Activity of ventro-posterior thalamus neurons during rotation and translation in the horizontal plane in the alert squirrel monkey

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ABSTRACT

The firing behavior of 107 vestibular-sensitive neurons in the ventro-posterior thalamus was studied in two alert squirrel monkeys during whole body rotation and translation in the horizontal plane. Vestibular-sensitive neurons were distributed primarily along the anterior and posterior borders of ventro-posterior nuclei; three clusters of these neurons could be distinguished based on their location and inputs. Eighty-four neurons responded to rotation; 66 (78%) of them responded to rotation only, and 18 (22%) to both rotation and translation. Forty-one neurons were sensitive to linear translation; 23 (56%) of them responded to translation only. The population rotational response to 0.5 Hz sinusoids with a peak velocity of 40°/s showed a gain of 0.23±0.15 spikes/s°/s, and phase lagging behind the angular velocity by −9.3±34.1°. Although rotational response amplitude increased with the stimulus velocity across the range 4-100°/s, the rotational sensitivity decreased with and was inversely proportional to the stimulus velocity. The rotational response amplitude and sensitivity increased with the stimulus frequency across the range 0.2-4.0 Hz. The population response to sinusoidal translation at 0.5 Hz and 0.1 g amplitude had a gain of 111.3±53.7 spikes/s/g, and lagged behind stimulus acceleration by −71.9±42.6°. Translational sensitivity decreased as acceleration increased, and this was inversely proportional to the square root of the acceleration. Results of this study imply that changes in the discharge rate of vestibular sensitive thalamic neurons can be approximated using power functions of the angular and linear velocity of spatial motion.
INTRODUCTION

The signals carried by neurons in the vestibular system provide an important source of cognitive perception of self-motion in space. The signals that originate at the vestibular end organs are conveyed to the brainstem vestibular nuclei. From there, they are forwarded to the thalamus, and are then sent to the cerebral cortex. The processing of these signals in the vestibular nuclei and various areas of the cerebral cortex, which are involved in perception of spatial motion, has been studied in great details (Khalsa et al. 1987; Grüsser et al. 1990; Gdowski and McCrea 1999; McCrea et al. 1999; Roy and Cullen 2001; Bremmer et al. 2002; Klam and Graf 2003; Cullen and Roy 2004; Dickman and Angelaki 2004; Gu et al. 2006; Klam and Graf 2006; Yakushin et al. 2006).

However, thalamic neuronal activity associated with these signals has been examined less extensively, and additional study is necessary to understand how motion signals are processed by the thalamic neurons that mediate passage of vestibular information to the cerebral cortex.

The focus of the present study is the ventro-posterior thalamus of the squirrel monkey, which contains neurons sensitive to spatial motion. In contrast to thalamic relay nuclei for other sensory modalities, no distinct nucleus associated with transmission of vestibular sensory signals has been identified. Instead, vestibular-related neurons appear to be distributed throughout the broad ventro-posterior portion of the thalamus (Büttner and Henn 1976; Liedgren et al. 1976; Büttner et al. 1977; Magnin and Fuchs 1977; Lang et al. 1979; Meng et al. 2007). These scattered neurons form projections to several cortical areas involved in processing self-motion signals including the parietal insular,

Previous studies in rhesus monkeys found that thalamic neurons sensitive to vestibular stimulation had low spontaneous discharge rate and irregular firing pattern when compared to brainstem and cerebellar neurons sensitive to vestibular stimulation (Büttner and Henn 1976; Büttner et al. 1977; Magnin and Fuchs 1977). The responses of thalamic neurons to passive whole body rotation in the horizontal plane have been reported to lead in phase the angular velocity (Büttner et al. 1977; Meng et al. 2007).

In this paper we present our observations on ventro-posterior thalamus neurons sensitive to whole animal rotation and/or translation in the horizontal plane. We have found these neurons to be clustered primarily on the borders of the ventro-posterior nuclei. The rotational sensitivity of the thalamic neurons is inversely proportional to stimulus velocity across the range 4-100°/s. The translational sensitivity of these neurons decreases with increasing acceleration across the range of 0.05-0.2 g, with the sensitivity inversely proportional to the square root of stimulus acceleration. Preliminary reports have been published elsewhere (Marlinski et al. 2004b; Marlinski et al. 2004a).

METHODS

Experiments were carried out on two alert squirrel monkeys (Saimiri sciureus) prepared for chronic recording from single neurons. Protocols were approved by the University of Chicago Institutional Animal Care and Use Committee, and were in
compliance with the National Institutes of Health guidelines for the care and use of animals in research.

*Surgical preparation*

Surgical procedures were carried out under sterile conditions in a central surgical suite with the assistance of local veterinarians. Anesthesia was initiated with ketamine (10 mg/kg, i.m.), and maintained with intravenous injection of remifentanil (0.025-0.075 µg/kg/min) and isoflurane inhalation (~1%). The animals were supported postoperatively with bupenorphine (0.03 mg/kg, i.m.) and sulfatrimethoprim (30 mg/kg, i.m.).

Details of the surgical preparation have been described previously (Gdowski and McCrea 1999; McCrea et al. 1999). Surgical preparation included cranial attachment of a head-holding acrylic frame oriented parallel to the cranial horizontal (Frankfurt) plane (Emmers and Akert 1963). The frame featured an aluminium ring, which allowed fine adjustment of head position, and served also as a support for an electrode micro-advance device. A teflon-coated coil of stainless steel wire (Cooner) was implanted in one eye for the recording eye movements using the magnetic search coil technique (Robinson 1963). Labyrinthine stimulating electrodes of teflon-coated silver wire (Medwire Corp.) were implanted bilaterally in the middle ear (Minor and Goldberg 1991).

*Experimental setup*

The monkey was seated on a perch situated on a revolving platform atop an actuator for rotational and translational movements. Mounted on the platform were
structures used for restraint of animal’s head and body, electromagnetic field coils for eye and head movement measurements, and a three-dimensional manipulator for orienting a recording electrode micro-drive.

The revolving platform was mounted on a linear sled (T3D, Trilogy Systems) with the translational axis in the horizontal plane. The platform supporting the monkey could be rotated around the yaw axis and locked at different angles relative to the translational axis. The linear sled was mounted on the top of rotary position servomotor (DDR, Kollmorgen), the axis of which was aligned with the earth vertical axis for producing yaw rotations. Motion profile commands were constructed using the Spike-2 (CED 1401) software, which controlled inputs to the servomotors.

During experiments, movements of the monkey’s body were restrained by a jacket tethered to table structures, while limbs were free to grasp hand and foot rails. Care was taken to keep the animal in a comfortable posture similar to that observed during voluntary seating in its cage. The head was restrained by attaching the chronically implanted aluminum ring to a vertical rod fixed to the table structures.

At the beginning of recording from the thalamus the lateral geniculate body (LG) served as a topographical landmark in the area of investigation. Location of the LG was estimated according to field potentials evoked by 1 ms flash illumination (Vivitar 2000) of the darkened recording room.

*Experimental protocol*

Vestibular stimulation was achieved with animal’s rotations around the earth
vertical axis and translations in the horizontal plane along naso-occipital and interaural axes. The rotational vestibular stimuli were 0.25-2.0 Hz sinusoids of 5-80°/s peak angular velocity, and the translational vestibular stimuli were 0.5-4.0 Hz sinusoids of 0.05-0.2 g (0.491-1.944 m/s²) peak acceleration.

