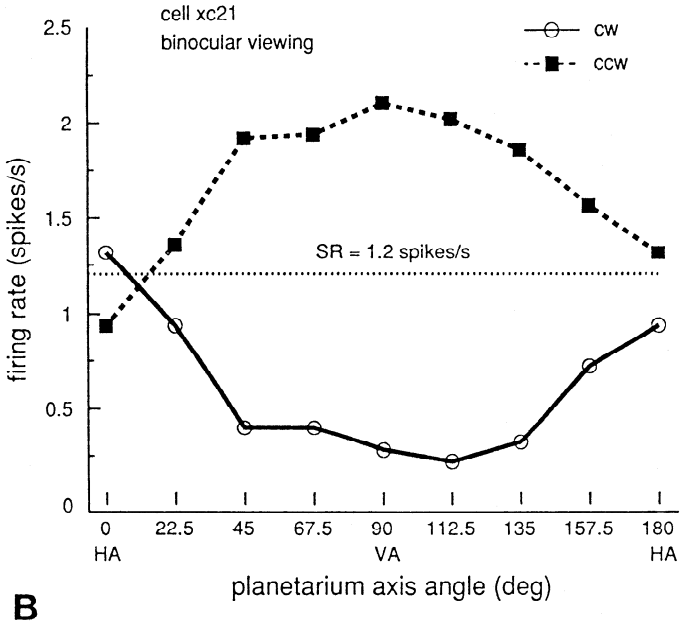


FIG. 3. Binocular elevation tuning curve for a VA neuron. *A*: PSTHs for rotation about each axis. Ordinate mark, 5 spikes/bin. *B*: firing rate, plotted as a function of axis of rotation for clockwise (CW) and counterclockwise (CCW) rotation. Dotted line represents spontaneous rate (SR). VA, vertical axis; HA, horizontal axis. Note that in *B*, complete sine wave tuning curve can be obtained if either CW or CCW profiles are shifted by 180° (e.g., 0° CW = 180° CCW). See text for details.

always 0°; refer to Fig. 1*C*). Both eyes remained exposed. A typical result is shown in Fig. 3. (In *B* of this figure and subsequent similar figures, the complete sine wave tuning can be envisioned by shifting either the counterclockwise or clockwise functions by 180°; i.e., 0° CW = 180° CCW.) This neuron responded best to rotation about axes near the vertical axis, but there was less modulation in response to rotation about axes close to the horizontal axis. However, it is evident from this figure that rotation about the horizontal axis did result in some modulation of the firing rate. The null axis appears to fall close to the 22.5° axis. Given that the best axis is usually ~90° from the null axis, the best axis for this cell was tilted forward to what we have designated as the vertical axis. This was typical for VA neurons. To determine the axis resulting in the maximal depth of modulation (best axis) for individual neurons, we applied a simple curve-fitting procedure to the elevation tuning curves. Each clockwise direction was taken as counterclockwise + 180°, the Fourier fundamental was fit to the tuning curve, and the phase was taken as the best axis (Graf et al. 1988). The resultant best axes for most of the 21 VA neurons, shown in Fig. 4, were tilted forward relative to the vertical axis. The mean best axis was 20.4° anterior to the vertical axis, which is approximately orthogonal to the normal visual horizon-

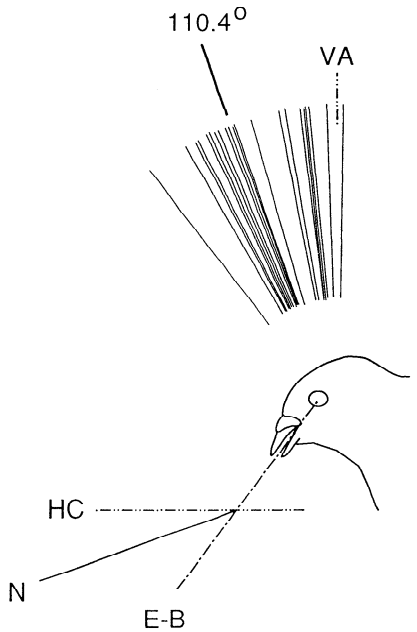


FIG. 4. Best axes for binocular stimulation of VA neurons. Best axes were calculated from best-fit sine waves of the binocular elevation tuning curves. Mean best axis is also indicated. HC, horizontal canal; N, normal visual horizontal; E-B, eye-bill axis. See text for details.

tal (N). That is, the mean preferred and nonpreferred directions of motion were approximately coincident with the normal visual horizon.

OCULAR DOMINANCE For 30 VA cells, ocular dominance was assessed and a seven-point, semiquantitative scale was used to categorize the data. This scale is the same as the five-point scale from Wylie et al. (1993), except monocular groups have been added. An histogram of the number of VA neurons in the seven ocular dominance groups is shown in Fig. 5. Ten cells were monocular: nine ipsilateral and one contralateral. Of the remaining 20 binocular cells, most showed a marked ipsilateral dominance.

For six binocular VA cells, elevation tuning curves were obtained under binocular and monocular viewing conditions. In Fig. 6, the ipsilateral elevation tuning curve (i.e., contralateral eye occluded) and contralateral elevation tuning curve (i.e., ipsilateral eye occluded) are shown for a VA neuron that had a slight ipsilateral dominance. The best axes for each of 12 cells were calculated from the monocular elevation tuning curves and are shown in Fig. 7. Included are data from six binocular and seven monocular cells. Note that the mean best axis for ipsilateral stimulation is tilted forward 11° to that for contralateral stimulation. For each of the six binocular neurons exposed to monocular stimulation of each eye, the best ipsilateral axis was tilted forward relative to the best contralateral axis (mean diff = 11.7°).

For most binocular VA cells tested (13 of 20), binocular stimulation resulted in greater modulation relative to stimulation of the dominant eye alone. This is illustrated for one cell in Fig. 8 that showed a marked ipsilateral dominance. For the other seven cells, the depth of modulation in response to binocular stimulation was similar to that in response to stimulation of the dominant eye alone.

H-135i axis neurons

Recordings were made from 34 H-135i neurons in the left flocculus. These neurons were maximally modulated by rotation about the H-135°i/45°c azimuth axis. For neurons in the left flocculus, an increase in firing rate resulted from counterclockwise rotation about this axis with respect to the left (ipsilateral) eye. This produced a flowfield such that there was upward motion in the ipsilateral hemifield at H-45°i, downward motion in the contralateral hemifield at H-135°c, counterclockwise rotary motion at H-135°i in the ipsilateral hemifield, and clockwise rotary motion about the H-45°c axis in the contralateral hemifield. The opposite direction of rotation resulted in strong inhibition. (For neurons in the right flocculus, the flowfield producing excitation would appear as clockwise rotation about the H-135°i in the right eye, and counterclockwise rotation about the H-45°c in the left eye.) Rotation about axes orthogonal to this, i.e., the vertical axis and the H-45°i/135°c axis, resulted in much less or no modulation of CS activity. Azimuth tuning curves were obtained from 19 cells by varying the horizontal axis of the planetarium in 22.5° steps within the horizontal plane (i.e., the elevation was always 0°; refer to Fig. 1*B*). A typical azimuth tuning curve for a H-135i cell under binocular viewing conditions is shown in Fig. 9. It is clear that rotation about the H-135°i/45°c axis (best axis) resulted in substantial modulation of the firing rate; however, very little modulation occurred to rotation about the H-45°i/135°c axis (null axis). The best axes for 19 H-135i neurons, as calculated from best-fit sine waves of the azimuth tuning curves, are shown in Fig. 10. Note that the best axes cluster about the H-135°i/45°c axis: the mean best axis was H-135.7°i.

