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Responses to Moving Visual Stimuli in Pretectal Neurons of the Small-Spotted Dogfish (*Scyliorhinus canicula*)

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Masseck OA, Hoffmann K-P. Responses to moving visual stimuli in pretectal neurons of the small-spotted dogfish (*Scyliorhinus canicula*). *J Neurophysiol* 99: 200–207, 2008. First published October 31, 2007; doi:10.1152/jn.00926.2007. Single-unit recordings were performed from a retinorecipient pretectal area (corpus geniculatum laterale) in *Scyliorhinus canicula*. The function and homology of this nucleus has not been clarified so far. During visual stimulation with a random dot pattern, 45 (35%) neurons were found to be direction selective, 10 (8%) were axis selective (best neuronal responses to rotations in both directions around one particular stimulus axis), and 75 (58%) were movement sensitive. Direction-selective responses were found to the following stimulus directions (in retinal coordinates): temporonasal and nasotemporal horizontal movements, up- and downward vertical movements, and oblique movements. All directions of motion were represented equally by our sample of pretectal neurons. Additionally we tested the responses of 58 of the 130 neurons to random dot patterns rotating around the semicircular canal or body axes to investigate whether direction-selective visual information is mapped into vestibular coordinates in pretectal neurons of this chondrichthyan species. Again all rotational directions were represented equally, which argues against a direct transformation from a retinal to a vestibular reference frame. If a complete transformation had occurred, responses to rotational axes corresponding to the axes of the semicircular canals should have been overrepresented. In conclusion, the recorded direction-selective neurons in the Cgl are plausible detectors for retinal slip created by body rotations in all directions.

INTRODUCTION

In teleosts the area pretectalis (APT) contains highly direction-selective neurons and is involved in optokinetic retinal image stabilization. Neurons in this nucleus respond direction specifically to temporonasal, nasotemporal as well as vertical movements (Klar and Hoffmann 2002). This is significantly different from tetrapods in which the pretectum and accessory optic system contains different nuclei coding for different directions of visual motion.

In mammals, the accessory optic system (AOS) is composed of the dorsal terminal nucleus (DTN), the medial terminal nucleus (MTN), and the lateral terminal nucleus (LTN). In addition, neurons in the nucleus of the optic tract (NOT) behave like those in the DTN. These neurons are highly directionally selective and respond over a wide speed range. The direction-selective neurons of the NOT and the DTN have a strictly ipsiversive motion preference (e.g., Collewijn 1976; Grasse and Cyander 1984; Hoffmann and Schoppmann 1981). In MTN and LTN vertical motion is represented (e.g., Grasse and Cyander 1982, 1984).

In amphibians, reptiles, and birds the nucleus lentiformis mesencephali (LM) is the visuomotor interface of the horizontal optokinetic nystagmus (frog: Fite 1985; Katte and Hoffmann 1980; turtle: Fan et al. 1995; bird: Fite et al. 1979; Fu et al. 1998; Winterson and Brauth 1985). Neurons in the LM code predominantly for ipsiversive motion, some are selective for contraversive and vertical motion (frog: Katte and Hoffmann 1980; turtle: Fan et al. 1995; pigeon: Winterson and Brauth 1985). The nucleus of the basal optic root (nBOR), a major nucleus of the AOS in tetrapods other than mammals, processes information about retinal slip for all directions of motion except horizontal ipsiversive (Dieringer et al. 1982; Fan et al. 1995; Gruberg and Grasse 1984; Zhang et al. 1999), which is represented by the LM.

It has been suggested that the AOS and its downstream targets transform visual motion signals from retinal coordinates into vestibular coordinates (Graf et al. 1988; Simpson et al. 1988; Wylie and Frost 1993). A vestibular reference frame is characterized by an alignment of the preferred directions with the response axes of semicircular canals (Graf et al. 1988), i.e.: the neuronal population should show a bias for rotation around axes that correspond to semicircular canal axes. Transformation of the visual motion information into a vestibular reference frame would facilitate combining visual and vestibular information in the computation of self movements and stabilizing gaze (Hengstenberg 1998; Wallman and Velez 1985; Wylie et al. 1998).

In contrast to other vertebrate groups, little is known about the visual input to gaze stabilization in chondrichtyans. A possible input, the retinorecipient corpus geniculatum laterale (Cgl), is composed of diencephalic and pretectal parts and, despite its name, has no evident homology with the mammalian corpus geniculatum laterale. Furthermore the oculomotor organization of chondrichthyans seems to be different from all other vertebrates investigated so far, in that the motoneurons of the medial rectus muscle are located contralaterally to their innervated muscle (elasmobranches: Graf and Brunken 1984). Also in lampreys the oculomotor organization is equally different from that of other vertebrates [for example, the horizontal semicircular canals are lacking (Simpson and Graf 1985)]. Here motoneurons of the medial rectus muscle are innervated ipsilaterally. Thus the underlying circuits of optokinetic control in sharks may differ from other species studied so far.