*Single unit recording*

Neuronal activity was recorded extracellularly with 4-7 MΩ epoxy-insulated tungsten microelectrode (A-M Systems). Penetrations were carried out with the help of a stereotaxically positioned guide-tube (25 gauge). The microelectrode was advanced into the thalamus using a micro-positioner (FHC) secured to the head-holding frame during experiments.

After two-stage amplification and $10^2$-$10^4$ Hz band-pass filtering of the microelectrode recording, the spikes were discriminated with a dual window discriminator (Bak). Trigger pulses generated by the discriminator were sent to the event channel of the CED 1401 device.

*Identification of neuronal inputs*

The area of the thalamus that we explored in this study was predominantly comprised of the ventro-posterior lateral and medial nuclei related to the processing of somatosensory signals. Spatial motion of the animal triggers neuronal responses to vestibular stimulation, as well as neuronal responses due to somatosensory and visual
stimuli. Our task was to isolate the neuronal responses related to the vestibular system from neuronal responses due to the other stimuli.

Somatosensory sensitivity of every neuron was examined by measuring its response to gentle touch of the hair and skin, and application of pressure to the head, trunk, extremities and the tail. When a neuron responded to any of these stimuli, the somatosensory receptive field was localized. Care was taken to avoid mechanical stimulation of this field during whole animal rotation or translation. If mechanical stimulation of such a field could not be excluded because of the animal’s body motion relative to the harness during vestibular stimulation, the neuron was considered sensitive to somatosensory input only. Several neurons sensitive to animal’s motion responded to stimuli applied to a somatosensory receptive field that was not in contact with the harness. We considered those neurons sensitive to both vestibular and somatosensory inputs.

Neuronal sensitivity to neck proprioception was tested with rotations of the trunk while the head was held stationary. We recorded from group of neurons that were responsive to both whole body and trunk rotations, thus had receiving vestibular and neck proprioceptive inputs. These neurons will be characterized in details in a subsequent report.

To identify neurons receiving vestibular input, the whole animal was manually rotated and translated in the illuminated room. During those motions the animal faced a wall covered with a pattern of alternating black-white undulating vertical stripes with randomly varying 2-4 cm width. If neuronal discharge rate was altered during such motion the illumination was switched off, and neuron’s sensitivity to motion was re-
tested in the dark. If the neuron did not respond during motion in darkness, it was considered sensitive to visual input only. If the neuron was responsive to motion in darkness, it was regarded as a neuron receiving vestibular input.

Data acquisition

Eye and head movements were monitored with a search coil system (Angle-Meter NT, Primelec). Platform rotational velocity was recorded with an angular velocity sensor (Watson). Linear translations along two orthogonal axes were recorded with the dual axis accelerometer (Kionix).

Analogue signals were low-pass filtered with 6 pole 7 kHz Butterworth filters (Frequency devices), digitized at 992 Hz with CED Power 1401, and saved on a computer for off-line analysis. In addition, unfiltered microelectrode recordings were sampled at the rate of 55.6 kHz, and were used for field potential analysis and checking the fidelity of spike discrimination.

Data analysis

Data analysis utilized routines written for the IGOR Pro (WaveMetric), and Excel (Microsoft) software environment.

Unit discharge rate was computed using a time-symmetric algorithm in which discharge rate was computed from the occurrence of spikes immediately before, after, and during the sampling. We considered a neuron to be sensitive to rotation or
translation if the discharge rate was altered by 10% or more. To determine neuronal sensitivity to the angular velocity or the linear acceleration, the discharge rate of a neuron was averaged over 12 or more rotational or translational sinusoids. Averages of motion stimulus and of the discharge rate were fitted with sinusoidal function, and the amplitude and phase shift of the fits were estimated. In neurons that could be silenced during off-direction of rotation, sinusoidal fitting was restricted to periods where linear relationship was observed between the discharge rate and angular velocity. Response nonlinearities due to inhibitory saturation were eliminated by removing parts of the response deviated from linearity (Chen-Huang and McCrea 1998). The coefficients of fit were obtained after exclusion of nonlinear part of the response. The ratio of the response amplitude to the peak angular velocity gave an estimate of the rotational sensitivity or gainR of a neuron (spikes/s/°/s). The ratio of the response amplitude to the peak linear acceleration gave an estimate of translational sensitivity the response or gainT of a neuron (spikes/s/g). The difference between phases of the stimulus and of the response gave an estimate of the response phase shift relative to the angular velocity or linear acceleration of the animal.

Quantitative estimates of responses of various neuronal groups are presented everywhere in the text as average ± standard deviation. Statistical difference between neuronal subgroup averages was verified using the two-tailed distribution t-test. Goodness of fit was assessed by the determination coefficient (R²) of correlation between the regression model and experimental data.
RESULTS

General characteristics of neuronal activity

The firing behavior of 1171 neurons in the ventro-posterior thalamus of alert squirrel monkeys was studied during whole body rotation and translation in the horizontal plane. In 21 cells the discharge rate was modulated during motion, but this response was attributable to stimulation of somatosensory receptive fields by relative motion of the monkey with respect to the harness restraint system. Thirty-five cells were sensitive to motion in the illuminated room only, and their responses were judged to be the result of visual stimulation. One hundred and seven neurons were sensitive to rotational or translational movements in the dark, in the absence of visual and somatosensory stimulation. We classified these cells as vestibular sensitive thalamic neurons. Except for a few neurons silenced during saccades, none of these neurons was sensitive to eye movements in the absence of head movements.

The background discharge rate in our sample of vestibular sensitive neurons varied between 5.1 and 84.6 spikes/s, and was 25.9±15.8 spikes/s on average. The mean rate of background activity that was observed in squirrel monkey was in the range of that reported for analogous neurons in the rhesus monkey: 10.1 spikes/s (Büttner et al. 1977), 17 spikes/s (Magnin and Fuchs 1977), 47.4 spikes/s (Meng et al. 2007).
Anatomical reconstruction of the recordings from the ventro-posterior thalamus

To identify the locations of vestibular-sensitive neurons in the ventro-posterior thalamus we analyzed recordings from identified individual cells and field potentials, and examined postmortem frontal sections of the brains with recognizable traces of microelectrode penetrations.

Reconstructions of recordings from the left thalamus of one of the monkeys are presented in Figure 1, panels A1 and A2, which show sagittal and frontal views of the area of recordings, respectively. Vestibular-sensitive neurons are depicted as red symbols: circles represent neurons responded to angular motion, squares represent neurons responsive to linear motion, and diamonds represent neurons responded to both angular and linear motion. Dark blue circles represent the location of recorded field potential evoked by a flash of light, and the location of cells generated spike bursts in response to this stimulus. These blue symbols are concentrated in an area that we identified as the lateral geniculate body (LG). Green circles indicate positions of recordings where vestibulo-cochlear nerve stimulation evoked recognizable field potentials, but where no neurons sensitive to vestibular stimuli were detected. It is very likely that this area corresponds to the thalamic auditory nucleus – the medial geniculate body (MG). Light blue circles represent cells responding to spatial motion of the animal in the illuminated room, but that were insensitive to the animal’s motion in the dark. We suggest that area to be a part of the lateral pulvinar (PuL). Gray circles represent cells with somatosensory input, which responded with instantaneous high amplitude increase in the firing rate to touch of the hair or gentle pressure onto muscles. In our judgment,
the gray symbol corresponds to the somesthetic relay nuclei, lateral and medial ventro-posterior (VPL and VPM). Detailed reconstructions of recordings from neurons sensitive to somatosensory inputs are shown in Figure 1, panels B-D. Panels B1 and B2 are sagittal and frontal view of recordings from forelimb related neurons, which were distributed over a large portion of the VP. Panels C1 and C2 are sagittal and frontal view of recordings from hindlimb- and tail- responsive neurons. These neurons were located primarily posterior and inferior to forelimb-responsive cells. Panels D1 and D2 are sagittal and frontal view of recordings from head related neurons, which were found in the medial part of the VP. Receptive fields of neurons with various somatosensory inputs are depicted with different symbols, indicated below the panels of Figure 1.