OCULAR DOMINANCE. Ocular dominance was tested for 20 H-135i cells and categorized using the seven-point scale. A frequency histogram of ocular dominance group is shown in Fig. 11. Four cells were monocular: three ipsilateral and

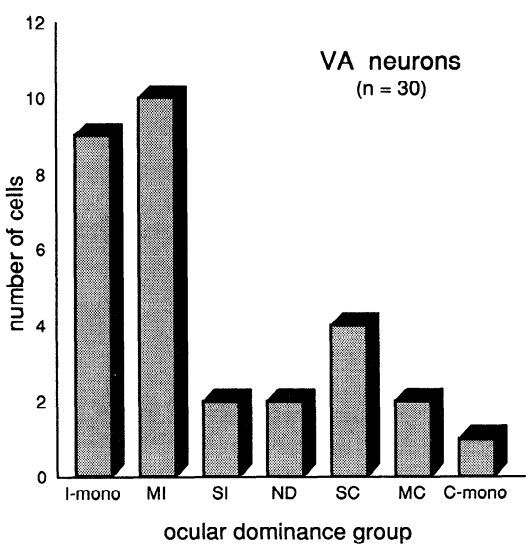


FIG. 5. Frequency histogram of ocular dominance group for VA neurons. I-mono, monocular ipsilateral; C-mono, monocular contralateral; MI, markedly ipsilateral dominant; MC, markedly contralateral dominant; SI, slightly ipsilateral dominant; ND, no dominance. Note that most cells are ipsilateral dominant or monocular-ipsilateral.

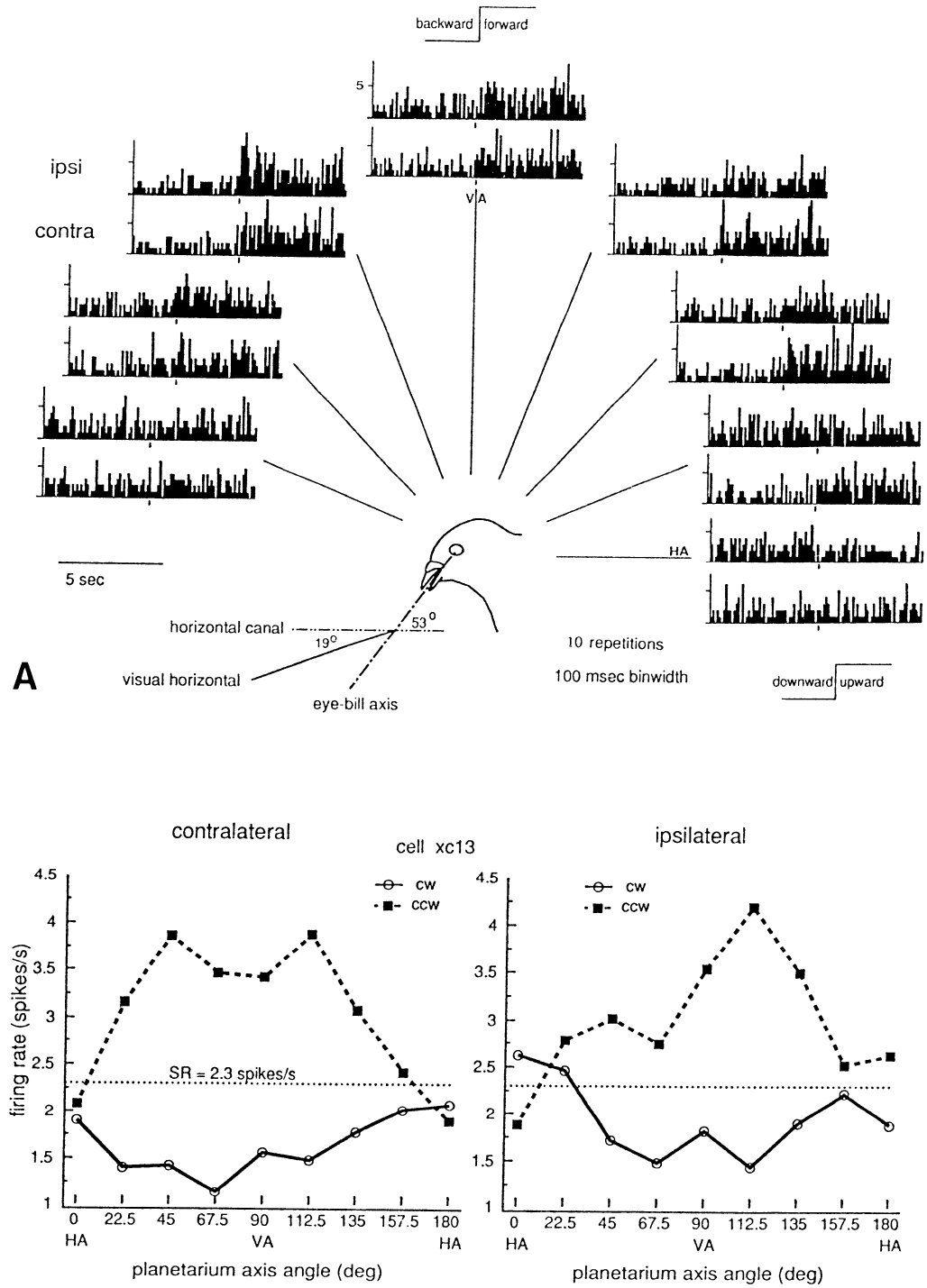


FIG. 6. Ipsilateral and contralateral elevation tuning curves for a VA neuron. *A*: PSTHs for rotation about each axis. Ordinate mark, 5 spikes/bin. *B*: firing rate, plotted as a function of axis of rotation for CW and CCW rotation. Dotted line represents SR. VA, vertical axis; HA, horizontal axis. See text for details.

one contralateral. The remaining 16 were binocular, although most of these showed an ipsilateral dominance.

