Research Note

Purkinje cells in the vestibulocerebellum of the pigeon respond best to either translational or rotational wholefield visual motion

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Summary. Using standard extracellular techniques, the response properties of neurons in the vestibulocerebellum of the pigeon to movement of a wholefield visual stimulus were determined. Complex spike activity of Purkinje cells was modulated in a direction-selective manner by the stimulus and 94% of cells were binocularly driven. Some neurons preferred the same direction of wholefield motion in both eyes, simulating optic flow which results from self-translation, while others preferred the opposite direction in each eye, simulating optic flow resulting from rotation. Four functional classes of neurons were found: (1) *Descent* cells preferred upward motion in both eyes; (2) *Ascent* neurons preferred downward motion in both eyes; (3) *Roll* cells preferred upward and downward motion in the ipsilateral and contralateral eyes respectively; and (4) *Yaw* cells preferred forward (temporal to nasal) and backward motion in the ipsilateral and contralateral eyes respectively. The observation that these neurons clearly distinguish rotational and translational optic flow patterns suggests they may play an important role in controlling locomotor activities of the pigeon.

Key words: Vestibulocerebellum − Binocular − Rotation − Translation − Pigeon

Movement of the eyes, head or body usually results in motion of the imaged scene across the entire retina in the opposite direction. Several lines of evidence suggest that this "wholefield" visual motion is analyzed by a distinct visual pathway, the Accessory Optic System (AOS), to generate compensatory head and eye movements thereby maintaining a stable retinal image (for review see Simpson 1984). In birds, the AOS consists of two major nuclei; the nucleus of the basal optic root (nBOR) and the pretectal nucleus lentiformis mesencephali (LM). Electrophysiological studies have demonstrated that

avian nBOR and LM neurons respond best to very large stimuli rich in visual texture (i.e. wholefield random dot patterns) moving in a particular direction in the contralateral visual field (Britto et al. 1981; Burns and Wallman 1981; Morgan and Frost 1981; Winterson and Brauth 1985; Wylie and Frost 1990a); however, only a few neurons are binocularly driven (Wylie and Frost 1990b).

Since self-motion results in visual flowfields in both eyes, one might expect that at some point in the AOS, visual information from both eyes would be combined so that flowfields resulting from translation and rotation of the bird could be distinguished. In species with lateral-eyes such as the pigeon, neurons preferring the same direction of optic flow in both visual fields could encode translation, and neurons preferring opposite directions of optic flow in the two eyes could encode rotation. For example, upward motion in both eyes would result from a downward translation or "descent" of the bird. In contrast, upward visual flow in one eye and downward visual flow in the opposite eye would result from self-rotation, specifically a "roll" of the bird.

The pigeon vestibulocerebellum receives bilateral projections from the LM and nBOR, directly via the mossy fibre system and indirectly via the inferior olive through the climbing fibre system (Brecha et al. 1980; Clarke 1977). It would be reasonable to expect that these cells respond best to translational visual flow which would result from ascent, descent, forward and backward motion, or rotational visual flow which would result from roll, pitch and yaw movements of the bird.