A photograph of the frontal section of the thalamus of another monkey is shown in the Figure 1, panel E. Within this part of the section, four microelectrode penetrations had been made. Reconstructed locations of neurons, which were identified during these penetrations, are indicated with different symbols superposed on the photograph. Red circles represent vestibular-sensitive neurons. White circles represent cells sensitive to animal rotation or translation only in light. Yellow symbols represent neurons with inputs from different parts of the body: diamonds, leg; squares, thigh; circles, tail.

Neurons sensitive to angular and/or linear motion of the animal in the horizontal plane were distributed primarily on anterior and posterior borders of a region that contained neurons responsive to somatosensory stimuli and corresponded to the complex of the ventro-posterior nuclei (VP). Within this area the separate clusters of vestibular sensitive neurons could be distinguished. One cluster was formed by neurons located in the posterior part of the VP, superior to the MG, and inferior to the PuL. These neurons
were surrounded by vestibular-insensitive cells activated by somatosensory stimuli, such as touch or pressure on the hind limb or tail. Among the vestibular-sensitive neurons studied we found units activated with a short latency of about 4 ms by electrical stimulation of the ipsilateral VIIIn (Fig. 1, F). Superior and posterior to this cluster was another group of vestibular-sensitive neurons that were enclosed by other cells responsive only to visual stimuli. Another cluster of vestibular-sensitive neurons was located in an area corresponding to the oral or superior part of the VP. Among these neurons were cells responsive also to somatosensory stimulation, such as touch of the shoulder or trunk.

*Responses to rotation*

We recorded from 84 neurons that responded to rotation, which constitute 76% of the entire sample of vestibular-sensitive neurons. They were divided into two groups based on their directional sensitivity: 37 neurons increased their discharge rate during ipsilateral rotation and thus showed type I responses according to the Duensing and Schaeffer classification (Duensing and Schaefer 1958); 47 neurons showed type II responses by increasing their discharge rate during contralateral rotation. No rotation-sensitive neurons with bi-directional responses were seen. Sixty-six neurons, 62% of the total sample or 78% of rotation-sensitive neurons, responded to rotation only. Eighteen neurons, 17% of the total or 22% of rotation sensitive neurons, were sensitive to both rotation and translation. A detailed classification of all neurons according to their rotational and translational responses is given Table 1.
Rotational responses were quite variable, both in the amplitude and phase relative to the animal’s motion velocity. The gain and phase of the responses of all rotation-sensitive neurons to sinusoids of 0.5 Hz frequency and 40°/s peak velocity are plotted in a polar graph in Figure 2. To distinguish between the different types of neurons the responsive cells are depicted with various symbols. Type I neurons are shown as diamonds and type II neurons as circles. Dark gray symbols represent neurons responding to rotation only, while light gray symbols represent neurons responding to both rotation and translation. To evaluate rotational sensitivity of the population as a whole a mean population response vector in polar coordinates was calculated (Batschelet 1981). The black diamond and circle represent the population mean response gain and phase of type I and type II neurons respectively. The sensitivity to rotational stimulation did not vary considerably between different groups of neurons. The average sensitivity of all type II neurons (0.25±0.16 spikes/s°/s) as a group seemed to be greater than that of type I neurons (0.20±0.13 spikes/s°/s), but the difference was not statistically significant (p=0.11). Population response sensitivity of both neuronal groups was approximately 10% smaller than the arithmetic average: it was 0.23±0.20 spikes/s°/s in type II neurons, and 0.17±0.17 spikes/s/deg/s in type I neurons (Fig. 2). Detailed data on responses of various neuronal sub-groups are presented in Table 2. In only one case was there a statistically significant difference in sensitivity between subgroups, namely, between type II neurons sensitive only to rotation and type I rotation-sensitive neurons, which were also sensitive to translation (p=0.04). Because of the similarity in the response magnitude across neurons of various types we pooled all of the data together and
calculated the average sensitivity of the entire population of rotation-sensitive cells:

\[ 0.23 \pm 0.15 \text{ spikes/s/°/s}. \]

For rotation sensitive neurons as a group the response phase relative to on-directional angular velocity was \(-9.3 \pm 34.1°\). The response phase varied widely, ranging from a phase lead of 73.7° to a phase lag of \(-88.3°\). This variability is reflected in the high standard deviation of the phase mean. Average responses of type II neurons had a greater phase lag \((-16.4 \pm 32.03°)\) than responses of type I neurons \((-1.81 \pm 36.82°)\), but the difference fell just short of statistical significance \((p=0.06)\). On average, the responses of type I and type II neurons sensitive to both rotation and translation lagged behind the angular velocity more than neurons sensitive to rotation only (Table 2). However, due to the high variability in phase shifts, the differences between all subgroups were statistically insignificant \((p>0.05)\).

**Rotational responses in dark and light**

We considered neurons to have vestibular input if they responded to angular or linear motion in darkness. To clarify whether the vestibular responses were modified by illumination, we compared rotational responses in light to responses in the dark in 32 of 84 rotation-sensitive neurons.

The phases of the rotational responses of these neurons in the light are plotted against the phases of responses in the dark (Fig. 3, C). The thick diagonal line indicates zero difference in phase, while two thin diagonal lines show phase shifts of +45° and −45°. The gain of rotational responses in the light versus the gain of responses in the...
dark is plotted in Figure 3, D. The diagonal line in this panel indicates constancy in the gain for responses under the two conditions.

Two groups of neurons could be distinguished on the basis of the phase shifts of their responses in the dark versus the illuminated room.

In one group we included neurons (27 of 32, 84%), which responses to rotations in the light and in the dark either did not change their phases, or the phase lead of responses in the light increased relative to the phase lead of rotational responses in the dark. Examples of representative neuron responses to rotations in the dark and in the light are shown in Figure 3, panels A1 and A2, respectively. In 18 neurons response phases in light deviated from response phases in the dark in the range of $-6.9$-$21.2$ deg, however, statistically those differences were indistinguishable ($p>0.05$). In 9 neurons the responses in the light increased their phase lead by $26.2$-$56.3$ deg, and these shifts were statistically significant ($p<0.01$). Despite the variability, all these neurons represented a continuum in respect to changes in phase of rotational responses in the darkness and in the illuminated room (Fig. 3, C, gray symbols). For all these neurons pooled together, the phase lead of responses in the light exceeded, on average, by $14.2 \pm 21.4^\circ$ the phase of responses in the dark, though this difference was statistically insignificant ($p=0.13$).