Azimuth tuning curves for five H-135i binocular neurons were performed under binocular and monocular viewing conditions. Ipsilateral and contralateral azimuth tuning curves for a cell that showed no dominance are shown in Fig. 12. Note that the maximal depth of modulation for ipsilateral and contralateral stimulation occurred in response to the rotation about the H-135°i and H-45°c axes, respectively. In contrast, little modulation occurred in response to rotation about the H-45°i or H-135°c axes. In Fig. 13 the best axes determined from best-fit sine waves of the azimuth tuning curves for ipsilateral and contralateral stimulation are shown for the five binocular cells tested

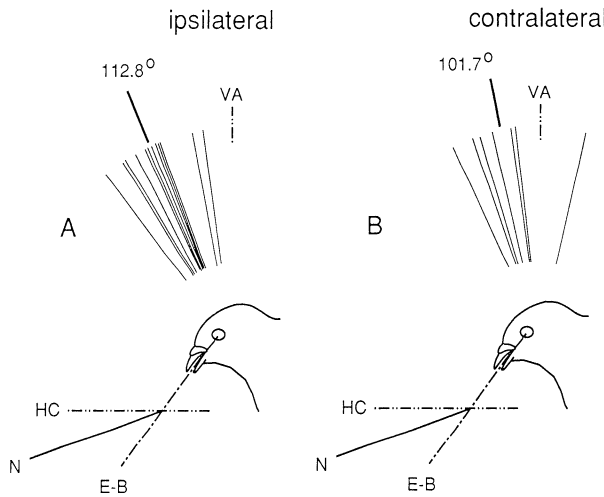


FIG. 7. Best axes for ipsilateral and contralateral stimulation of VA neurons. Best axes were calculated from best-fit sine waves of elevation tuning curves. Mean best axes are also indicated. HC, horizontal canal; N, normal visual horizontal; E-B, eye-bill axis. See text for details.

with monocular stimulation and two ipsilateral-monocular cells. The best axes for ipsilateral stimulation cluster at about H-135°i, and those for contralateral stimulation clustered at about H-45°c. The mean best axes for ipsilateral and contralateral stimulation were H-137.0°i and H-47.8°c, respectively. (Note that these two values represent the same direction about the same axis; i.e., CCW about the 135i° axis = CW about the 45c° axis).

As with the VA neurons, for most H-135i cells tested (11 of 15), binocular stimulation resulted in greater modulation relative to stimulation of the dominant eye alone. In Fig. 14 this is shown for a cell that had a slight contralateral dominance.

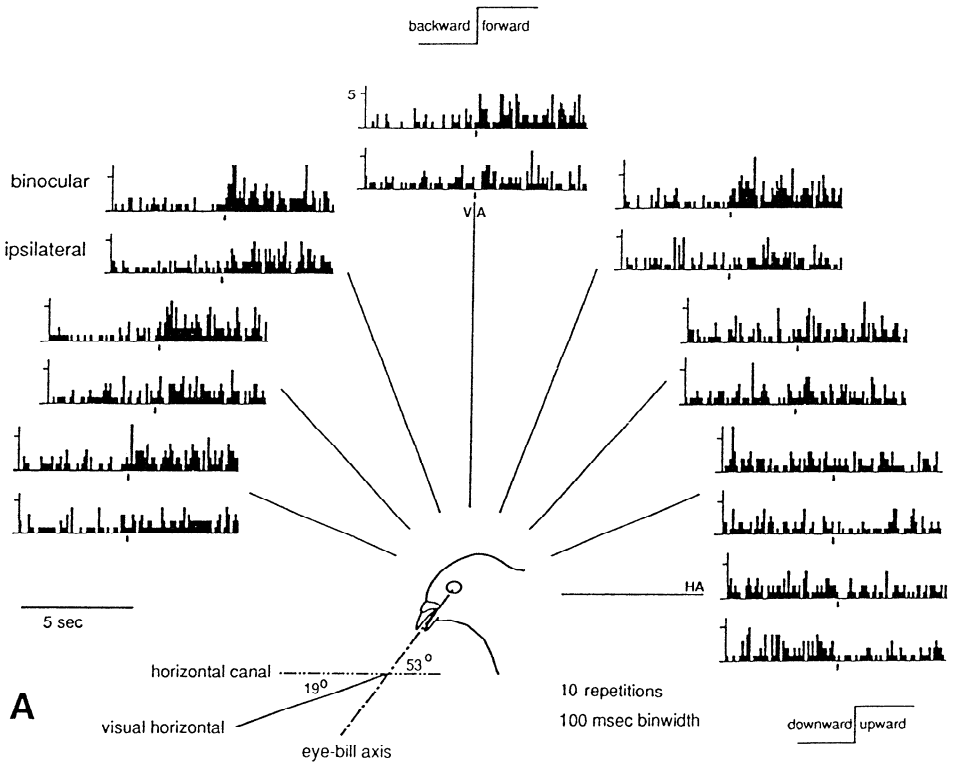
RECEPTIVE FIELD STRUCTURE. The direction selectivity of localized subfields of the receptive fields of eight H-135i neurons (7 binocular and 1 monocular-ipsilateral) were determined by stimulating circumscribed regions of each hemifield with largefield stimuli (the smallest of which measured 45° × 120°). Figure 15 shows the results of a such an investigation for two neurons. The neuron in Fig. 15*A* was presented with alternating upward and downward largefield motion restricted to one of the shaded areas, either the anterior 45°, central 90°, or posterior 45° of the ipsilateral or contralateral hemifield. (The stimulus measured 120° vertically.) For all neurons tested, stimulation of the ipsilateral anterior 45° or central 90° with upward motion increased the firing rate, whereas downward motion inhibited the cell. Stimulation of the ipsilateral posterior 45° did not affect the firing rate of the cell. In every case, in the anterior 45° of the contralateral hemifield, upward motion excited the cell and downward motion caused inhibition. In contrast, in the central 90° of the contralateral hemifield, downward motion excited the cell and upward motion resulted in inhibition. As with the ipsilateral field, stimulation of the contralateral posterior 45° did not produce any response. Figure 15*B* shows the response of a neuron to stimulation of circumscribed areas of the contralateral hemifield with alternating either upward/downward or backward/forward largefield motion. When the stimulus was restricted to the an area anterior to the best axis (i.e., to the anterior 45° of the contralateral hemifield), the neuron was excited by upward motion and inhibited by downward motion. When the stimulus was restricted to the an area posterior to the best axis (i.e., to the central 90° of the contralateral hemifield), the neuron was excited by downward motion and inhibited by upward motion. If these neurons respond to rotation, one would expect that the neuron would be excited by backward visual motion above the best axis. Similarly one would expect that the neuron would be excited by forward motion in an area below the best axis. However, as Fig. 15*B* shows, when the stimulus was restricted to areas above and below the best axis, the neuron was not modulated by alternating forward and backward motion. This suggests that H135i neurons have a "bipartite" receptive field. The receptive field consists of subfields that respond best to opposite directions of vertical motion.

DISCUSSION

This study showed that CS activity of Purkinje cells in the lateral aspect of the VbC (flocculus) of the pigeon was modulated by rotational wholefield visual motion. Neurons could be grouped into two classes on the basis of the preferred axis of rotation. VA neurons responded best to rotation about the vertical axis (yaw rotation), such that there was forward and backward motion in the ipsilateral and contralateral hemifields, respectively. Rotation about horizontal axes resulted in little or no modulation. H-135i neurons in the left flocculus responded best to counterclockwise rotation (with respect to the ipsilateral eye) about the H-135°i/45°c axis. Basically, this rotation produces wholefield motion with an upward component in the anterior 135° of the ipsilateral hemifield and anterior 45° of the contralateral hemifield and wholefield motion with a downward component in the posterior 135° of the contralateral hemifield and posterior 45° of the ipsilateral hemifield. Rotation in the opposite direction inhibited the cell, and rotation about the vertical axis and H-45°i/135°c axes had little affect on the cells' firing rates.