In this preliminary report we describe purkinje cells in the pigeon vestibulocerebellum that respond to wholefield stimulation of the visual fields of both eyes. Some neurons responded best to translational optic flow, while others preferred rotational optic flow. Standard extracellular techniques were used to record the complex spike activity of Purkinje cells in the vestibulocerebellum of urethane-anaesthetized pigeons. Details of preparation, stimulus control and recording have been reported elsewhere (Frost et al. 1988; Wylie and Frost 1990a, 1990b). Two large tangent screens were oriented parallel
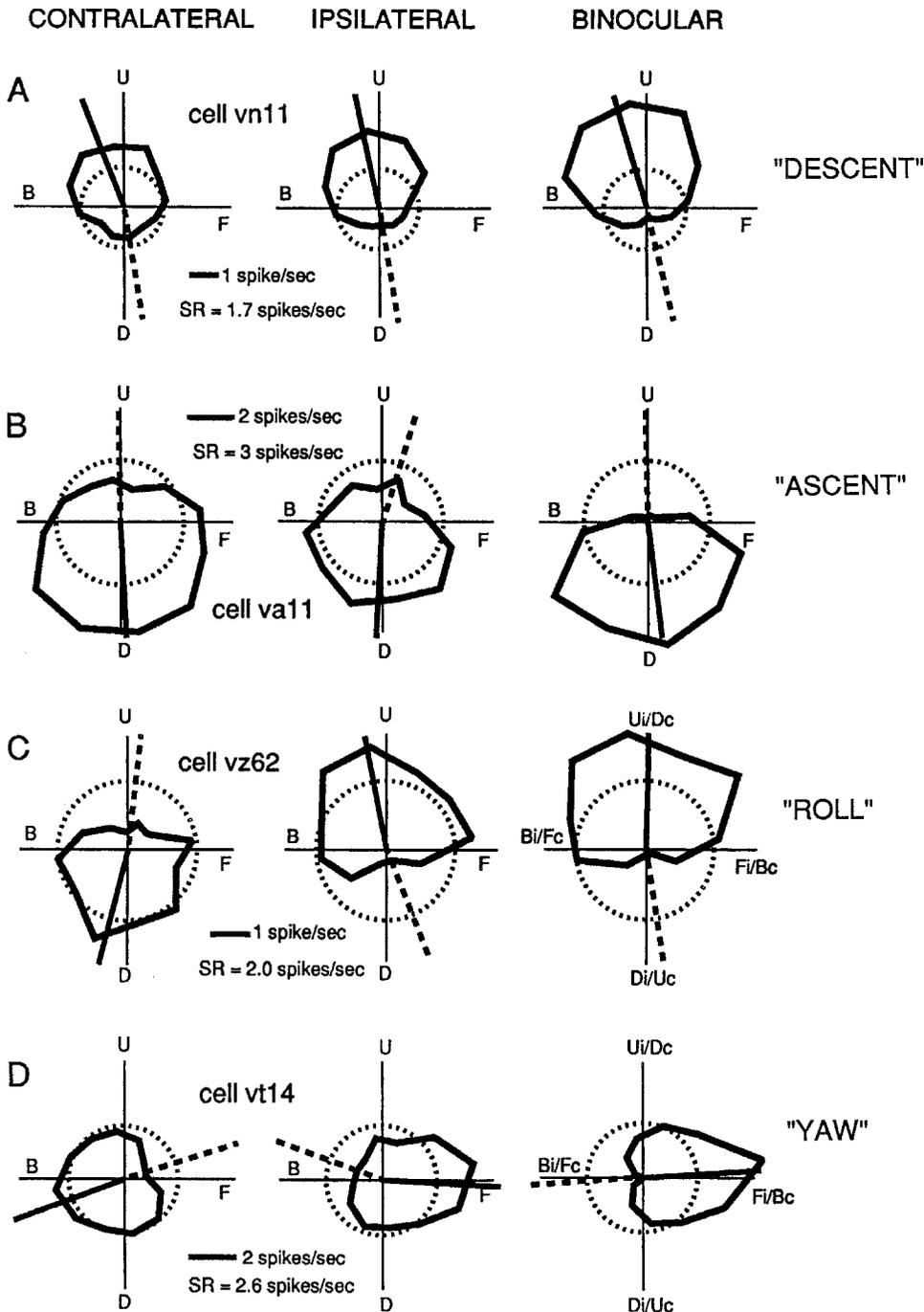
CONTRALATERAL   IPSILATERAL   BINOCULAR

Fig. 1A–D. Direction-selective complex spike activity of purkinje cells in the pigeon vestibulocerebellum. Directional tuning curves of four cells are shown. The firing rate in response to wholefield motion as a function of the direction of stimulus motion is plotted in polar coordinates. The spontaneous firing rate is represented by the dotted circle. Directional Tuning curves for contralateral and ipsilateral stimulation, as well as binocular in-phase (A, B) or antiphase (C, D) are shown. The cells in A and B prefer the same direction of wholefield motion in both eyes and thus respond best to optic flow resulting from translation. The cells in C and D prefer opposite directions of motion in the two eyes and thus respond best to optic flow resulting from rotation

to each other and placed 55 cm on either side of the bird's head. A wholefield stimulus, consisting of a random dot pattern which measured approximately 100° × 100°, was backprojected onto each screen. The directional tuning characteristics of each unit were assessed by moving the wholefield stimulus in 12 different directions, 30° apart. Spike counts were averaged over 5–10 sweeps (duration = 4s) of each direction. The directional tuning curves were performed separately for each eye (monocular) or binocularly. The binocular directional tuning curves were performed with the direction of motion either the same in both eyes (in-phase; eg. ipsi = upward, contra = upward; ipsi = backward (nasal to temporal), con-

tra = backward) or with the direction of motion opposite in either eye (antiphase; e.g. ipsi = upward, contra = downward; ipsi = forward, contra = backward).

