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Binocular neurons in the nucleus lentiformis mesencephali in pigeons: responses to translational and rotational optic flowfields

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Abstract

The pretectal nucleus lentiformis mesencephali (LM) receives direct input from the contralateral retina and is dedicated to the analysis of optic flowfields resulting from self-motion. The activity of 126 LM neurons in response to optic flow stimuli was recorded. As with previous studies, it was found that most neurons (~90%) exhibited direction-selectivity to large-field stimuli moving in the contralateral hemifield. However, some neurons (~10%) responded to stimulation of both eyes and had receptive field structures conducive for detection of particular patterns of optic flow resulting from either self-translation or self-rotation. These binocular neurons were maximally responsive to panoramic optic flowfields simulating either translational or rotational optic flow.

Keywords: Optokinetic; Pretectum; Accessory optic system; Self-motion

Because the environment consists of stationary objects and surfaces, as one moves through the environment optic flow occurs across the entire retina [6]. In the pigeon vestibulocerebellum (VbC), the complex spike activity of Purkinje cells is modulated by optic flow stimuli. These neurons have large, binocular (virtually panoramic) receptive fields (RFs) and respond best to particular patterns of optic flow resulting from either self-translation or self-rotation [12,15,16,18]. The optic flow input to the pigeon VbC arises, via the medial column of the inferior olive (IO), from the nucleus of the basal optic root (nBOR) of the accessory optic system (AOS) and the pretectal nucleus lentiformis mesencephali (LM) [1,2,5]. Most neurons in the nBOR and LM have large RFs in the contralateral hemifield and prefer large-field stimuli moving in a particular direction [3,11,14]. However, a small sub-population (<10%) of nBOR neurons have RFs in both the ipsilateral and contralateral eyes and, like VbC cells, respond to either translational or rotational optic flow [13,17]. In this report, I show that a small sub-population of LM neurons have binocular RFs and prefer particular patterns of translational or rotational optic flow.

Using standard extracellular techniques, the activity of 126 LM neurons was recorded in anaesthetized pigeons. Detailed methods for anaesthesia, surgery, extracellular recording, and data collection have been described previously [16,17]. Anaesthetized animals were placed in a stereotaxic device and, using the atlas of Karten and Hodos [8] as a guide, a section of bone and dura was removed to allow access to LM on the left side of the brain. Recordings were made with glass micropipettes filled with 2 M NaCl (4–5 μm tip diameter). Extracellular potentials were amplified, filtered and fed to a window discriminator. TTL pulses, each representing a single spike time, were analyzed using a Cambridge Electronic Designs (CED) 1401Plus, and peri-stimulus time histograms (PSTHs) were constructed using Spike2 software (CED). Once a cell was isolated, a large (about 90 × 90°) handheld stimulus, consisting of a random pattern of lines, dots and squiggles, was moved in various directions throughout both the ipsi- and contralateral hemifields.

Of the 126 LM cells, 113 (89.7%) responded to large-field stimuli moving in the contralateral visual field, but were insensitive to stimuli moving in the ipsilateral hemifield. Of these monocular cells, 112 were direction-selective: 48 (43%) preferred forward (temporal to nasal) motion, whereas 46 (41%), 14 (12.5%) and four (3.5%) preferred backward, upward and downward motion, respectively. These findings are in agreement with previous studies of the pigeon LM in that most neurons prefer large-field stimuli moving horizontally, but usually there is a greater bias to cells preferring forward motion [3,11]. One mono-

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cular cell showed an omnidirectional response as described by Fu et al. [3]. This cell was excited by large-field motion, irrespective of the direction of motion.

Some cells (13; 10.3%) responded to motion of large-field stimuli in both the ipsilateral and contralateral visual fields. Of these binocular cells, seven preferred the opposite directions of motion in the two hemifields. For species with laterally placed eyes, such an RF arrangement is ideal for analyzing optic flow resulting from self-rotation [13,18]. The other six binocular cells had a RF arrangement ideally suited for the analysis of optic flow resulting from self-translation.