Neurons with strikingly similar properties have been found in the rabbit VbC by Graf et al. (1988) and Kano et al. (1990b). These studies also found VA neurons responding best to forward and backward motion in the ipsilateral and contralateral hemifields, respectively; however, Graf et al. (1988) noted that most VA neurons in the rabbit were monocular, responding only to the ipsilateral eye. This may be because, in the accessory optic system (AOS) of the rabbit, which provides the input to those areas of the IO projecting to the VbC, there are few neurons that prefer backward motion (Maekawa et al. 1984). But neurons responding best to backward wholefield motion are prevalent in the pigeon AOS (Gioanni et al. 1984; Wylie and Frost 1990). Nevertheless, in this study ⅔ of the VA cells showed a marked ipsilateral dominance or were monocular-ipsilateral. Thus, for VA neurons in both the rabbit and pigeon, there is a bias toward ipsilateral dominance.

The finding of neurons responding best to rotation about the H-135°/45°c axis (H-135i neurons) is also in agreement with the findings of Graf et al. (1988) and Kano et al. (1990b) in the rabbit VbC. Graf et al. (1988) described two



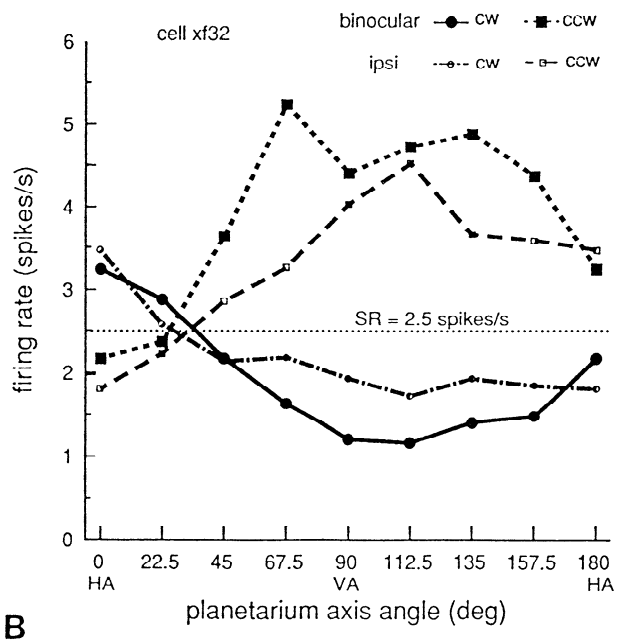


FIG. 8. Comparison of binocular stimulation and stimulation of the dominant eye (ipsilateral) for a VA neuron. Binocular and ipsilateral (dominant eye) elevation tuning curves are shown. This cell was classified as markedly ipsilateral dominant. *A*: PSTHs for rotation about each axis. Ordinate mark, 5 spikes/bin. *B*: firing rate, plotted as a function of axis of rotation for CW and CCW rotation. Dotted line represents SR. VA, vertical axis; HA, horizontal axis. See text for details.

types of neurons responding to rotation about the H-135°i axis: anterior axis neurons and posterior axis neurons. Both types of neurons preferred the same direction of rotation about the H-135°i axis: counterclockwise with respect to the ipsilateral eye. The distinction between anterior axis and posterior axis neurons was based primarily on ocular dominance, but also the inclination of the best axis was slightly different for the two groups. Anterior axis neurons were contralateral dominant and posterior axis neurons were ipsilateral dominant. In the present study, no such distinction was found. Although some H-135i neurons exhibited an ocular dominance, many neurons displayed no dominance (see Fig. 11). There were not enough data available to discern a possible distinction on the basis of the inclination of the best axis.

In the present study, the H-135i neurons were found to have a bipartite receptive field structure, as is the case for some neurons in the rabbit VbC, IO, VTRZ and MTN (Graf et al. 1988; Kano et al. 1990b; Leonard et al. 1988; Simpson et al. 1981, 1988a,b, 1989a,b). With respect to the CS activity of Purkinje cells in the rabbit VbC, the bipartite ipsilateral receptive field responds best to upward motion in

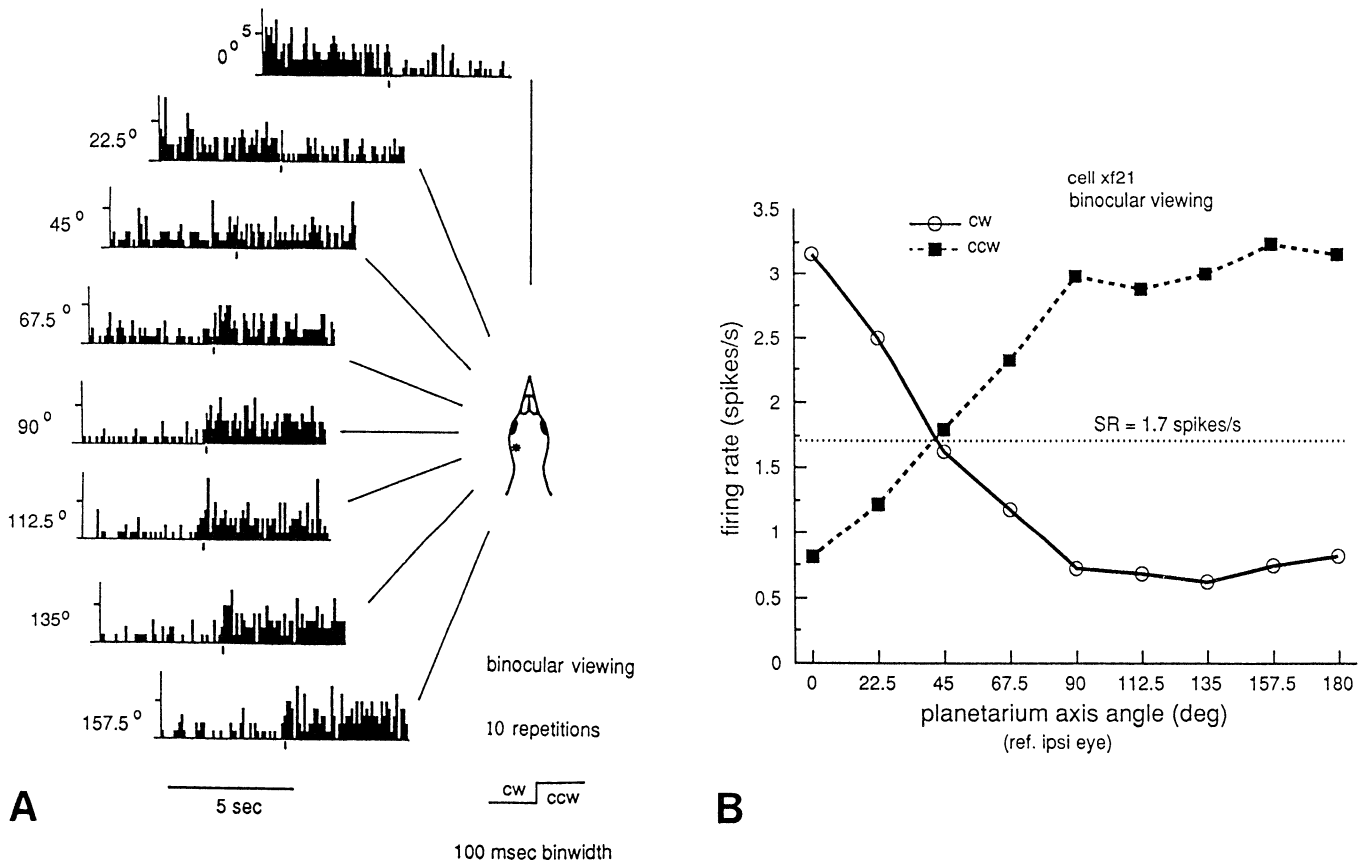


FIG. 9. Binocular azimuth tuning curve for an H-135i neuron. *A*: PSTHs for rotation about each axis. Ordinate mark, 5 spikes/bin. *, side of recording site. *B*: firing rate, plotted as a function of axis of rotation for CW and CCW rotation. Dotted line represents SR. See text for details.