Recordings were made from 137 Purkinje cells (109 single-units and 28 multi-units) in folia IXc, d and X of 30 pigeons. The most lateral aspect of the pigeon vestibulocerebellum is about 4.5 mm from the midline. The medial-lateral position of the recording sites ranged between 1.0 and 3.5 mm lateral to the midline. Complex spike (CS) activity in folia IXc, d and X exhibited direction selectivity in response to the wholefield motion; however, the movement of small spots or bars were ineffective in modulating the cells' firing rates. With the
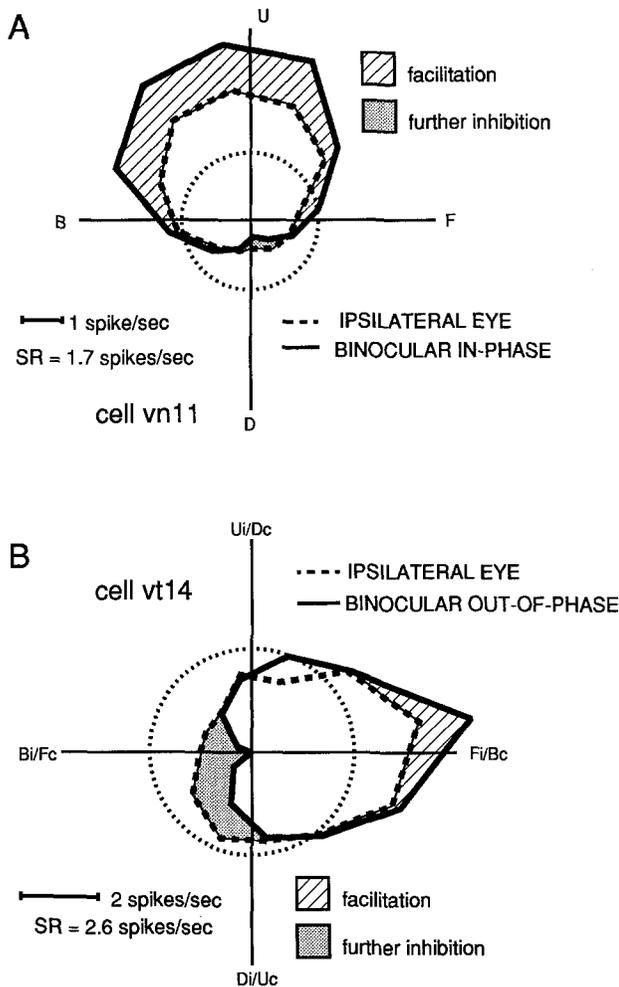
A

U

facilitation

further inhibition

B

F

●——● 1 spike/sec
SR = 1.7 spikes/sec

- - - IPSILATERAL EYE
—— BINOCULAR IN-PHASE

cell vn11

D

Ui/Dc

B

cell vt14

- - - IPSILATERAL EYE
—— BINOCULAR OUT-OF-PHASE

Bi/Fc

Fi/Bc

●——● 2 spikes/sec
SR = 2.6 spikes/sec

facilitation

further inhibition

Di/Uc

Fig. 2A, B. Binocular facilitation of the cells shown in Fig. 1A and 1D. In **A**, the response to wholefield stimulation of the ipsilateral (dominant) eye is compared with the response to binocular in-phase stimulation. Note that in-phase upward stimulation results in facilitation of the response relative to ipsilateral upward stimulation alone, and in-phase downward stimulation results in additional inhibition of the firing rate relative to ipsilateral downward stimulation alone. In **B**, the ipsilateral tuning curve is compared to that resulting from binocular antiphase stimulation. Antiphase stimulation in the preferred direction results in a greater firing rate relative to wholefield stimulation in the preferred direction in the ipsilateral eye alone, and antiphase stimulation in the non-preferred direction results in more further inhibition relative to monocular stimulation

exception of eight units, all were binocular, and the ipsilateral eye was slightly dominant for most cells. Directional tuning curves of four binocular neurons are shown in Fig. 1. These represent the four functional classes that we have identified. The cell in Fig. 1A responded best to upward wholefield motion in both visual fields, and was inhibited by downward motion in both eyes. Thus, this cell would respond best to visual flow which results from a downward translation, e.g. *descent*. Seventy-six single-units and thirteen multi-units responded in this manner. The cell in Fig. 1B is the opposite, responding best to downward wholefield motion in both eyes. This type of visual flow would result from an upward translation, e.g. *ascent*. Only eight single-units and two multi-units were classified as ascent cells. Unlike

these two cell types, the neurons in Fig. 1C and D prefer visual flow which results from rotation. The cell in Fig. 1C prefers upward and downward motion in the ipsilateral and contralateral eyes respectively, a flow pattern which results from a *roll* of the bird (U/D in the nomenclature of Kano et al. 1990). Five single-units and four multi-units were classified as roll cells. The cell in Fig. 1D prefers backward motion in the contralateral eye and forward motion in the ipsilateral eye. This flow pattern would result as the bird made an ipsiversive horizontal head rotation, e.g. a *yaw* movement (F/B cells in the nomenclature of Kano et al. 1990, and *vertical axis* neurons using the nomenclature of Graf et al. 1988). Fourteen single-units and seven multi-units responded in this manner.