Of the seven rotation cells, six preferred forward motion in the contralateral hemifield and backward motion in the ipsilateral hemifield. The other cell showed the opposite direction preference (Fig. 1). These rotation cells were further studied with a 'planetarium' projector that produced panoramic rotational flowfields. This was modelled on that designed by Simpson and colleagues [7,9,10], and has been described in detail elsewhere [15,17]. In a darkened room, this device projected a flowfield onto the walls, ceiling and floor of the room. The rotational flowfield oscillated about a particular axis at a frequency of 0.1 Hz, and the dots moved at a constant velocity of 1–2°/s. The planetarium was suspended above the bird in gimbals such that the axis of rotation could be positioned to any orientation in 3-D space.

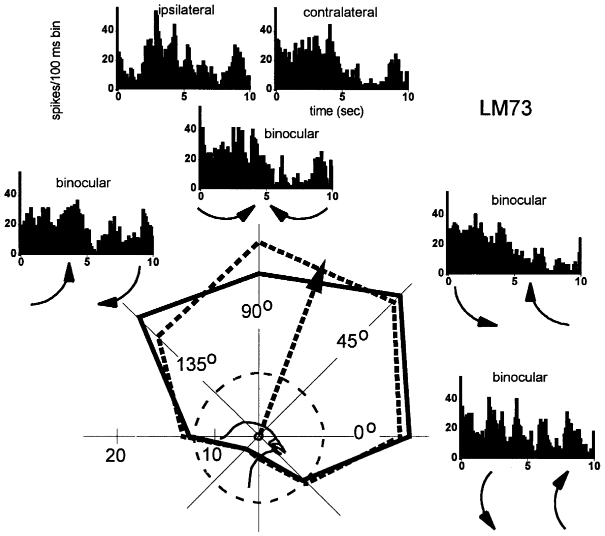

Fig. 1. Responses of a binocular LM neuron to rotation about the vertical axis (VA). PSTHs show the responses to rotational optic flow, (produced by the planetarium), about four axes in the saggital plane (elevation tuning curve). Each PSTH was summed from five sweeps, and each sweep consisted of 5 s of rotation about the axis in one direction, followed by 5 s of rotation in the opposite direction. The curved arrows indicate the direction of head rotation that produces the flowfield (i.e. opposite to the direction of rotational optic flow). For all four axes, the response for binocular viewing is shown, but for rotation about the VA, responses to monocular stimulation of the ipsi- and contralateral hemifields are also shown. A polar plot of elevation tuning, firing rate (spikes/s) as a function of the axis of rotation, is also shown. The broken curve represents the best fit cosine to the tuning curve and the broken arrow represents the peak of the cosine (i.e. the best axis). The broken circle represents the spontaneous rate, which was determined from several instances when the neuron was presented with a stationary stimulus.

Fig. 1 shows the responses of a cell to rotational optic flow produced by the planetarium. PSTHs of the responses to rotation about four axes in the saggital plane are shown. This neuron responded best to rotation about the vertical axis (VA), in the direction that produced backward motion in the contralateral eye and forward motion in the ipsilateral eye.

In Fig. 1, the responses to rotation about the VA are also shown for monocular stimulation of the ipsilateral and contralateral eyes. A quantitative index of ocular dominance (OD) was calculated by taking the ratio of the depth of modulation to stimulation of the dominant vs. the non-dominant eye. The depth of modulation for each eye was determined as the average firing rate to motion in the preferred direction minus the average firing rate to motion in the anti-preferred direction. The OD for the neuron shown in Fig. 1 was 4.1c, indicating a marked contralateral dominance. Of the 13 binocular neurons, 11 had a marked contralateral dominance ($OD > 2$). The average of the OD index was 4.2c (±1.4 (SEM); range 1.1–15.0c).

Six of the binocular LM neurons preferred optic flow patterns that would result from self-translation. When tested with the handheld stimulus, these cells preferred the same direction of motion in the lateral margin of each visual field. Such a RF arrangement is ideal for analyzing translational optic flow [13,18]. For example, one neuron preferred downward motion in both eyes, which would result from upward translation. Four neurons preferred backward motion in the lateral regions of both visual fields, and one neuron preferred forward motion in the lateral regions of both eyes. These neurons were further studied with a translator that projected a panoramic translational optic flowfield onto the floor, walls and ceiling of the darkened room. This device, described in detail elsewhere [16], produced a translational flowfield, with a focus of expansion (FOE) at one 'pole', a focus of contraction (FOC) at the opposite 'pole', and laminar flow at the 'equator'. The device was mounted in gimbals such that the axis of the spherical translational flowfield could be positioned to any orientation within 3-D space.