the anterior 135° and downward motion in the posterior 45° of the hemifield, and the bipartite contralateral receptive field responds best to upward motion in the anterior 45° and downward motion in the posterior 135° of the hemifield (Kano et al. 1990b). In the present study only the contralateral field was found to be bipartite, because no responses were obtained from stimulation of the posterior 45° of either hemifield. However, the absence of a response from stimulation of this area may be attributed to the fact that only a small portion of the visual field was stimulated, because the posterior blind field measures ~45° in pigeons (Martin and Young 1983). Also, pieces of the stereotaxic device obscured part of the posterior visual field. It is probable that the ipsilateral receptive fields in the pigeon VbC

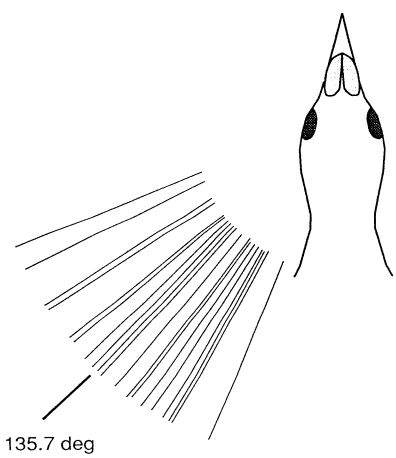


FIG. 10. Best axes for binocular stimulation of H-135i neurons. Best axes were calculated from best-fit sine waves of the binocular azimuth tuning curves. Mean best axis is also indicated. See text for details.

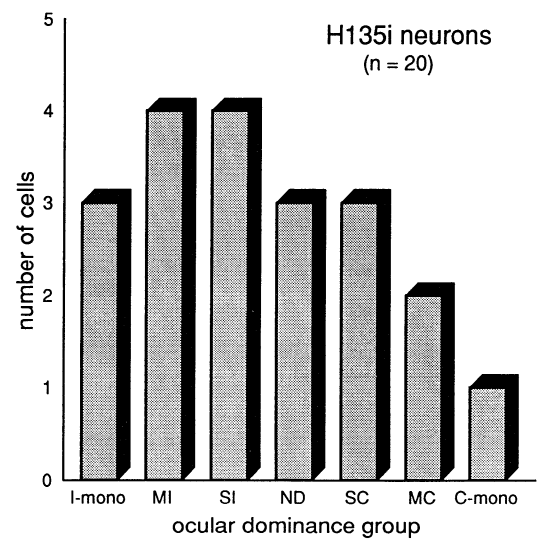


FIG. 11. Frequency histogram of ocular dominance group for H-135i neurons. I-mono, monocular ipsilateral; C-mono, monocular contralateral; MI, markedly ipsilateral dominant; MC, markedly contralateral dominant; SI, slightly ipsilateral dominant; ND, no dominance. Note that most cells are ipsilateral dominant.

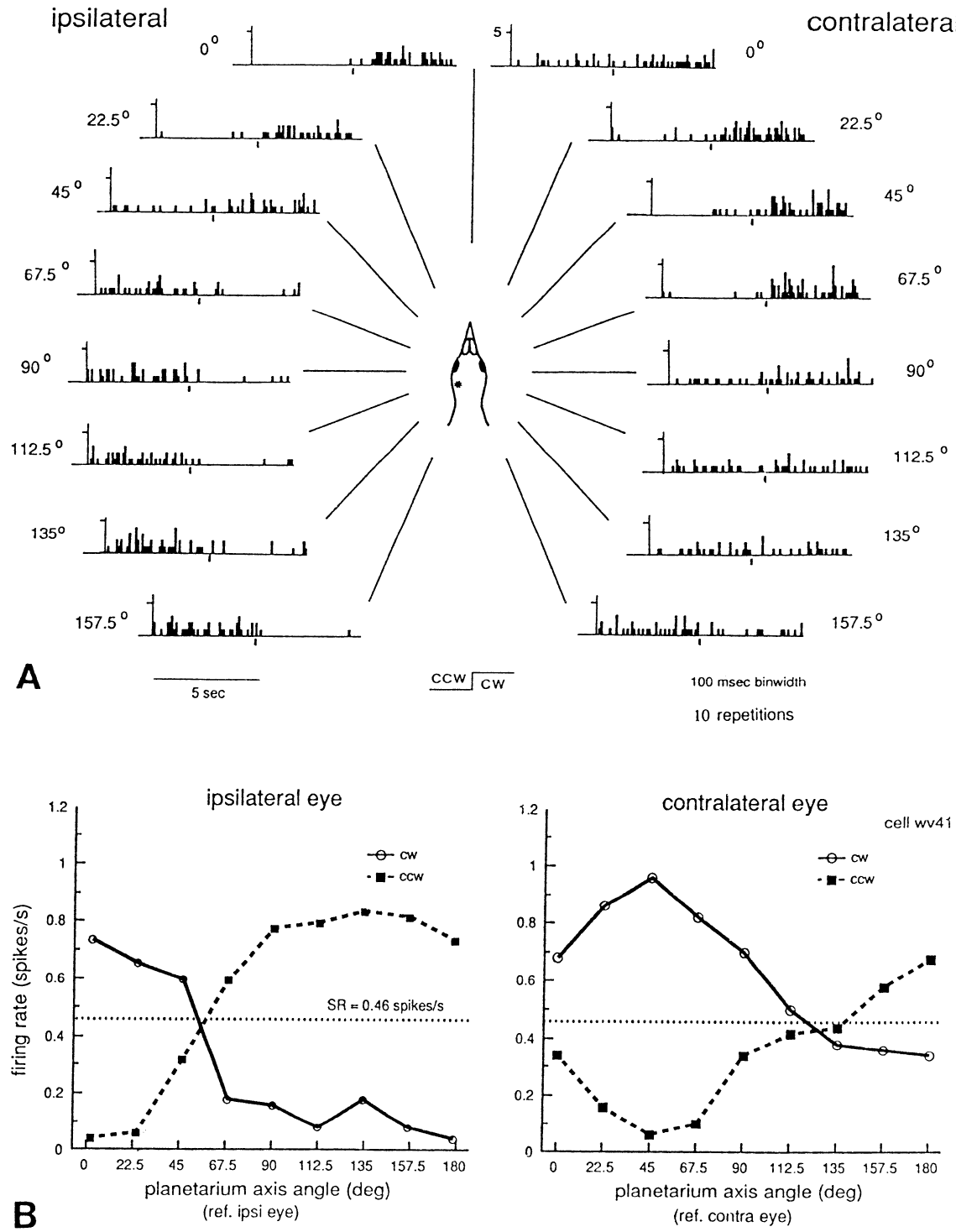


FIG. 12. Ipsilateral and contralateral azimuth tuning curves for an H-135i neuron. *A*: PSTHs for rotation about each axis. Ordinate mark, 5 spikes/bin. *, side of recording site. *B*: firing rate, plotted as a function of axis of rotation for CW and CCW rotation. Dotted line represents SR. See text for details.

were bipartite in view of the fact that the best axis for monocular stimulation of the ipsilateral eye with the planetarium projector was the H-135°i axis.