Although a quantitative analysis of the data is not yet available, preliminary results suggest a functional longitudinal organization of the pigeon vestibulocerebellum. The translation cells (ascent and descent) are always found medial to the rotation cells (roll and yaw).

It is evident in Fig. 1 that binocular wholefield motion in the preferred direction in both visual fields results in greater excitation relative to monocular stimulation of either eye. Likewise, binocular wholefield motion in the non-preferred direction results in increased inhibition relative to monocular stimulation. This is more clearly illustrated in Fig. 2 where the binocular tuning curve is compared with the monocular tuning curve of the ipsilateral (dominant) eye for two cells. In A, upward binocular in-phase stimulation results in a facilitation of the response relative to monocular upward motion in the ipsilateral eye. Moreover, downward binocular in-phase stimulation results in further inhibition, relative to monocular downward motion in the ipsilateral eye. In B, antiphase stimulation with the preferred direction of motion in both eyes, forward and backward in the ipsilateral and contralateral eyes respectively, results in facilitation relative to forward stimulation in the ipsilateral eye alone. Likewise binocular stimulation in the opposite direction results in further inhibition relative to backward stimulation in the ipsilateral eye.

It has been demonstrated in species of other vertebrate classes that cerebellar neurons respond to binocular wholefield visual motion (Ansorge and Grüsser-Cornehls 1977; Blanks and Precht 1983; Blanks et al. 1977; Ghelarducci et al. 1975; Graf et al. 1988; Kano et al. 1990; Kusunoki et al. 1990; Waespe and Henn 1981). Graf et al. (1988), using a rotating planetarium as a projector, have shown that neurons in the flocculus of the rabbit respond best to visual flow simulating a head rotation in the plane of one of the three pairs of semicircular canals (see also Leonard et al. 1988). *Vertical axis* neurons respond best to visual flow resulting from rotation about the horizontal canal. These resemble the *yaw* neurons found in the present study, with the exception that Graf et al. found most of them to be monocular, responding best to forward motion in the ipsilateral eye. Graf et al. (1988) described two types of *roll* neurons, each responding to visual rotation about a particular pair of vertical semicircular canals: *posterior axis* and *anterior axis* neurons. Most *anterior axis* and all *posterior axis*

neurons were binocular. For many neurons each mono-cular receptive field was *bipartite*, i.e. the neuron's direction preference depended on the location of the stimulus in the visual field (see also Simpson et al. 1988; Soodak and Simpson 1988). For example, in the ipsilateral receptive field of *posterior axis* neurons, downward motion was preferred in the temporal 45 deg, and upward motion was preferred nasal to this. Based on their findings, one might expect that the roll cells we identified respond best to stimulation about either pair of the vertical semicircular canals. Using handheld stimuli we looked for bipartite receptive fields, however, these stimuli were ineffective in modulating the cell's firing rate. Moreover, the cell's firing rate was not well modulated when the wholefield stimulus was restricted to various parts of the visual field. To resolve the question of whether the roll units are organized with respect to the semicircular canals, our future research will use a planetarium projector.

In the present study most pigeon vestibulocerebellum cells responded best to translational optic flow patterns. Graf et al. (1988) did not find any neurons in the rabbit flocculus which responded best to translation, but it is possible that this type of unit might not have been seen when a rotating planetarium projector is used for wholefield stimulation. However, more recently, Kano et al. (1990) and Kusunoki et al. (1990) recorded from Purkinje cells in the nodulus and flocculus of the rabbit, using essentially the same methodology as in the present study. Although they found that CS activity was modulated by wholefield motion, most cells were monocular. Those that were binocular, preferred rotational visual flow, either roll or yaw. None of the cells preferred translational visual flow.

In contrast, cells in the medial aspect of the pigeon vestibulocerebellum clearly prefer translational optic flow. These translation neurons may be mediating retinal image stabilization in response to translational optic flow, such as occurs in the visually driven stereotypical head-bobbing behaviour in pigeons (Freidman 1975; Frost 1978). Moreover, when landing, but not during take-off, pigeons head-bob (Davies and Green 1988). The predominance of *descent* neurons over *ascent* neurons reported here is consistent with the notion that the pigeon vestibulocerebellum participates in the control of head-bobbing behaviour.

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