Rotational sensitivity was not altered with illumination: the gain for responses in the light was not different from the gain for responses in the dark, deviating by only $0.03\pm0.12$ spikes/s/$^\circ$/s, on average, and the difference was not significant ($p=0.61$) (Fig. 3, D, gray symbols).

Another, smaller group comprised neurons (5 of 32, 16%) responded to rotations in the light in a different way. The responses of one of these neurons to rotations in the
dark and in the light are shown in Figure 3, panels B1 and B2, respectively. These neurons were distinguished by a substantial increase in the phase lag of their responses in the light compared to their responses in the dark. In each of these neurons the difference between phases of the responses was statistically significant (p<0.01 in four neurons, and p<0.025 in one neuron). On average, the phase shift of responses in the dark and in the light was $-52.6 \pm 12.3^\circ$ (Fig. 3, C, black symbols). Phases of averaged responses to rotation in two distinct conditions differed significantly (p<0.01, paired t-test with two-tail distribution). Rotational sensitivity in the light was not higher than in the dark, although their average estimates diverged by $0.11 \pm 0.15$ spikes/s/°/s, the difference was not statistically significant (p=0.22) (Fig. 3, D, black symbols).

The constancy in rotational sensitivity in the major group of neurons is an indication that in the thalamus, the vestibular signal is processed independently from visual signals. The small increase in responsiveness observed in a part of these neurons during rotation in light more likely reflects an increase in background activity due to a general elevation of sensory inputs in the illuminated environment, rather than a response to specific visual stimuli.

A significant increase in the phase lag of responses in the light, seen in a small group of rotation sensitive neurons, may reflect a transition in which their responses instead of being related to rotational velocity began to relate to position. These neurons were nested among visually sensitive cells, and were primarily located superior and posterior in the explored area, which we identified as the PuL. It is very likely that they represent pulvinar visually sensitive cells that also receive vestibular input. One result of
the vestibular input to these cells may be an increase in their sensitivity to the visually perceived movement of surroundings during self-motion.

**Rotational response as a function of velocity**

In 15 neurons we recorded responses to rotations for varying velocities, which ranged from 4 to 100 °/s. In all these neurons we saw that the response amplitude increased with the rotational velocity. This increase, however, was not linear. A ratio of the response amplitude to the amplitude of the rotational stimulus, defined as response gain, decreased with increasing stimulus velocity. Figure 4 illustrates the changes in the absolute and relative magnitude of the responses to 1 Hz rotational sinusoids. Panels A-E show responses of a neuron that were symmetrical during excitatory and inhibitory parts of the cycle. Panels F-H show responses of a neuron with inhibitory saturation during rotation with the highest of used peak velocities. The rotational gain of the 15 neurons is plotted as a function of the peak angular velocity in Figure 4, I. The data are modeled by the power function shown as a gray line. The fit yields an estimate of average gain = 7.8 × (velocity)^{-0.9}, R^2 = 0.54. To simplify the equation, we set an exponent (power) to negative unity, and obtained gain = 11.3 × (velocity)^{-1}, which can be written as gain = 11.3/velocity. It follows from this ratio that for the range of velocities tested, the correlation between gain and angular velocity appears to be quite straightforward: rotational sensitivity is inversely proportional to the velocity of rotation.

The phase of responses to rotations with different angular velocities did not vary consistently in the cells we studied (Fig. 4, J).
Rotational response as a function of frequency

In nine neurons the rotational responses were tested with two to five frequencies in the range of 0.2-4.0 Hz. The responses of one of those neurons are shown in Figure 5, panels A-C. The response amplitude increased with the rotational frequency. Rotational sensitivity, or gain_R, also increased with the rotational frequency. This increase in gain_R was not linear. Gain_R is plotted as a function of the rotational frequency in Figure 5.

The phase of rotational responses of different neurons varied substantially between a phase lead of 90° to a phase lag of −60° relative to the velocity of rotation. In most cases, the responses slightly led the rotational velocity or were in phase with it. There was no significant change in the phase of responses as the rotational frequency increased (Fig. 5, E).

Responses to translation

Forty-one neurons (38% of our entire sample) were sensitive to linear translation. Twenty-three of these neurons (56%) responded to translation only, and 18 of them (44%) responded to both translation and rotation. We did not study the spatial distribution of translational responses, and we restricted testing to translations along two cardinal axes: interaural and naso-occipital. Sixteen cells (39%) responded to translations along the interaural axis. Twenty-two neurons (54%) responded to translations along the naso-occipital axis. The latter group included six neurons responded to the second
harmonic of translational sinusoid, they were of type III according to the classification of Duensing and Schaeffer (1958). All other neurons showed unidirectional response preference. Three neurons (7%) responded similarly to translation along both axes. A detailed classification of these translation-sensitive neurons is given in the Table 1.

Sensitivity (gain\textsubscript{T}) and phase shift of translational responses were calculated relative to the peak acceleration of sinusoidal motion. Figure 6 uses polar coordinates to display the gain\textsubscript{T} (A) and phase (B) of responses to interaural and naso-occipital translations with 0.5 Hz frequency and 0.1 g peak acceleration. The gain\textsubscript{T} and phase of the population responses of subgroups of neurons sensitive to ipsi- or contralateral interaural translation, and fore or aft naso-occipital translation, were calculated as polar coordinates of a mean vector (Batschelet 1981). The arithmetic average gain\textsubscript{T} and phase were calculated to estimate the variability across the responses of individual neurons. The results of this analysis of the different subtypes of the translation sensitive neurons are summarized in the Table 3.

The translational response gains were similar in neurons sensitive only to translation and in those sensitive to both translation and rotation. In addition, they were similar among neurons showing different directional sensitivities to translation. The only differences in average gain\textsubscript{T} were between neurons responsive only to translation along the interaural axis and neurons responsive to both translations along the interaural axis and to yaw rotation (Table 3). These differences, however, were statistically insignificant (p=0.17), and probably result from the small sample size. Because of this similarity in translational sensitivity, we grouped the data together and calculated the average
sensitivity of the whole sample of translation-sensitive neurons to be $111.3 \pm 53.7$ spikes/s/g.

The phase of the responses to translation varied significantly among neurons, but in general, translational responses lagged behind peak stimulus acceleration. Estimates of response phase shifts, which are shown in Table 3, were calculated relative to on-directional acceleration of linear motion. No statistically significant differences were found in comparing the averaged response phases to the population response phases of neuronal subgroups sensitive to translation only or to both translation and rotation. The same was found when comparing the averaged response phases to the population response phases of neuronal subgroups sensitive to translation along one of the cardinal axes. On average, the response phase shift in all translation-sensitive neurons relative to on-directional translation was $-71.9 \pm 42.6^\circ$. This result shows that translational responses of thalamic neurons lagged behind the acceleration of linear motion, but led the linear motion velocity.

In nine neurons we tested responses to translations with various frequencies and accelerations. Exemplary responses from one of these neurons are shown in Figure 7, panels A-C. The $\text{gain}_T$ in this neuron decreased with increasing acceleration. The same was true in the other cells, and is visible in the plot of $\text{gain}_T$ versus translational acceleration (Fig. 7, D). The relationship between $\text{gain}_T$ and translational acceleration was not linear, and was best approximated with a power function. The data are fit with the equation $\text{gain}_T = 53.7 \times \text{acceleration}^{-0.49}$, $R^2 = 0.26$ (Fig. 7, D, solid gray line). In the equation the exponent (power) is equal to $-1/2$, which means that the sensitivity to translational acceleration was inversely proportional to the square root of the
acceleration. Bearing in mind that acceleration is proportional to the square of velocity we can assume that translational gain is inversely proportional to linear stimulus velocity, and thus is similar to what we have found in the relationship between the neuronal rotational gain and stimulus angular velocity. In contrast, the phase of the translational responses did not vary with the acceleration in the neurons tested (Fig. 7, E).