Scyliorhinus canicula is one of the more primitive members of the Galeomorpha, which represents 73% of all living sharks (Reperant et al. 1986). Thus this species represents a good

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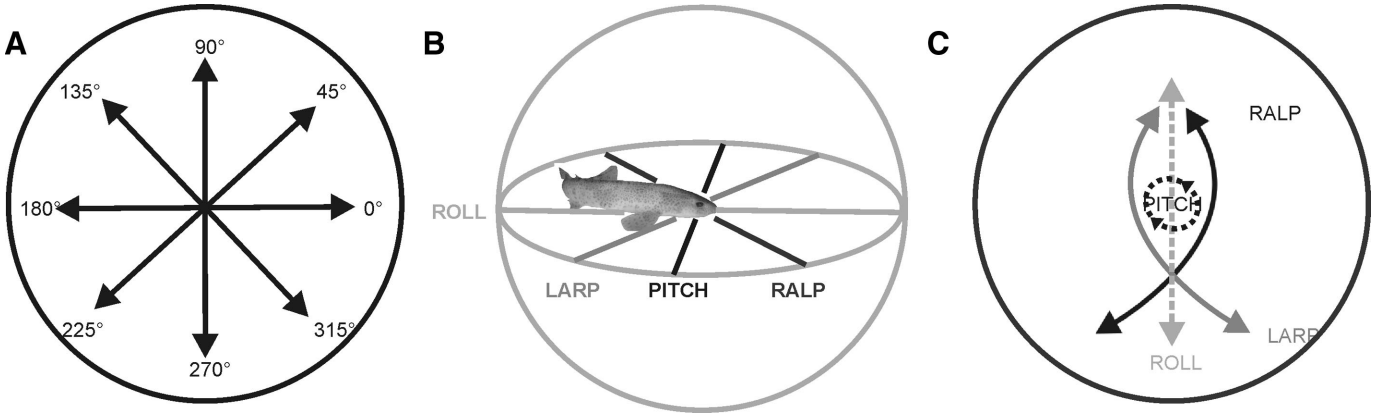

FIG. 1. *A*: illustration of stimulus directions seen by the central 60° of the retina during linear stimulation. *B*: illustration of stimulus axes used in the horizontal plane, i.e., axes of rotation of the planetarium to test for a vestibular reference frame. LARP, left anterior right posterior axis of the fish. How clockwise and counterclockwise rotation around the LARP axis appears on the right central retina is shown in *C* and in the supplementary movies, PITCH transverse axis, RALP right anterior left posterior axis, ROLL longitudinal axis.[1] *C*: stimulus movements seen by the central retina during stimulation around LARP, RALP, ROLL, and PITCH axes.

model for studying the evolution of visuo-motor pathways. Previous studies presumed that the retinofugal system of *S. canicula* resembles that of actinopterygians (Smeets 1981) in that as in osteichthyes, the optic nerves are completely crossed. Two retinorecipient nuclei in the pretectum were described in *S. canicula*, the Cgl and the nucleus pretectalis (Pret) (Smeets 1981; Reperant et al. 1986). However, a structure corresponding to the nucleus of the basal optic root (nBOR), a key component of the accessory optic system in tetrapods, does not seem to be present in *S. canicula* (Smeets et al. 1983). The aim of this study was to investigate the pretectum of the small spotted dogfish (*Scyliorhinus canicula*) with electrophysiological and histological methods to locate the visuo-motor interface coding retinal slip subserving the optokinetic reflex in chondrichthyans. In particular, we ask whether the pretectum of chondrichthyans shows evidence of a transformation from a retinal into a vestibular reference frame.

METHODS

Data from 14 *S. canicula* provided by the Observatoire Oceanologique de Banyuls, the Biologische Anstalt Helgoland and the Aquazoo-Löbbecke Museum were included in the present study. Animal were at least half a year old, between 10 and 50 cm in length and included animals of both sexes. All experiments were approved by the local authorities (Regierungspräsidium Arnsberg) and carried out in accordance with the Deutsche Tierschutzgesetz of 12 April 2001, the European Communities Council Directive of 24 November 1986 (S6 609 EEC) and National Institutes of Health guidelines [1]for care and use of animals for experimental procedures.

Animals were anesthetized during surgery in a bath containing 0.1% MS222. After additional local anesthesia with 2.5% lidocaine, a craniotomy was performed to allow access to the left tectum opticum and pretectum. After surgery the animals were immobilized with pancuroniumbromide (0.6 mg/kg) and transferred to a transparent recording hemisphere (diameter: 70 cm) where they were artificially ventilated with cooled sea water (14°C). Single-unit recordings with glass-coated tungsten microelectrodes or glass micropipettes (impedance: 1–2.5 MΩ) were made in the left pretectum. Receptive field sizes were qualitatively tested with single dots (diameter: 4–10°) produced by a hand lamp. For quantitative investigation of the responses to movement, the visual stimulus consisted of random light dots projected into the hemisphere by a planetarium projector centered above the fish's head. The planetarium, consisting of a spherical shell (diameter: 15 cm) with small holes in it attached to a computer-controlled motor. A lamp inside the shell produced an optokinetic stimulus, covering the whole visual field of the right eye with dots sized from 2 to 4° in diameter and 1 cd/m^2 in luminance on the translucent hemisphere (for further information, see Simpson et al. 1988). The following stimulus movements were presented in the whole visual field of the right eye.

Linear motion stimuli (testing for a retinal reference frame)

Four axes of linear motion were used to clarify, whether a bias for horizontal or vertical movements exists among neurons in the pretectum of chondrichthyans: horizontal movements from temporal to nasal (0°) and nasal to temporal (180°), vertical movements from ventral to dorsal (90°) and from dorsal to ventral (270°), oblique movement from temporo-ventral to naso-dorsal (45°) and naso-dorsal to temporo-ventral (225°), and oblique movements from naso-ventral to temporo-dorsal (135°) and from temporo-dorsal to naso-ventral (315°). All eight stimulus directions produce near linear movements on the fish's central retina. We call this the retinal reference frame, as all linear stimuli correspond to straight movements on the central retina (Fig. 1*A*).