It should be noted that the boundaries between the upward and downward subfields of the bipartite receptive fields of neurons in the MTN (Simpson et al. 1988a,b), VTRZ (Simpson et al. 1988a,b), and IO (Leonard et al. 1988; Simpson et al. 1981) in the rabbit are not always coincident with the H-135°c/45°i axis. In these studies of the rabbit AOS, using a small spot stimulus moving across different areas of the visual field, several variants of the bipartite receptive field organization were found. For example, for one VTRZ cell, the boundary between the upward and downward subfields was at H-50°i and H-100°c in the ipsilateral and contralateral receptive fields, respectively (Simpson et al. 1988a). Nevertheless, under binocular

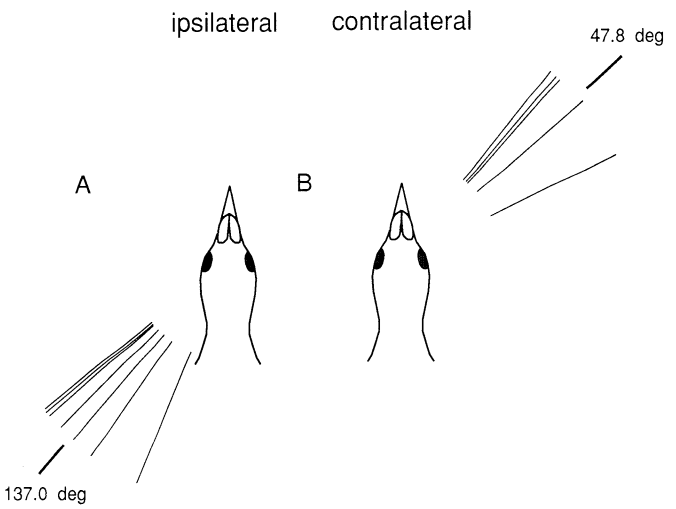


FIG. 13. Best axes for ipsilateral and contralateral stimulation of H-135i neurons. Best axes were calculated from best-fit sine waves of monocular azimuth tuning curves. Mean best axes are also indicated. Note that mean best axes for ipsilateral and contralateral stimulation represent same direction of rotation about same axis; i.e., CCW-137°i = CW-47°i). See text for details.

viewing conditions, this cell responded best to rotation about the H-135°c/45°i axis. It may also be the case in the pigeon VbC that the subfield boundaries within the bipartite receptive fields do not fall exactly at the H-135°i/45°c axis. However, the CS activity of Purkinje cells in the pigeon did not respond adequately to small stimuli to allow such a determination.

Coordinate system of the visual input to the rotation cells in the VbC: semicircular canal or extraocular muscle coordinates?

Because the VbC receives input from both the AOS and the vestibular system, one would expect that both use the same coordinate system. This study has provided evidence that the climbing fiber visual input to rotation cells in the VbC is organized with the respect to the reference frame of the vestibular canals. That is, the CS activity of Purkinje cells in the pigeon VbC responds best to flowfields resulting from a head rotation's maximally stimulating one of the three pairs of the semicircular canals. This is also the case in the rabbit, in which both the CS and SS activity of Purkinje cells are organized in vestibular coordinates (Graf et al. 1988; Simpson et al. 1989a,b). Moreover, stimulation of the rabbit flocculus results in rotation of one or both eyes about either the vertical axis or the H-135°i/45°c axis (Simpson et al. 1989b).

Instead of a reference frame based on the orientation of the semicircular canals, Purkinje cell responses in the flocculus could be organized with respect to the output of the system, which is primarily to extraocular premotor neurons (pigeon, Arends and Zeigler 1991a,b). In fact, Simpson and Graf (1981, 1985) have shown that the extraocular muscles and the vestibular canals have similar spatial frame of reference. That is, the pulling action of a given extraocular muscle is approximately in the plane of the semicircular canal from which it receives its primary input. For example, the line of action of the superior rectus is nearly parallel to the ipsilateral anterior canal, and the line of action of the superior oblique is approximately parallel to the ipsilateral posterior canal. This relationship exists in both lateral- and frontal-eyed animals, which emphasizes its importance: with the evolution of frontal eye placement, the insertion points of the extraocular muscles on the globe changed to preserve the relationship between the semicircular canals and the extraocular muscles (Simpson and Graf 1981, 1985). However, this relationship is only approximate. In the rabbit, for example, the action of the paired vertical recti rotate the eye about the H-148°i, but maximal stimulation of the ipsilateral anterior/contralateral posterior canal pair results from rotation about the H-139°i axis (Simpson et al. 1989a,b). Because of the close correspondence be-