**Convergence of rotational and translational inputs**

Among neurons sensitive to vestibular stimulation were 18 cells (17% of our entire sample) that responded to both rotational and translational stimulation. These cells showed no directional preferences in their responses. They were almost equally divided into neurons with type I and type II rotational responses. The fraction of these neurons sensitive to naso-occipital translations was equal to the fraction of neurons sensitive to interaural translations. The details of these results are listed in Table 1.

Responsiveness to angular and linear motion varied between these neurons. We did not find that the sensitivities to rotational and translational stimuli varied in direct proportion with each other.

**DISCUSSION**

In our study of ventro-posterior thalamus neurons sensitive to vestibular stimulation we concentrated on cells that were responsive to rotation and/or translation in the horizontal plane only. We found these neurons to be distributed across a wide area in
the ventro-posterior thalamus. Our observations are in agreement with those of Büttner and colleagues (1977), Magnin and Fuchs (1977) and Meng and colleagues (2007) who reported that the neurons sensitive to rotation in rhesus monkeys were scattered within the limits of the ventro-posterior nuclei, and were intermingled with other cells that did not receive vestibular input. Our data are also in accord with the results of Liedgren and colleagues (1976), who studied neuronal activity in the ventro-posterior thalamus in the squirrel monkey. They found that neurons responsive to vestibular nerve stimulation were not confined to one cell group, but were dispersed among the various somatosensory nuclei, mostly in the oral part of pulvinar, and the oral and caudal parts of the VPL, while no vestibular sensitive neurons were detected in the VPM or in the central part of the VPL.

We observed that the vestibular-sensitive neurons in the ventro-posterior thalamus were not randomly distributed; instead, vestibular-sensitive neurons were grouped into separate clusters. One cluster was located within the midst of adjoining areas that we recognized as posterior region of the VP, an area of the PuL, and the superior part of the MG. This cluster therefore coincides with the inferior part of the nucleus ventralis posterior, pars posterior (VPP), identified by Akbarian et al. (1992) as the main source of thalamic projections to the parieto-insular vestibular cortex (PIVC) in the squirrel monkey. This cluster is very likely to be analogous to the “vestibular cluster” of large, multiangular cells that emerges from the dorsal aspect of MG in the macaque monkey (Craig 2004). Another distinct cluster of vestibular-sensitive neurons was situated superior and posterior to the one described above. We suggest that these neurons, which were surrounded by cells sensitive only to visual stimuli, were located in the PuL. A
third distinctive cluster of vestibular-sensitive neurons was observed in the area that we classified as the superior border of the VP. This observation is in agreement with the data of Liedgren et al. (1976), who identified in the oral part of the VPL a majority of cells combining short-latency vestibular responses and somatosensory responses from proximal parts of the limbs and trunk. It is possible that these different clusters of vestibular-sensitive neurons in the ventro-posterior thalamus correspond to distinct, separate sources of projections from the thalamus to different cortical areas involved in the processing of vestibular signals, as described by Akbarian et al. (1992). Using retrograde labeling of thalamo-cortical neurons with HRP in squirrel monkeys, these researchers found that the parieto-insular vestibular cortex (PIVC) received input mainly from the posterior part of ventro-posterior nuclei (VPP), the somatosensory cortical area 3aV received input mainly from the superior region of ventro-posterior nuclei, and the association parieto-temporal cortical area T3 received input mainly from the oral and medial pulvinar.

Most of our vestibular-sensitive neurons responded to rotation in the horizontal plane. The average rotational sensitivity of these neurons, which was estimated for responses to 0.5 Hz sinusoids with 40°/s peak velocity, was 0.23 spikes/s/°/s.

We found that despite the extensive variation between neurons the mean response phase generally followed changes in the angular velocity. This echoes studies of the phase shift of thalamic neuron responses in the rhesus monkey (Büttner et al. 1977; Magnin and Fuchs 1977; Meng et al. 2007). There are, however, some quantitative differences between those studies and ours. In the rhesus monkey experiments the response had been found to lead the angular velocity by 10-30°, whereas we found a
small phase lag of $-9.3^\circ$ for the response in the squirrel monkey. It is reasonable to compare response phase shifts of thalamic neurons with those recorded from vestibular nuclei neurons. In the gerbil brainstem it was found that vestibular-sensitive neurons responded to 0.1-2 Hz sinusoids with $60^\circ$/s amplitude in phase with rotational velocity (Kaufman et al. 2000). In alert rhesus monkeys, the rotational responses of vestibular nuclei neurons lead the angular velocity; three different studies in monkeys have produced very similar estimates of response phase lead: $2-35^\circ$ over the frequency range 0.2-0.93 Hz (Fuchs and Kimm 1975), $\leq 10^\circ$ at frequencies above 0.2 Hz (Buettner et al. 1978), and 20 deg at 0.5 Hz (Dickman and Angelaki 2004). According to the data from the rhesus monkey, the mean thalamic neuron response to rotation shows a phase lead that exceeds the response of vestibular nuclei neurons. This difference in response phases suggests that the rotational signal is rapidly transmitted between the vestibular nuclei and the thalamus. In contrast, our data indicate that the thalamic neuron response has a small lag behind the vestibular nuclei neuron response, suggesting that a small delay occurs in processing signals in the vestibulo-thalamic pathway.

In the available literature examining rotational responses of thalamic neurons we did not find reports on the relationship between rotational sensitivity and angular velocity. Büttner et al. (1977) analyzed gain as a function of the stimulus frequency. In their experiments, however, rotations with different frequencies were performed with different angular velocities. If in the plots of their paper the rotational velocities are substituted for the corresponding frequencies it can be seen that the response gain decreased with increasing peak velocity. A similar relationship between rotational sensitivity and the angular velocity is seen in the vestibular nuclei neurons. For example,
Schneider and Anderson (1976) found that the response gain in gerbils decreased with increasing angular velocity, and in the most sensitive neurons the response gain showed an almost logarithmic decrease with increasing stimulus velocity. Dickman and Angelaki (2004), who analyzed response gain as a function of stimulus frequency, found that the increase in gain followed an increase in frequency. In fact, at frequencies where response gain increased, the peak angular velocity was not the same, but decreased from 30°/s to 15 and 7.5°/s, thus indicating the decrease in gain with increase in the rotational velocity.

We observed that the phase of responses to rotations with different angular velocities but fixed stimulus frequency did not vary consistently. A similar constancy in response phase during rotational stimulation at different velocities was observed in thalamic units of rhesus monkeys (Magnin and Fuchs 1977). These results suggest that the temporal relationship between stimulus and rotational response of thalamic neurons is not affected by the speed of rotational movement, at least within the range of angular velocities examined.