Rotational stimuli (testing for a vestibular reference frame)

In addition, four axes of rotational axes in the horizontal plane were tested (Fig. 1, *B* and *C*) to find out whether the strongest responses were elicited by rotations around axes of the vertical semicircular canals. Around every axis, the planetarium turned in clockwise (CW) and counterclockwise (CCW) directions leading to image motion on the right retina like that during the following body movements. *1*) Roll (planetarium rotation around the longitudinal axis of the fish), body rotation around this axis leads to upwards motion (roll up) or downwards motion in the central retina (roll down). *2*) LARP (planetarium rotation around the left anterior right posterior axis of the fish). Rotation around this axis leads to a visual stimulus, which corresponds to a maximal activation of either the right anterior vertical semicircular canal (left ear up, LARP up) or the left posterior vertical semicircular canal (left ear down, LARP down). *3*) Pitch (planetarium rotation around the transverse axis of the fish): nose down (pitch up) or nose up (pitch down). *4*) RALP (planetarium rotation around the right anterior left posterior).

[1] The online version of this article contains supplemental data.

Visual stimuli resulting from a rotation around the RALP-axis correspond to a maximal activation of either the right posterior vertical semicircular canal (left ear up, RALP up) or the left anterior vertical canal (left ear down, RALP down). The angles selected for the LARP and RALP axes are based on vestibular canal orientation (own dissection) and physiological studies on other species (e.g., Simpson and Graf 1985; Simpson et al. 1988). Stimulus speed was kept constant at 10°/s. Each trial consisted of a stationary phase (0–2,000 ms), a rotation in CW direction (2,000–5,000 ms), another stationary phase (5,000–7,000 ms), and a rotation in CCW direction (7,000–10,000 ms).

Data analysis

Action potentials were converted to TTL pulses by a window discriminator. In some experiments, data acquisition involved storing TTL pulses on the audiotrack of a videotape for manual off-line analysis with a counter. In the remaining experiments preamplified signals were acquired with CORTEX (NIMH, Laboratory of Neurophysiology. Version 5.96), and off-line analysis was performed with a customized Matlab (version 7.0.1) program.

To test for direction selectivity the weighted preferred direction vector was calculated as following.

First the rectangular coordinates of the mean vector are calculated, where eight angles α_i are given (i.e.: $\alpha_1 = 0°$, $\alpha_2 = 45°, \ldots$, corresponding to the sampled stimulus directions), m_i represents mean activity in the corresponding angle α_i and

$$n = \sum_{i=1}^{8} m_i.$$

$$x = \frac{\sum_{i=1}^{8} m_i * \cos \alpha_i}{n}, \quad y = \frac{\sum_{i=1}^{8} m_i * \sin \alpha_i}{n} \text{ from which we get } r = \sqrt{x^2 + y^2}.$$

Where r is the length of the mean vector. The value of the mean angle θ is now determined by the angle having the following cosine and sin

$$\theta = \cos^{-1}\left(\frac{x}{r}\right), \ \theta = \sin^{-1}\theta\left(\frac{y}{r}\right)$$

The four neighboring directions of the weighted preferred direction vector were compared with the four opposite directions with a *t*-test or a rank sum test. Only neurons with a P value <0.01 were taken as direction selective. Null direction is taken as the direction with the lowest response. Weighted preferred direction vectors have the advantage that all responses, even in the null direction, are taken into account to estimate preferred direction and tuning width. The length of the mean vector (r) was taken as the tuning width index (TWI), with values near 1 indicating no dispersion of the mean values (i.e., all except 1 direction have null activity).

To test for axis-selective cells a multi comparison test (1-way ANOVA) was applied, activity of the preferred axis had to be significantly different from all other directions. To look for unimodal, bimodal, or uniform distribution of the whole population a Rayleigh test was used.

Histological procedures

At the end of the experiments electrolytic lesions (10-s, 10-μA, anodic and cathodic) were made to identify the recording sites. In some experiments, tetramethylrhodaminedextrane (MW 3000, anionic, lysine fixable, Molecular Probes, administered in 0.3 M PBS) was applied iontophoretically (positive current pulses 7 s on/3 s off, 10 μA for 30 min) via the recording pipettte to verify the recording side. The fish were deeply anesthetized and perfused transcardially with 0.9% saline followed by 4% paraformaldehyde in 0.1 M phosphate buffer (PB, pH 7.4) containing 10% sucrose. To avoid blood coagulation, 0.1 ml heparin was injected into the ventricle immediately before the perfusion. Brains were removed and stored overnight in the same fixative at 4°C. The next day the brains were cryoprotected with 30% sucrose in 0.1 M PB for another 24 h. The brains were then embedded in chicken albumin (Sigma), and 30-μm sections were cut in a frontal plane on a cryostat. Two series were collected, the first was stained with cresylviolet to reveal cytoarchitecture, the second was stained with a combination of a myelin stain (Gallyas) and cresyl violet or according to Klüver-Barrera (Romeis and Böck 1989). Brain regions were named following the nomenclature of Smeets and coworkers (1983).