Fig. 2 shows the responses of a binocular neuron, (that preferred forward motion in both eyes), to translational optic flow along four axes in the horizontal plane. PSTHs in response to translation in both directions along each axis are shown, as is a polar plot of the azimuth tuning curve. These data show that this neuron was maximally modulated in response to translation along the horizontal axis oriented at approximately 45° ipsilateral (i) azimuth but showed little modulation in response to translation along the orthogonal axis (45° contralateral (c) azimuth). Translation in the direction producing a FOC at 45°i azimuth resulted in maximal excitation whereas translation in the opposite direction

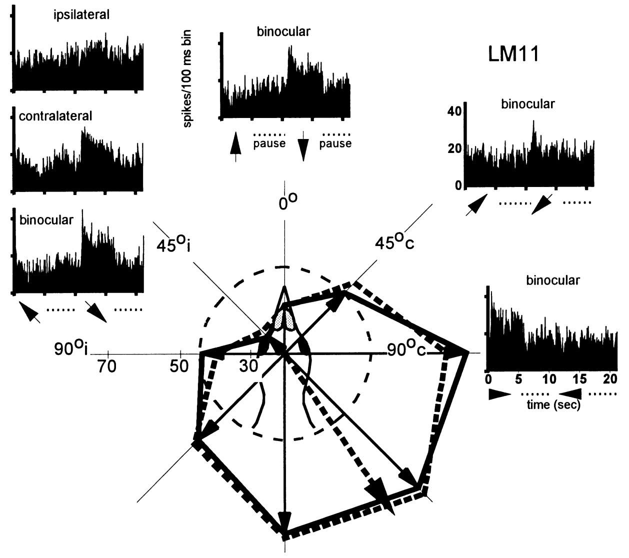

Fig. 2. Responses of a translation sensitive binocular LM neuron. PSTHs show the responses of this neuron to translational optic flow, (produced by the translator), along four axes in the horizontal plane (azimuth tuning curve). The PSTHs are summed from four sweeps, where each sweep consisted of 5.3 s of motion in one direction, followed by a 5.3 s pause, followed by 5.3 s in the opposite direction, followed by a 5.3 s pause. The orientation of each arrow reflects the orientation of the axis of the translator, and the arrowheads point in the direction in which the animal would move to produce such a flowfield. That is, the arrowheads point toward the FOE in the flowfield. For all four axes, the response for binocular viewing is shown, but for translation along the axis oriented at 45°i azimuth, responses to monocular stimulation of the ipsi- and contralateral hemifields are also shown. A polar plot of azimuthal tuning is also shown. The broken arrow indicates the peak of the best fit cosine (broken line) to the tuning curve and the broken circle represents the spontaneous rate.

resulted in maximal inhibition. PSTHs of the responses to translation along the best axis for monocular stimulation of the ipsi- and contralateral eyes are also shown. Note the marked contralateral dominance (OD = 2.2c), and the fact that binocular stimulation resulted in a greater depth of modulation relative to stimulation of the dominant eye alone.

When tested with the translator, four neurons (those that preferred backward motion in the lateral regions of both eyes) also responded best to translational optic flow along a horizontal axis, approximately 45° from the midline (34.4–62.3°). These neurons showed a clear bipartite RF structure. The bipartite RF was first shown for rotation sensitive neurons in the AOS, IO, and VbC of rabbits by Simpson and colleagues [7,9,10]. These RFs consisted of a region that preferred upward motion adjacent to a region that preferred downward motion. The best stimulus was a rotational optic flowfield with the axis of rotation at the boundary of the two regions of the bipartite RF [7,9,10].

In Fig. 3 a bipartite RF is shown, but for a neuron that preferred translational optic flow. In response to the translator, this neuron responded best to an optic flowfield with the FOE at approximately 45°c azimuth.