Our results on the relationship between response to rotation and stimulus frequency are in a good agreement with the data of Büttner et al. (1977) and Meng et al. (2007), who studied the rotational responses of thalamic neurons in rhesus monkeys. Their estimate of the absolute gain was 0.56 spikes/s°/s at 0.1 Hz, and 0.54 spikes/s°/s at 0.5 Hz. They reported that for their sample of neurons, the responses were in phase with or led the stimulus velocity by 10-30°. The relationship between the response gain and rotational frequency in the range of 0.2-4 Hz for the thalamic neurons in the squirrel monkey (this work) and those recorded in the rhesus monkey (Büttner et al. 1977; Meng et al. 2007) are generally similar to what has been seen in the vestibular nuclei neurons in
gerbils (Schneider and Anderson 1976), and in monkeys (Buettner et al. 1978; Dickman and Angelaki 2004). In both vestibular nuclei and thalamic neurons, the response gain increased with the stimulus frequency. A substantial difference between these two groups of neurons is the magnitude of their rotational sensitivity. In our sample of thalamic neurons, the average gain of 0.45 spikes/s/°/s at 1 Hz was about two times lower than that of the vestibular nuclei neurons recorded by Buettner et al. (1978), who found it to be 0.77 spikes/s/°/s, or Dickman and Angelaki (2004) who found it to be 0.9 spikes/s/°/s at 1 Hz frequency. In both thalamic and vestibular nuclei neurons the rotational responses tended to increase their phase lead relative to angular velocity, but this tendency did not reach statistical significance for either type of neuron.

Our estimate of the mean translational sensitivity of thalamic neurons (111 spikes/s/g) was almost identical to the average sensitivity (103.8 spikes/s/g) estimated for thalamic neurons sensitive to translation in the rhesus monkey (Meng et al. 2007). A difference in translational sensitivity had been found between vestibular nuclei neurons with only otolith input and those with both otolith and canal inputs: the gain of the translational responses of the latter type of neurons (219 spikes/s/g) was almost twice as high as that calculated for the former (134 spikes/s/g) (Dickman and Angelaki 2002). In our sample of thalamic cells, we did not see significant differences in sensitivity between neurons responsive to translation only and neurons responsive to translation and rotation. In acute and chronic experiments in cats and monkeys it has been found that responses of vestibular nuclei neurons to activation of otolith afferents were in phase with the velocity of motion (Tomlinson et al. 1996; Schor et al. 1998; Dickman and Angelaki 2002). In a detailed study Dickman and Angelaki (2002) reported that translation-sensitive vestibular
nuclei neurons could be divided into three groups according to their response dynamics: the most common group showed a responses phase lag of less than $-60^\circ$ relative to acceleration, another group showed a lag between 0 and $-50^\circ$, and a third group showed a modulated firing rate almost in phase with acceleration. Taken together, these findings indicate that the phases of translational responses are distributed between stimulus acceleration and velocity, and on average correlate more tightly with velocity. Similar temporal relationship between neuronal response and translational stimulus is seen during processing of motion signal in vestibular-sensitive thalamic neurons.

A convergence of rotational and translational inputs was seen in 17% of the vestibular-sensitive thalamic neurons we studied. We suggest that small proportion of neurons with convergence of signals from different end-organs, which were identified in our sample of cells, was the result of limitation of motion to the horizontal plane only. For comparison, Meng and colleagues (2007) reported that 90% of thalamic neurons they recorded in the rhesus monkey were sensitive to both rotational and translational stimuli. In the vestibular nuclei the number of neurons sensitive to both rotational and translational stimuli has differed from study to study. In decerebrated cats a convergence of both inputs was found in 17–21% of all cells recorded, according to Zhang et al. (2001) and Schor et al. (1998). In the alert gerbil a convergence of the inputs was seen in 38% of neurons (Kaufman et al. 2000). Fully half of the neurons recorded in the alert rhesus monkey vestibular nuclei have been reported to be sensitive to both motion stimuli (Tomlinson et al. 1996; Dickman and Angelaki 2002).

In our experiments, we found that sensitivities to translational and rotational stimuli were independent of each other, and high sensitivity to one input did not
necessarily mean high sensitivity to the other. This could result from spatial separation
of the canal and otolith organ inputs from the vestibular nuclei. The former have been
found primarily in the superior and lateral vestibular nuclei, while the latter have been
found more posterior in the lateral, medial, and descending nuclei; both inputs overlap in
the lateral vestibular nucleus (Zhang et al. 2001). In the thalamic neurons that receive
projections from the midst of that overlap, the inputs from canal and otolith organs could
be equal, while in other thalamic neurons one of the inputs could be larger than the other.

Our results imply that changes in the discharge rate of thalamic neurons, which
code motion in the horizontal plane, can be approximated with power functions of the
velocity of displacement. Such a compressed functional relationship between neuronal
response and stimulus is common in the sensory systems (Stevens 1970; Johnson et al.
2002; Drew and Abbott 2006). These power relationships have been considered to be an
effective strategy for neuronal responses to encode stimuli that vary across a wide
dynamic range (Stevens 1970; Dayan and Abbott 2001). Since the range of self-motion
velocities overlaps four decades in the decimal scale, the demands are high for vestibular-
sensitive neurons to effectively encode signals of motion. The idea that neuronal
responses to sensory stimuli can be expressed as a power law correlates with quantitative
measures of how these stimuli are cognitively perceived. The psychophysical law of
Weber, as modified by Stevens, postulates that sensation is a power function of the
stimulus magnitude (Stevens 1961). The overall efficiency of the relationship between
neuronal activity coding spatial motion and the subjective perception of that motion from
the vestibular activity is quite effective: the accuracy in subjective estimates of
translations and rotations in the horizontal plane have been found to closely match the
actual magnitude and velocity of the spatial displacement (Israel et al. 1997; Jurgens et al. 1999; Marlinsky 1999b; Marlinsky 1999a; Becker et al. 2000; Mittelstaedt and Mittelstaedt 2001).

ACKNOWLEDGEMENT

Authors are grateful to Michael Graziano and John Jackson for their work in building the experimental setup, and Dr. Timothy Belton for discussion the material and help in preparation of the manuscript.

GRANTS

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LEGENDS TO FIGURES

Fig. 1. Location of vestibular sensitive neurons in the ventro-posterior thalamus. A1 and A2: Sagittal and frontal views of recording sites from the left VP region of one animal. Red symbols represent vestibular sensitive neurons: circles are neurons responding to rotation; squares, neurons responding to translation; diamonds, neurons responding to both rotation and translation. Dark blue circles represent locations of field potentials evoked by a flash of light, and cells activated by this stimulus. Green circles show locations of field potential evoked by VIII nerve stimulation, and neurons insensitive to motion. Gray circles represent neurons sensitive to somatosensory stimuli. Light blue circles represent cells responsive to moving visual stimuli, but insensitive to animal’s motion in darkness. B1 and B2: Sagittal and frontal views of recording sites from somatosensory neurons with forelimb receptive fields. C1 and C2: Sagittal and frontal views of recording sites from neurons with hindlimb- and tail-receptive fields. D1 and D2: Sagittal and frontal view of recordings from neurons with head-receptive fields. Receptive fields of somatosensory neurons are indicated with different symbols shown below the panels. E: Frontal section of the left thalamus of a second animal. Vertical lines are superposed on traces of gliosis caused by four penetrations. Red circles represent vestibular sensitive neurons. Yellow symbols indicate location of cells sensitive to touch at various points on an animal’s body: diamond, foot; circle, thigh; square, tail. White circles represent cells responsive to moving visual stimuli. F: VPP neuronal responses to contralateral VIII nerve stimulation. Superposition of nine recordings. Abbreviations: CM, centrum medianum; FR, formatio reticularis; LG, lateral
geniculate body; MD, nucleus medialis dorsal; MG, medial geniculate body; NR, nucleus ruber; P, posterior nucleus; Pd, nucleus peripeduncularis; PuL, pulvinar lateralis; PuO, pulvinar oralis; VPL, nucleus ventro-posterior lateralis; VPP, nucleus ventro-posterior, pars posterior. See text for details.