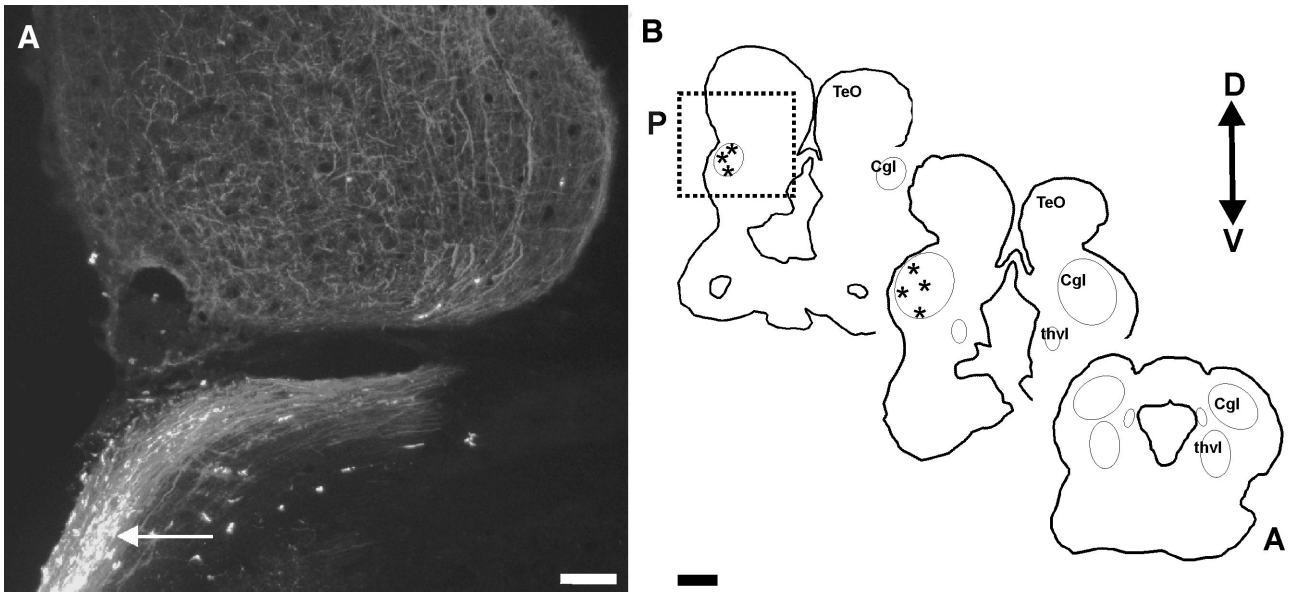

FIG. 2. *A*: photomicrograph of a frontal section showing the injection of tetramethylrhodaminedextran into the Cgl. ←, application side. Scalebar represents 100 μm. *B*: sketch of frontal sections through the diencephalon and pretectum. ⋆, location of microlesions and tetramethylrhodaminedextran application. ⋯, position of the photomicrograph in *A*. A, anterior; D, dorsal; P, posterior; V, ventral; Cgl, corpus geniculatum laterale; TeO, tectum opticum; thvl, thalamus ventralis, pars lateralis. Scale bar represents 1 mm.

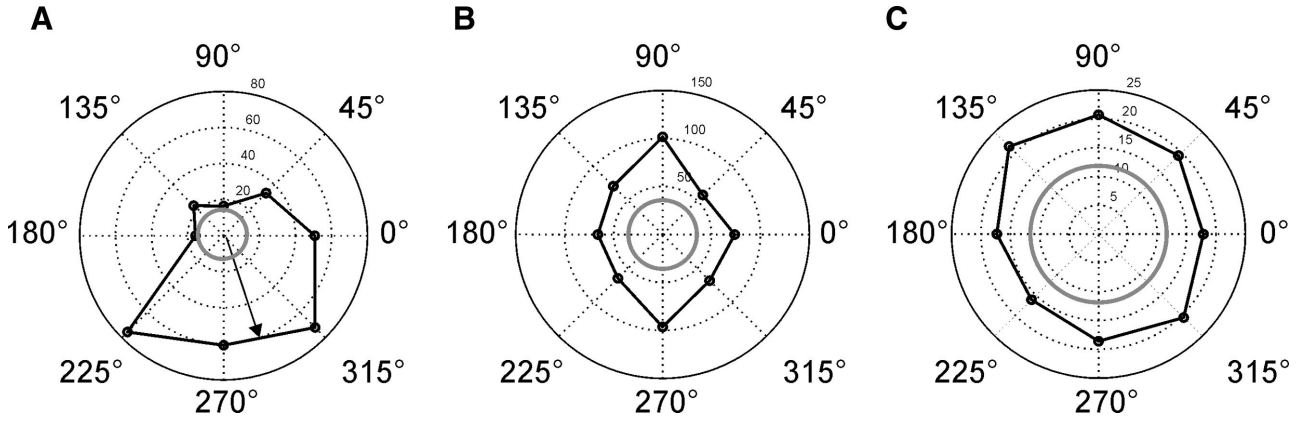

FIG. 3. Polar plots of cells that were measured with linear stimuli. Radials represent direction of stimulus motion, dash-dotted circles represent activity in spikes per second; gray circle represents mean spontaneous activity in spikes per second. *A*: direction-selective neuron. *B*: axis-sensitive neuron. *C*: motion-sensitive neuron.

RESULTS

Linear stimuli on the central retina

Altogether 130 visual neurons in the pretectum of 14 sharks were recorded during whole field visual stimulation with a stimulus velocity of 10°/s. The five reconstructed microlesions and the two rhodamine injections were all located in caudal parts of the pretectum within the so called corpus geniculatum laterale (Fig. 2, *A* and *B*). All of these lesions and rhodamine injections were located in the pretectal parts of the Cgl.