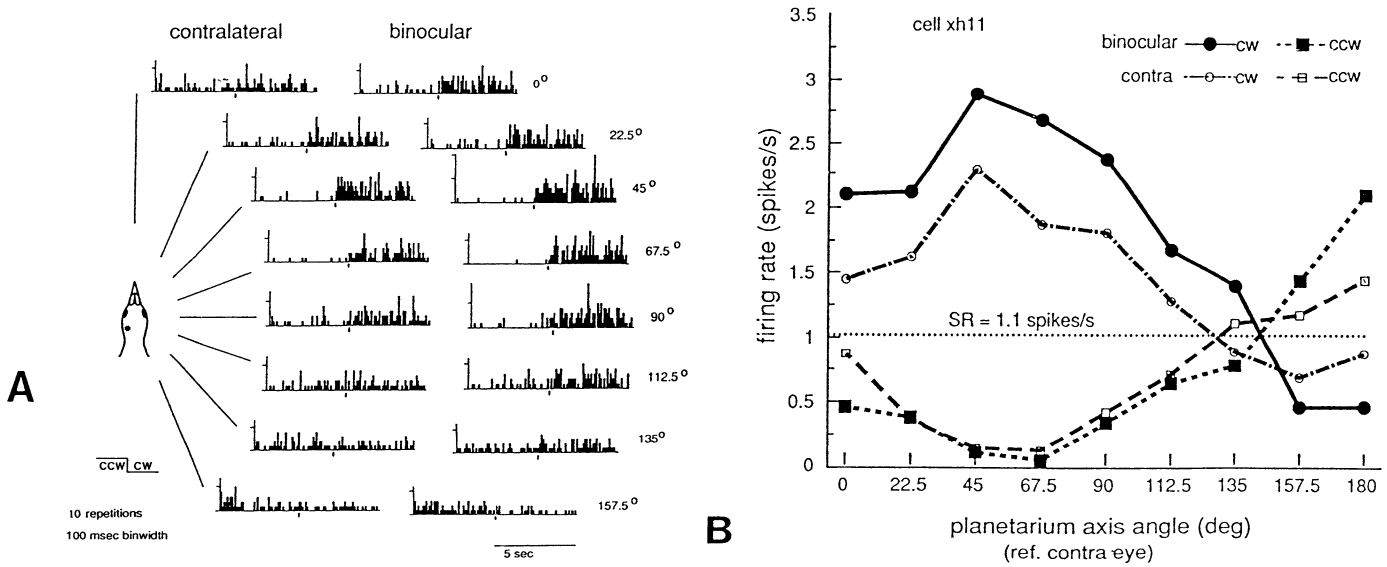


FIG. 14. Comparison of binocular stimulation and stimulation of dominant eye (contralateral) of an H-135i neuron. Binocular and contralateral azimuth tuning curves are shown. This cell was classified as slightly contralateral dominant. *A*: PSTHs for rotation about each axis. Ordinate mark, 5 spikes/bin. *, side of recording site. *B*: firing rate, plotted as a function of axis of rotation for CW and CCW rotation. Note that binocular stimulation resulted in a greater depth of modulation. See text for details.

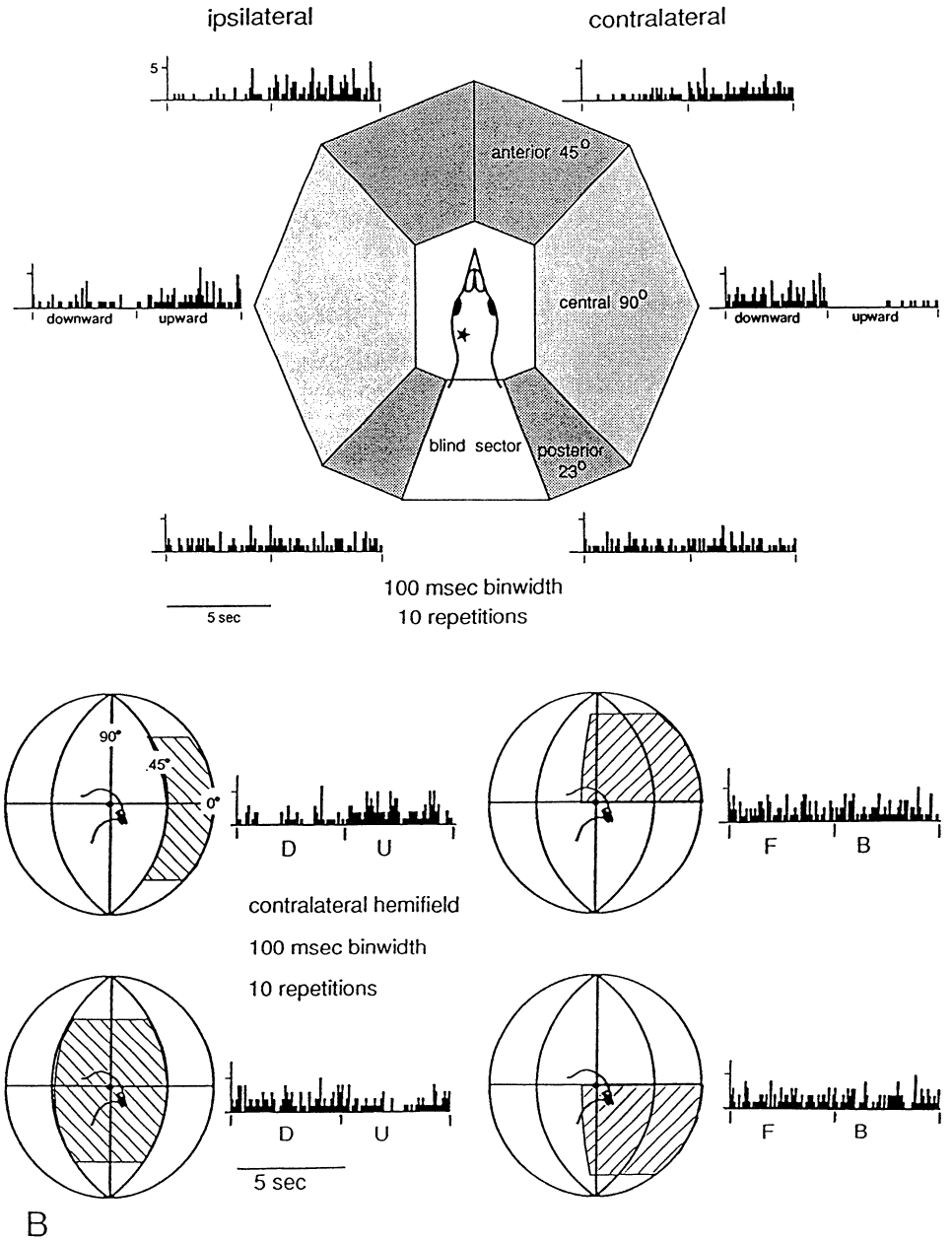


FIG. 15. Bipartite receptive field structure of an H-135i neuron. *A*: separate zones indicated on diagram refer to circumscribed areas of visual field areas that were stimulated with alternating upward and downward largefield motion. Ordinate mark, 5 spikes/bin. *, side of recording site. Blind sector is based on measurements of Martin and Young (1983). Note that cell responded best to upward motion in ipsilateral-central 90°, ipsilateral-anterior 45°, and contralateral-anterior 45°. However, cell responded best to downward motion in contralateral-central 90°. *B*: response of a cell to either *1*) alternating upward and downward motion in front and behind the best axis or *2*) alternating backward and forward motion above and below the best axis. If this neuron truly responded best to rotation, neuron would be excited by backward motion above axis and forward motion below best axis. These data suggest that these rotation-sensitive receptive fields are bipartite, with apposed regions responding to opposite directions of vertical largefield motion.

tween these two systems, it would be very difficult to determine whether the visual inputs are organized with respect to the semicircular canals or extraocular muscles. In fact, the best axis of visual rotation for the posterior axis neurons in the rabbit is H-143°i (Simpson et al. 1989a,b).

In the present study, for the VA neurons it was found that the best axes for the ipsilateral and contralateral eyes were different. The mean best axis for contralateral stimulation was tilted back 11° relative to that for ipsilateral stimulation. That is, the preferred direction for stimulation of the contralateral eye was not collinear to that of the ipsilateral eye, but was, on average, 11° downward. Similarly, in the accompanying paper (Wylie et al. 1993), it was shown for yaw cells that the preferred direction of motion for the contralateral eye was not opposite to that for the ipsilateral eye, but was ~30° downward. Interestingly, Nye (1969) reports that the lines of action of the medial and lateral rectus are not collinear. In the illustration provided by Nye (1969), the line of action of the lateral rectus is ~15° downward from that of the medial rectus. A simple dissection of the pigeon eye illustrates this obvious asymmetry of the horizontal recti. Although definitive conclusions would be premature, the data obtained from ipsilateral and contralateral wholefield stimulation of the VA neurons are consistent with the notion that the visual responses of neurons are organized in eye-muscle coordinates.