Fig. 2. Gain and phase of rotational responses. Circles represent type II neurons; diamonds, type I neurons. Dark gray symbols depict neurons responsive to rotation only; light gray symbols, neurons responsive to both rotation and translation. The black circle and diamond, respectively, represent population mean gain and phase for type I and type II neurons. The gainR is presented as a radius of the plot; response phase is shown as angular shift relative to rotational velocity.

Fig. 3. Rotational responses of vestibular-sensitive neurons in darkness and in light. A and B: Responses of two different neurons are shown in rows. Left column (A1, B1): responses in darkness. Right column (A2, B2): responses in the light. In each panel the upper trace represents head angular velocity (H') in °/s; the middle trace shows the raster record of unit activity; and the lower histogram is an average discharge rate (spikes/s), with a superposed sinusoidal function fit. Gain and phase shift relative to rotational velocity are given in each panel. The monkey graphic indicates the mode of motion. wbr, whole body rotation. C: Responses phase of in light is plotted versus response phase in the dark. The thick diagonal line indicates no phase difference of responses in two conditions. Two thin diagonals indicate phase lead of 45° and phase lag of -45° for responses in the light. Two groups of neurons (see text) are indicated as gray and black
symbols. D: Gain of responses in the light is plotted versus gain of responses in the dark. The diagonal line indicates no difference across the two conditions. Gray and black symbols are same as in C.

Fig. 4. Rotational response as a function of angular velocity. A-E: Neuron with symmetrical excitatory and inhibitory firing rate modulation in response to 1 Hz sinusoids with increasing angular velocity. F-H: Neuron with inhibitory saturation of the firing rate in response to high velocity rotation. The peak velocity, the amplitude of a sinusoidal fit to the response, and response gain are given in each panel. Traces on panels are as in Fig. 2. I: Neuronal response gain \( R \) plotted as a function of peak angular stimulus velocity. The gray curve is an exponential function fit (see text). J: Response phase shift plotted as a function of peak angular stimulus velocity. In panels I and J the black symbols are data from the neuron shown in A-E, the gray symbols are data from the neuron shown in F-H.

Fig. 5. Rotational response as a function of angular stimulus frequency. A-C: Representative neuron responses to 40°/s peak velocity sinusoids with increasing frequency (0.5, 1, and 2 Hz). The stimulus frequency, the amplitude of a sinusoidal fit to the response, and response gain are given in each panel. Traces on panels are as in Fig. 2. D: Neuronal response gain \( R \) plotted as a function of the rotational frequency. G: Response phase plotted as a function of the rotational frequency. Black circles in panels D and E are data from the neuron shown in panels A-C.
Fig. 6. Gain and phase of neuronal responses to linear translation along the interaural (A) and naso-occipital (B) axes. Circles represent type I neurons; diamonds represent type II neurons. Dark gray symbols represent neurons responsive to translation only, light gray symbols represent neurons responsive to both translation and rotation. Black circles are the population mean gain and phase. The $\text{gain}_T$ is presented as a radius of the plot; response phase is shown as angular shift relative to translational acceleration.

Fig. 7. Translational responses as a function of linear acceleration. A-C: Representative neuron responses to 1, 2 and 4 Hz sinusoids with 0.15, 0.21, and 0.1 g peak acceleration. In each panel the upper trace is linear acceleration, with the other traces as in Fig. 2. D: Neuronal translational gain plotted as a function of peak linear acceleration. The superimposed gray line is a power function fit. G: Response phase plotted as a function of peak linear acceleration. Black circles in panels D and E are data from the neuron shown in panels A-C. The monkey graphic indicates the mode of motion, wbt, whole body translation.
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Stevens SS (1961) To honor Fechner and repeal his law. Science 133: 80-86
Table 1. *Classification of neurons according to their rotational and translational responses.*

<table>
<thead>
<tr>
<th>Type</th>
<th>N</th>
<th>Proportion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total sample</td>
<td>107</td>
<td>100%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Rotation sensitive</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All</td>
<td>84</td>
<td>76% of total</td>
</tr>
<tr>
<td>Type I</td>
<td>37</td>
<td>44% of rotation all</td>
</tr>
<tr>
<td>Type II</td>
<td>47</td>
<td>56% of rotation all</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rotation sensitive only</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All</td>
<td>66</td>
<td>62% of total, 78% of rotation all</td>
</tr>
<tr>
<td>Type I</td>
<td>29</td>
<td>44% of rotation only</td>
</tr>
<tr>
<td>Type II</td>
<td>37</td>
<td>56% of rotation only</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Rotation and translation sensitive</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All</td>
<td>18</td>
<td>17% of total, 22% of rotation all, 44% of transl. all</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Rotational response</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Type I</td>
<td>8</td>
<td>44% of rotation and translation</td>
</tr>
<tr>
<td>Type II</td>
<td>10</td>
<td>56% of rotation and translation</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Translation sensitive</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All</td>
<td>41</td>
<td>38% of total</td>
</tr>
<tr>
<td>Interaural</td>
<td>16</td>
<td>39% of translation all</td>
</tr>
<tr>
<td>Naso-occipital</td>
<td>22</td>
<td>54% of translation all</td>
</tr>
<tr>
<td>Interaural + naso-occipital</td>
<td>3</td>
<td>7% of translation all</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Translation sensitive only</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All</td>
<td>23</td>
<td>21% of total, 56% of translation only</td>
</tr>
<tr>
<td>Interaural all</td>
<td>7</td>
<td>30% of translation only</td>
</tr>
<tr>
<td>Interaural ipsi</td>
<td>5</td>
<td>71% of translation only, interaural</td>
</tr>
<tr>
<td>Interaural contra</td>
<td>2</td>
<td>29% of translation only, interaural</td>
</tr>
<tr>
<td>Naso-occipital</td>
<td>14</td>
<td>61% of translation only</td>
</tr>
<tr>
<td>Naso-occipital fore</td>
<td>6</td>
<td>75% of translation only, naso-occipital</td>
</tr>
<tr>
<td>Naso-occipital aft</td>
<td>2</td>
<td>25% of translation only, naso-occipital</td>
</tr>
<tr>
<td>Naso-occipital fore + aft</td>
<td>6</td>
<td>26% of translation only</td>
</tr>
<tr>
<td>Interaural + naso-occipital</td>
<td>2</td>
<td>9% of translation only</td>
</tr>
<tr>
<td>Interaur. + naso-occ. contra</td>
<td>2</td>
<td>100% of interaural + naso-occipital</td>
</tr>
<tr>
<td>Interaur. + naso-occ. fore</td>
<td>2</td>
<td>100% of interaural + naso-occipital</td>
</tr>
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</table>
### Translational response