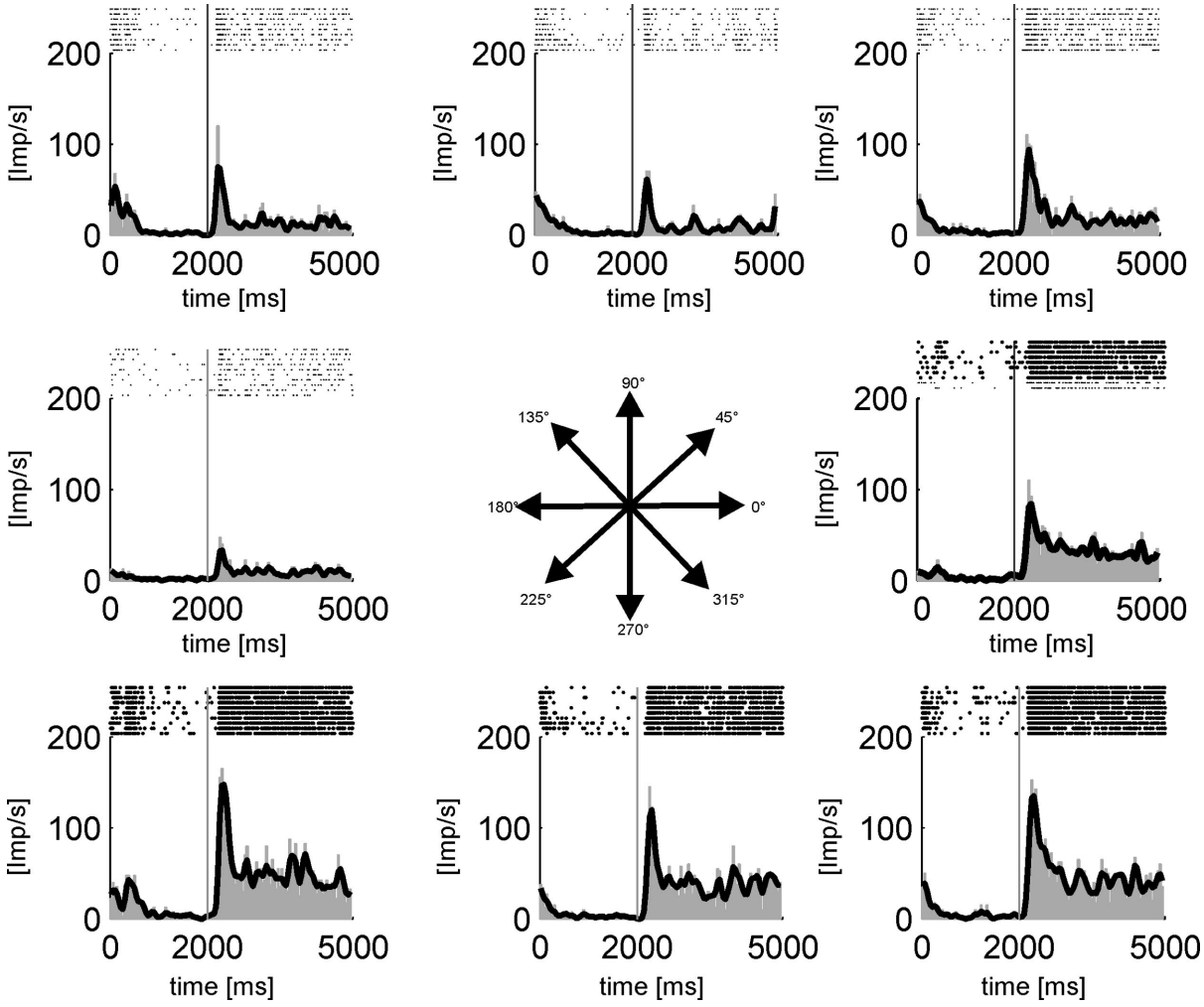

FIG. 4. Peristimulus time histograms and raster plots of a direction-selective neuron in the left Cgl of *S. canicula* as tested through the right eye with a linear stimulus moving at a velocity of 10°/s. Black line represents spike density function, which is based on a Gaussian filtering of the spike train; 0- to 2,000-ms stationary phase, 2,000- to 5,000-ms linear movement in direction of the assigned angle. Angles give direction of the linear movement seen be the central retina (see Fig. 1*A*).

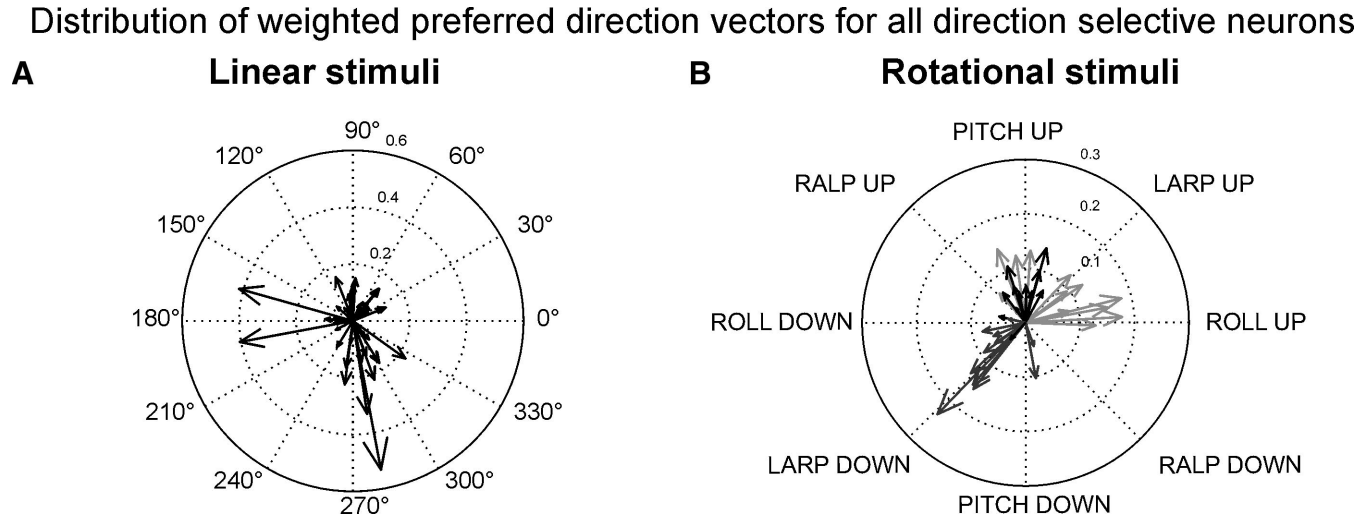

FIG. 5. *A*: each arrow represents the weighted preferred direction of 1 direction-selective neuron recorded with the linear stimulus. *B*: polar plot of weighted preferred directions for rotation around axes in the horizontal plane. Each shade represents neurons which were recorded in the same animal. Legend see Fig. 3.