In response to the handheld stimulus, the neuron was excited by backward motion in the lateral region, but showed the opposite direction preference in the anterior region of the contralateral hemifield. In Fig. 3, direction tuning curves of the responses to large-field drifting gratings (produced by a VSGThree, Cambridge Research Services) restricted to either the lateral or anterior regions of the contralateral hemifield are shown. This neuron preferred backward (nasal to temporal) motion in the central (lateral) region, and forward (temporal to nasal) motion in the anterior 45° of the contralateral hemifield. Given this bipartite RF structure, it is not surprising that the optimal response occurred to a translational flowfield with a FOE at approximately 45°c azimuth.

In this study I have shown that a subpopulation of neurons in the pigeon LM have binocular RFs and respond best to flowfields resulting from either self-translation or self-rotation. With the use of the translator and planetarium, the axis preferences for translation and rotation-sensitive neurons were determined, as has been done for Purkinje cells in the VbC. In the flocculus of the VbC, cells prefer rotational

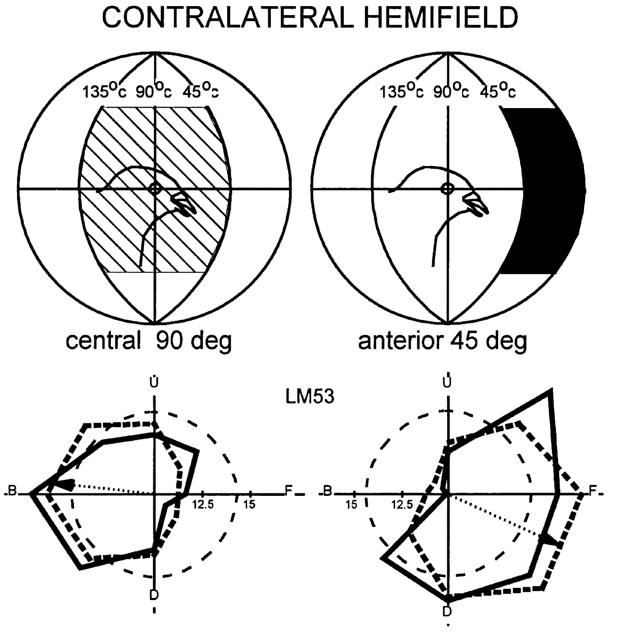

Fig. 3. The bipartite receptive field (RF) of a translation sensitive neuron. This neuron responded best to a translational flowfield with the FOE at approximately 45°c azimuth. The responses to drifting gratings restricted to the central 90° (left) or the anterior 45° (right) of the contralateral hemifield are shown. Directional tuning in these regions is shown in the polar plots, where firing rate (spikes/s) is plotted as function of the direction of large-field motion in polar coordinates. The broken arrow indicates the peak of the best fit cosine (broken line) and the broken circles represent the spontaneous rate. Note that this cell preferred backward (nasal to temporal; B) motion in the central 90°, and forward (temporal to nasal; F) motion in the anterior 45° of the contralateral hemifield. U, up; D, down.

optic flow about either the VA or a horizontal axis oriented at 45°c azimuth [7,15]. In the ventral uvula and nodulus, cells prefer translational optic flow along either the VA, or one of two horizontal axes oriented 45° to the midline [12,16]. Some nBOR neurons have binocular RFs and respond best to rotational or translational optic flow [17]. It also appears that the frame of reference for self-translation and self-rotation seen in the VbC, (VA, and horizontal axes 45° to the midline) [7,9,10,12,16], is reflected in the binocular neurons in the LM and nBOR [17]. However, two facts suggest that the LM and nBOR play minor roles compared to the VbC. First, the binocular LM and nBOR neurons represent small subpopulations, whereas a vast majority (>80%) of the VbC neurons have binocular RFs [13,15–18]. Second, most of the binocular LM and nBOR neurons show a marked OD, whereas the VbC neurons show a slight OD or are equidominant [13,15–18]. Clearly further integration of binocular inputs takes place in the IO.

It is known that the LM receives a direct retinal input from the contralateral eye [4], but how is it that some neurons have binocular RFs? I suggest that this might arise from a projection from the ipsilateral nBOR. The nBOR sends a massive projection to the ipsilateral LM and receives input from the contralateral nBOR [1].

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