<table>
<thead>
<tr>
<th>Description</th>
<th>Value</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Interaural all</td>
<td>9</td>
<td>50% of rotation and translation</td>
</tr>
<tr>
<td>Interaural ipsi</td>
<td>2</td>
<td>22% of rotation and translation interaural</td>
</tr>
<tr>
<td>Interaural contra</td>
<td>7</td>
<td>78% of rotation and translation interaural</td>
</tr>
<tr>
<td>Naso-occipital all</td>
<td>8</td>
<td>44% of rotation and translation</td>
</tr>
<tr>
<td>Naso-occipital fore</td>
<td>4</td>
<td>50% of rotation and translation naso-occipital</td>
</tr>
<tr>
<td>Naso-occipital aft</td>
<td>4</td>
<td>50% of rotation and translation naso-occipital</td>
</tr>
<tr>
<td>Interaural + naso-occipital</td>
<td>1</td>
<td>6% of rotation and translation</td>
</tr>
<tr>
<td>Interaural + naso-occ. ipsi</td>
<td>1</td>
<td>100% of interaural + naso-occipital</td>
</tr>
<tr>
<td>Interaural + naso-occ. fore</td>
<td>1</td>
<td>100% of interaural + naso-occipital</td>
</tr>
</tbody>
</table>
Table 2. *Rotational responses.*

<table>
<thead>
<tr>
<th>Neuron rotational type</th>
<th>Gain&lt;sub&gt;R&lt;/sub&gt; average</th>
<th>Phase average</th>
<th>Gain&lt;sub&gt;R&lt;/sub&gt; vector sum</th>
<th>Phase vector sum</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Neurons sensitive to rotation only</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Type I</td>
<td>0.22 ± 0.14</td>
<td>0.21 ± 36.5</td>
<td>0.18 ± 0.18</td>
<td>1.3 ± 36.5</td>
</tr>
<tr>
<td>Type II</td>
<td>0.26 ± 0.17</td>
<td>-14.1 ± 26.4</td>
<td>0.24 ± 0.19</td>
<td>-12.5 ± 26.6</td>
</tr>
<tr>
<td>Type I + II</td>
<td>0.24 ± 0.16</td>
<td>-7.8 ± 36.5</td>
<td>0.22 ± 0.19</td>
<td>-7.3 ± 31.8</td>
</tr>
<tr>
<td><strong>Neurons sensitive to rotation and translation</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Type I + transl.</td>
<td>0.17 ± 0.09</td>
<td>-8.0 ± 42.0</td>
<td>0.13 ± 0.15</td>
<td>-10.3 ± 42.1</td>
</tr>
<tr>
<td>Type II + transl.</td>
<td>0.22 ± 0.15</td>
<td>-19.8 ± 45.1</td>
<td>0.17 ± 0.21</td>
<td>-21.4 ± 45.3</td>
</tr>
<tr>
<td>Type I + II</td>
<td>0.20 ± 0.13</td>
<td>-8.0 ± 42.9</td>
<td>0.15 ± 0.18</td>
<td>-16.8 ± 43.0</td>
</tr>
<tr>
<td><strong>Total sample</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Type I all</td>
<td>0.20 ± 0.13</td>
<td>-1.8 ± 36.8</td>
<td>0.17 ± 0.17</td>
<td>-1.4 ± 36.9</td>
</tr>
<tr>
<td>Type II all</td>
<td>0.25 ± 0.16</td>
<td>-15.3 ± 30.8</td>
<td>0.23 ± 0.20</td>
<td>-14.1 ± 31.0</td>
</tr>
<tr>
<td>Type I + Type II</td>
<td>0.23 ± 0.15</td>
<td>-9.3 ± 34.1</td>
<td>0.20 ± 0.17</td>
<td>-9.1 ± 34.1</td>
</tr>
</tbody>
</table>

Gain<sub>R</sub>, spikes/s/deg/s. Phase relative to angular velocity, deg.
Table 3. *Translational responses.*

<table>
<thead>
<tr>
<th>Neuronal sensitivity</th>
<th>GainT average</th>
<th>Phase average</th>
<th>GainT vector sum</th>
<th>Phase vector sum</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Translation along interaural axis</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Transl. only ipsi</td>
<td>125.4 ± 69.1</td>
<td>-59.4 ± 41.5</td>
<td>91.3 ± 118.3</td>
<td>-56.0 ± 14.3</td>
</tr>
<tr>
<td>Transl. + rot. ipsi</td>
<td>68.6 ± 23.3</td>
<td>-53.3 ± 27.7</td>
<td>64.9 ± 39.2</td>
<td>-53.3 ± 36.7</td>
</tr>
<tr>
<td>Transl. ipsi</td>
<td>109.2 ± 63.5</td>
<td>-57.8 ± 35.9</td>
<td>83.4 ± 99.1</td>
<td>-55.1 ± 18.4</td>
</tr>
<tr>
<td>Transl. only con</td>
<td>124.5 ± 76.8</td>
<td>-89.2 ± 44.1</td>
<td>85.3 ± 127.2</td>
<td>-93.4 ± 27.4</td>
</tr>
<tr>
<td>Transl. + rot. con</td>
<td>104.4 ± 37.1</td>
<td>-64.6 ± 55.7</td>
<td>73.8 ± 89.1</td>
<td>-62.1 ± 27.3</td>
</tr>
<tr>
<td>Transl. con</td>
<td>114.1 ± 55.9</td>
<td>-75.0 ± 51.2</td>
<td>77.1 ± 104.4</td>
<td>-77.6 ± 29.3</td>
</tr>
<tr>
<td>Transl. ipsi + con</td>
<td>113.6 ± 61.1</td>
<td>-69.1 ± 45.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Translation along naso-occipital axis</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Transl. only fore</td>
<td>115.2 ± 43.9</td>
<td>-62.1 ± 48.3</td>
<td>86.4 ± 94.4</td>
<td>-61.4 ± 28.7</td>
</tr>
<tr>
<td>Transl. + rot. fore</td>
<td>108.9 ± 46.6</td>
<td>-70.8 ± 56.1</td>
<td>78.3 ± 96.6</td>
<td>-67.0 ± 25.5</td>
</tr>
<tr>
<td>Transl. fore</td>
<td>112.4 ± 43.0</td>
<td>-66.1 ± 49.5</td>
<td>81.6 ± 91.7</td>
<td>-63.8 ± 26.6</td>
</tr>
<tr>
<td>Transl. only aft</td>
<td>121.6 ± 71.4</td>
<td>-73.8 ± 29.5</td>
<td>110.5 ± 91.5</td>
<td>-73.7 ± 18.0</td>
</tr>
<tr>
<td>Transl. + rot. aft</td>
<td>92.6 ± 57.8</td>
<td>-99.2 ± 20.7</td>
<td>88.6 ± 65.5</td>
<td>-99.2 ± 9.3</td>
</tr>
<tr>
<td>Transl. aft</td>
<td>108.7 ± 63.5</td>
<td>-85.1 ± 27.8</td>
<td>96.7 ± 82.5</td>
<td>-85.4 ± 15.0</td>
</tr>
<tr>
<td>Transl. fore + aft</td>
<td>110.7 ± 57.1</td>
<td>-74.6 ± 41.3</td>
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<td></td>
</tr>
<tr>
<td><strong>Total sample</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Translational all</td>
<td>111.3 ± 53.7</td>
<td>-71.9 ± 42.6</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

GainT, spikes/s/g. Phase relative to linear on-acceleration, deg.