Forty-five (35%) of the recorded neurons were significantly direction selective ($P < 0.01$), 10 (8%) were axis selective ($P < 0.01$), and 75 (58%) were sensitive to motion but neither direction nor axis selective during whole field stimulation with a stimulus velocity of 10°/s. Figure 3 shows an example of each neuronal class: a direction-selective neuron (*A*), an axis-selective neuron (*B*), and a motion-selective neuron (*C*). None of the direction- and axis-selective neurons showed a clear inhibition to motion in the null direction; instead, responses were nearly all above spontaneous activity (Figs. 3 and 4). The responses of a typical linear direction-selective neuron are shown in Fig. 4. The neuron responds to each direction of motion with a transient response at movement onset and tonic firing above the rate of spontaneous activity (15 imp/s). No clear inhibition in the null direction (180°, mean activity, 16 imp/s) occurs. The neuron ceased firing only during stationary phases of the stimulus.

Most of the direction-selective neurons tested had broad tuning curves with large receptive field, spanning nearly the whole lower horizontal visual field of the right eye. (azimuth: 20–150°, elevation: −20°, −45°).

Weighted preferred directions of the 45 direction-selective neurons were uniformly distributed, i.e., there was no bias for horizontal movements from temporal to nasal as found in the pretectum or dorsal terminal nucleus of tetrapods (Fig. 5*A*).

Additionally 17 neurons were recorded with stimulus velocities of 5 and 20°/s as well as 10°/s. (Table 1). In general, direction-selective responses occurred more frequently at lower velocities, whereas axis-sensitive neurons behave complementary. The percentage of motion selective cells is stable over all tested stimulus velocities.

TABLE 1. *Percentage of direction-, axis-, and motion-selective neurons for different velocities*

	Direction Selective	Axis Selective	Motion Selective
5°/s, %	30	17	53
10°/s, %	18	35	47
20°/s, %	12	35	53

Each column represents one neuron class, each row a certain velocity. The table shows the percentage of neurons that were found at the given stimulus velocity. Altogether 17 neurons were recorded with 5, 10, and 20°/s.

Axis of rotation in the horizontal plane

Fifty-eight neurons in four animals were recorded during whole field stimulation with a stimulus velocity of 10°/s created by the planetarium rotating around axes in the horizontal plane. Thirty-six of them were significantly direction selective (62%), 3 were axis selective (5%), and 19 were motion sensitive (33%). Examples of each neuron class are shown in Fig. 6. A characteristic peristimulus time histograms (PSTH) of a direction-selective neuron recorded with axes in the horizontal plane is depicted in Fig. 7. As we found with linear motion stimulation, the responses in each axis and direction were above the spontaneous activity (15 imp/s). Almost all direction-selective neurons recorded with the rotational stimuli showed no inhibition to motion in the null direction.

Thirty-seven neurons were recorded with both linear and rotational motion. Twenty (54%) of them were direction selective stimulated by the planetarium rotating in the horizontal plane, and 18 (48%) of them were direction-selective for linear stimuli. There was no difference in the tuning width of direction-selective neurons for linear and rotational stimulus movement, i.e., the tuning width was not narrower for the horizontal axes nor was the length of the weighted preferred direction vectors significantly different (*t*-test, $P = 0.345$). If we consider the distribution of weighted preferred directions, a very similar picture as for the linear stimuli appears (Fig. 5*B*). The preferred directions in our sample of pretectal neurons can be uniformly assigned to the axes in the horizontal plane, i.e., a uni- or bimodal distribution can be rejected ($P = 0.001$). If a transformation into a vestibular reference frame would take place, our sample of Cgl neurons should show a uni-or bimodal distribution superimposed to the RALP or LARP axes as it has been shown for the rabbit (Graf et al. 1988). Hence it seems unlikely that transformation and coding of preferred directions occurs strictly in vestibular coordinates.

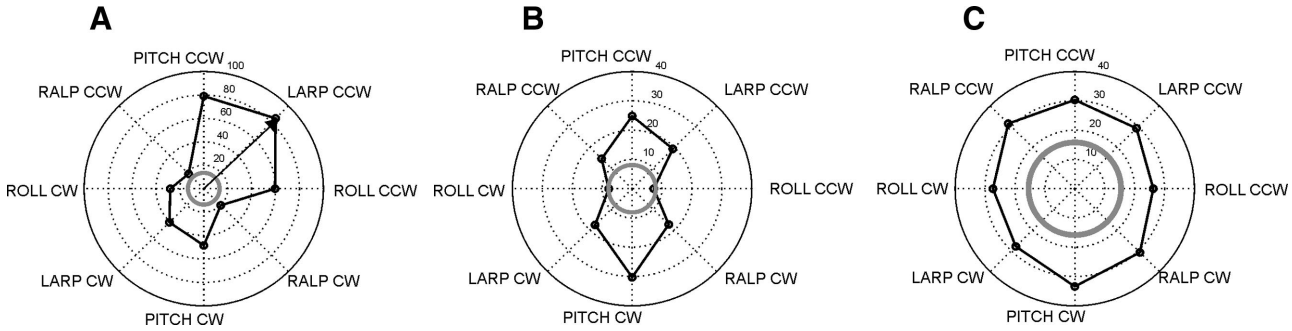

FIG. 6. Polar plots of cells that were measured with rotational stimuli. *A*: direction-selective neuron. *B*: axis-sensitive neuron. *C*: motion-sensitive neuron. Legend see Fig. 3.