The correspondence between the visual, eye muscle, and vestibular reference frames exists as long as the eyes are in their resting position in the orbit. As soon as the eyes change their position in the orbit, the reference frames are no longer aligned. This may not pose a great problem for the pigeon. First, the pigeon's resting eye position is maintained during various behaviors, including walking, perching, and flying (Erichsen et al. 1989). Second, during head-free optokinetic nystagmus much, and at times all, of the optomotor response is accomplished by head movement,

with the eyes remaining relatively stationary within the orbit (Gioanni 1988).

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REFERENCES

ARENDS, J. J. A. AND ZEIGLER, H. P. Organization of the cerebellum in the pigeon (*Columba livia*). I. Corticonuclear and corticovestibular connections. *J. Comp. Neurol.* 306: 221–244, 1991.

ARENDS, J. J. A. AND ZEIGLER, H. P. Organization of the cerebellum in the pigeon (*Columba livia*). III. Corticovestibular connections with eye and neck premotor neurons. *J. Comp. Neurol.* 306: 273–289, 1991b.

BALDO, M. V. C. The spatial arrangement of the semicircular canals of the pigeon. *Braz. J. Med. Biol. Res.* 23: 915–917, 1990.

ERICHSEN, J. T., HODOS, W., EVINGER, C., BESSETTE, B. B., AND PHILLIPS, S. J. Head orientation in pigeons: postural, locomotor and visual determinants. *Brain Behav. Evol.* 33: 268–578, 1989.

GIOANNI, H. Stabilising gaze reflexes in the pigeon (*Columba livia*). I. Horizontal and vertical and optokinctic eye (OKN) and head (OCR) reflexes. *Exp. Brain Res.* 69: 567–582, 1988.

GIOANNI, H., REY, J., VILLALOBOS, J., AND DALBERA, A. Single unit activity in the nucleus of the basal optic root (nBOR) during optokinetic, vestibular and visuo-vestibular stimulations in the alert pigeon (*Columba livia*). *Exp. Brain Res.* 57: 49–60, 1984.

GRAF, W., SIMPSON, J. I., AND LEONARD, C. S. Spatial organization of visual messages of the rabbit's cerebellar flocculus. II. Complex and simple spike responses of purkinje cells. *J. Neurophysiol.* 60: 2091–2121, 1988.

KANO, M., KANO, M.-S., KUSUNOKI, M., AND MAEKAWA, K. Nature of the optokinetic response and zonal organization of climbing fibre afferents in the vestibulocerebellum of the pigmented rabbit. II. The nodulus. *Exp. Brain Res.* 80: 238–251, 1990a.

KANO, M.-S., KANO, M., AND MAEKAWA, K. Receptive field organization of climbing fiber afferents responding to optokinetic stimulation in the cerebellar nodulus and flocculus of the pigmented rabbit. *Exp. Brain Res.* 82: 499–512, 1990b.

KARTEN, H. J. AND HODOS, W. *A Stereotaxic Atlas of the Brain of the Pigeon (Columba Livia)*. Baltimore, MD: Johns Hopkins Press, 1967.

KUSUNOKI, M., KANO, M., KANO, M.-S., AND MAEKAWA, K. Nature of the optokinetic response and zonal organization of climbing fibre afferents in the vestibulocerebellum to the pigmented rabbit. II. The flocculus. *Exp. Brain Res.* 80: 225–237, 1990.

LEONARD, C. S., SIMPSON, J. I., AND GRAF, W. Spatial organization of visual messages of the rabbit's cerebellar flocculus. I. Typology of inferior olive neurons of the dorsal cap of Kooy. *J. Neurophysiol.* 60: 2073–2090, 1988.

MAEKAWA, K., TAKEDA, T., AND KIMURA, M. Responses of the nucleus of the optic tract neurons projecting to the nucleus reticularis tegmenti pontis upon optokinetic stimulation in the rabbit. *Neurosci. Res.* 2: 1–25, 1984.

MARTIN, G. R. AND YOUNG, S. R. The retinal binocular visual field of the pigeon (*Columba livia*: English racing homer). *Vision Res.* 23: 911–915, 1983.

NALBACH, H.-O., WOLF-OBERHOLLENZER, F., AND KIRSCHFELD, K. The pigeon's eye viewed through an ophthalmoscopic microscope: orientation of retinal landmarks and significance of eye movements. *Vision Res.* 30: 529–540, 1990.

NYE, P. The monocular eye movements of the pigeon. *Vision Res.* 9: 133–144, 1969.

SIMPSON, J. I. AND GRAF, W. Eye-muscle geometry and compensatory eye movements in lateral-eyed and frontal-eyed animals. *Ann. NY Acad. Sci.* 374: 20–30, 1981.

SIMPSON, J. I. AND GRAF, W. The selection of reference frames by nature and its investigators. In: *Adaptive Mechanisms in Gaze Control: Facts and Theories*, edited by A. Berthoz and G. Melvill-Jones. Amsterdam: Elsevier, 1985, p. 1–15.

SIMPSON, J. I., GRAF, W., AND LEONARD, C. The coordinate system of visual climbing fibres to the flocculus. In: *Progress in Oculomotor Research*, edited by A. F. Fuchs and W. Becker. Amsterdam: Elsevier, 1981, p. 475–484.

SIMPSON, J. I., GRAF, W., AND LEONARD, C. Three-dimensional representation of retinal image movement by climbing fiber activity. *Exp. Brain Res. Suppl.* 17: 323–337, 1989a.

SIMPSON, J. I., LEONARD, C. S., AND SOODAK, R. E. The accessory optic system of rabbit. II. Spatial organization of direction selectivity. *J. Neurophysiol.* 60: 2055–2072, 1988a.

SIMPSON, J. I., LEONARD, C. S., AND SOODAK, R. E. The accessory optic system: analyzer of self-motion. *Ann. NY Acad. Sci.* 545: 170–179, 1988b.

SIMPSON, J. I., VAN DER STEEN, J., TAN, J., GRAF, W., AND LEONARD, C. S. Representations of ocular rotations in the cerebellar flocculus of the rabbit. In: *Progress in Brain Research*, edited by J. H. J. Allum and M. Hulliger. Amsterdam: Elsevier, 1989b, vol. 80, p. 213–223.

WYLIE, D. R. AND FROST, B. J. Visual response properties of neurons in the nucleus of the basal optic root of the pigeon: a quantitative analysis. *Exp. Brain Res.* 82: 327–336, 1990.

WYLIE, D. R. AND FROST, B. J. Purkinje cells in the vestibulocerebellum of the pigeon respond best to either translational or rotational wholefield visual motion. *Exp. Brain Res.* 86: 229–232, 1991.

WYLIE, D. R., KRIPALANI, T., AND FROST, B. J. Responses of pigeon vestibulocerebellar neurons to optokinetic stimulation. I. Functional organization of neurons discriminating between translational and rotational visual flow. *J. Neurophysiol.* 70: 2632–2646, 1993.