A clustering of preferred directions appears, as in each penetration a bias for a particular axis of rotation and direction is visible (see different shaded symbols in Fig. 5*B*), although our histology failed to show a clear segregation of preferred stimulus directions among different recording sites. Possibly a segregation on a smaller scale as in mammals is present.

DISCUSSION

Visual responses to moving stimuli

We recorded direction-selective neurons in the corpus geniculatum laterale in the pretectum of the small-spotted dogfish. All direction-selective neurons responded best to large slowly moving (5 and 10°/s) random-dot stimuli and had large receptive fields. These uniform response characteristics in our recordings lead us to suppose that the Cgl in chondrichthyans may represent a part of their AOS. In addition the Cgl receives direct retinal input (Smeets 1981; Reperant 1986) and projects directly to the nucleus oculomotorius and to the cerebellum (O. A. Masseck, unpublished observations), which underlines its function in eye movement control. Also the presence of motion sensitive neurons resembles the functional characteristics like in the NOT in mammals (Schoppmann and Hoffmann 1979) or LM in pigeons (Fu et al. 1998). Ibbotson and Mark (1994) suggested that motion-sensitive neurons might prevent ocular following responses during saccades. Also our third neuron class (axis-selective neurons) has been described in the LM of pigeons (Fu et al. 1998). Therefore our data suggest that the anatomical nomenclature of the caudal part of the Cgl, where direction-selective neurons are located, should be reconsidered. Although no definitive anatomical or morphological data support the homology of Cgl to the LM, we propose to rename it LM (nucleus lentiformis mesencephali) because of its functional similarities to the LM of amphibians, reptiles, and birds.

Lack of inhibition

In our sample of direction-selective neurons, suppression of spike activity below the spontaneous level was not observed even during stimuli moving in the null direction. What might be responsible for the lack of suppression in the null direction? One possibility is that the neuronal connectivity is different, i.e., the separation of the input from retinal ganglion cells with different preferred directions is not as strict as in other vertebrates, so that input from a small percentage of the afferent ganglion cells might not be direction selective or might be excitatory in the null direction of the pretectal direction-selective neurons. Alternatively direction-selective retinal ganglion cells might lack inhibition in the null direction. Direction selectivity in retinal ganglion cells is mediated by GABAergic mechanisms (Caldwell et al. 1978), and a series of experiments by Bonaventure and Jardon (Bonaventure et al. 1983, 1992; Jardon et al. 1992) on monocular OKN in frog and chicken showed that intravitreal eye injections of GABA agonists and antagonist could modulate OKN gain and even alter the asymmetry of monocular OKN. So it is possible that the underlying GABAergic or cholinergic mechanisms involved in directional selectivity might not be as specific as in mammals.

Inhibition in the null direction is not necessarily required to stabilize gaze during self-movements. In a push-pull system, it is the activity difference that counts. For example, temporo-nasal stimulus movement seen by the right eye leads to strong activation of neurons with TN preferred direction in the left Cgl, whereas neurons with NT preferred direction are activated much more weakly in their null direction. The activity of TN preferring neurons may, in turn, be relayed to motoneurons in the nucleus oculomotorius initiating a contraction of the right medial rectus muscle. Conversely, the NT preferring neurons might lead to a much weaker contraction of the right lateral rectus muscle. Overall this would lead to an eye movement to the left being executed. A direct activation of abducens motoneurons via the Cgl is also conceivable, as Chochran et al. (1984) assumed a direct linkage of the pretectum to the oculomotor and abducens nuclei in the frog and unpublished data from our lab (B. Guerke, unpublished observations) showed direct projections from the area pretectalis (APT) to the oculomotor und abducens nuclei in the trout.

Distribution of preferred directions

In contrast to some tetrapods, no segregation of coding retinal slip during self- motion around different axes into distinct nuclei seems to occur in chondrichthyans, perhaps because a structure homologous to the nucleus of the basal optic root is missing in *S. canicula* (Smeets et al. 1983). This uniform distribution of preferred directions in fish seems to represent the primitive condition. This result fits well to the parcellation theory suggested by Ebbeson (1980), which states that "nervous systems become more complex, not by one system invading another, but by a process of parcellation." It seems likely that during evolution one nucleus for encoding

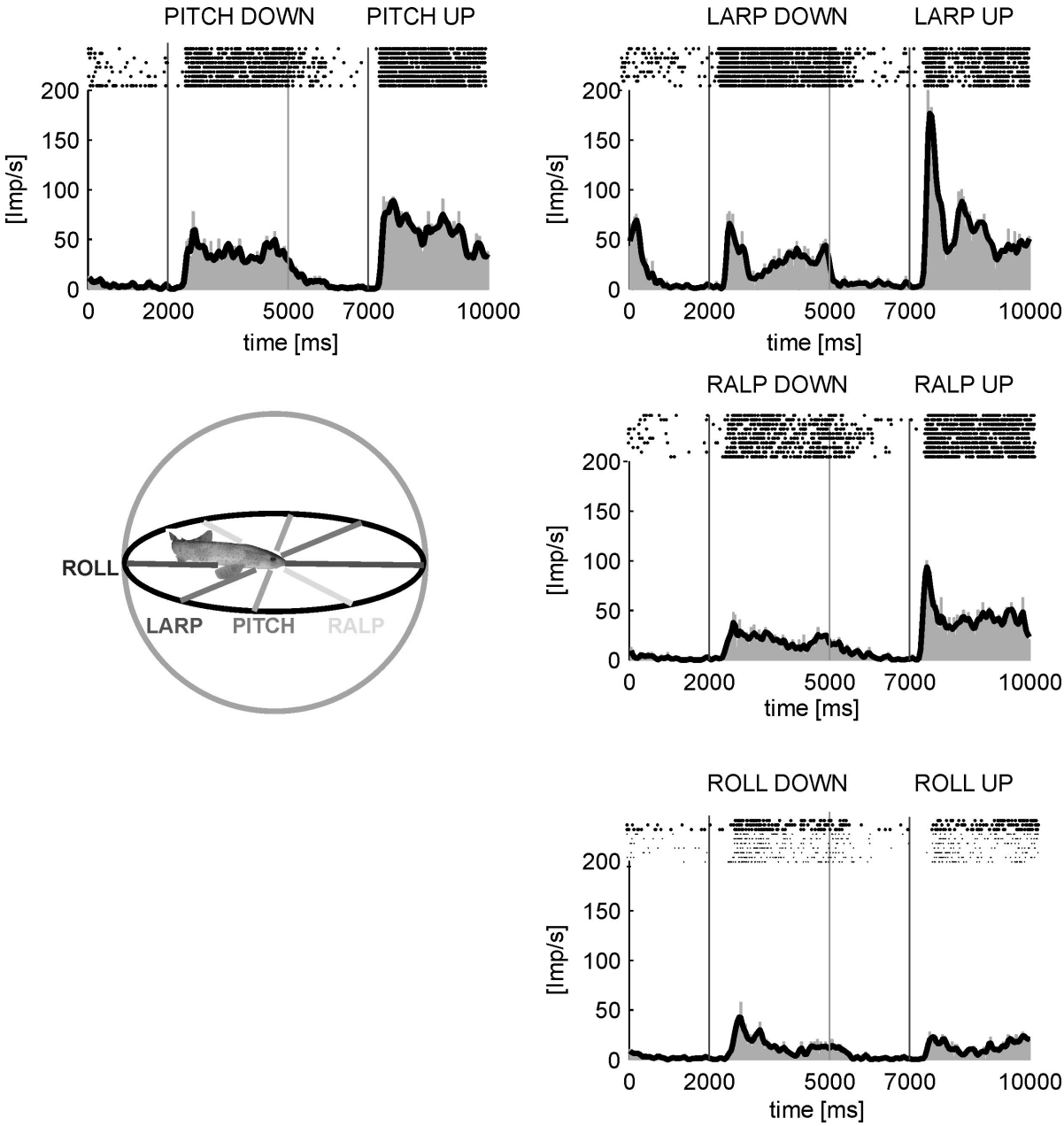

FIG. 7. Peristimulus time histograms and raster plots of a direction-selective neuron in the left Cgl of *S. canicula* as tested through the right eye with a rotational stimulus. Black line represents spike density function, which is based on a Gaussian filtering of the spike train; 0- to 2,000- and 5,000- to 7,000-ms stationary phase; 2,000- to 5,000-ms rotation in CW direction; and 7,000- to 10,000-ms rotation in counterclockwise (CCW) direction. PITCH DOWN, clockwise rotation of the planetarium around the interaural axis of the fish; PITCH UP, counterclockwise rotation of the planetarium around the interaural axis of the fish direction. Rotation around the PITCH axis result in circular motion on the central retina (see Fig. 1*C*); LARP DOWN, CW rotation of the planetarium around the left anterior to right posterior axis of the fish; LARP UP, same axis as LARP CW but rotation in CCW direction; ROLL DOWN, rotation of the planetarium around the longitudinal axis of the fish in CW direction; ROLLUP, rotation in CCW direction. Stimulation around the ROLL axis results in vertical (up-down, down-up) movements on the central retina (see Fig. 1*C*); RALP DOWN, planetarium rotation around the right anterior to left posterior axis of the fish in CW direction; RALP UP, rotation in CCW direction.

retinal slip splits up into a more complex system were different directions of retinal slip are encoded in different nuclei. Our findings additionally support the existence of a monocularly organized oculomotor system as described for some fish (goldfish: Easter et al. 1974; sandlance and pipefish: Fritsches and Marshall 2002) and the chameleon (Gioanni et al. 1993). However, further behavioral studies of the optokinetic system in chondrichtyans are needed to verify or refute a monocular organization.

Vestibular reference frame

Strict coding in vestibular coordinates was not found in the Cgl, i.e., neurons recorded with both linear and rotational stimuli showed no significant bias for the rotational stimuli although half of the tested axes correspond to semicircular canal axes. So far a transformation of reference frames has been shown in mammals (Simpson et al. 1988) and birds (Wylie and Frost 1999; Wylie et al. 1998), it is

questionable whether neurons in the LM and nBOR of other tetrapods show a transformation from a visual into a vestibular reference frame already in the LM and nBOR. Further studies are needed to clarify this question. It is also possible that transformation to a vestibular reference frame occurs later in the processing of visual inputs to the vestibular nuclei (Graf et al. 1988; Leonard et al. 1988; Wylie et al. 1993).

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GRANTS

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