Optokinetic and vestibular responsiveness in the macaque rostral vestibular and fastigial nuclei

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Abstract

We recorded from rostral vestibular and rostral fastigial nuclei neurons that did not respond to eye movements during three-dimensional (3D) vestibular and optokinetic stimulation (OKS). The majority of neurons in both areas (76% and 69% in VN and FN, respectively) responded during both rotational and translational motion. Preferred directions scattered throughout 3D space for translation but showed some preference for pitch/roll over yaw for rotation. VN/FN neurons were also tested during OKS while monkeys suppressed their optokinetic nystagmus by fixating a head-fixed target. Only a handful of cells (VN: 17%, FN: 6%) modulated during 0.5 Hz OKS-suppression, but the number of responsive cells increased (VN: 40%, FN: 48%) during 0.02 Hz OKS. Preferred directions for rotation and OKS were not matched on individual neurons and OKS gains were smaller than the respective gains during rotation. These results were generally similar for vestibular and fastigial nuclei neurons. We conclude that optokinetic-vestibular convergence might not be as prevalent as earlier studies have suggested.

Introduction

Many studies have qualified the responses of primate vestibular nuclei (VN) and rostral fastigial nuclei (FN) neurons with no eye movement-related activity during rotation and translation (VN: Angelaki and Dickman 2000; Dickman and Angelaki 2002; Chen-Huang and Peterson 2006; Musallam and Tomlinson 2002; FN: Buettner et al.)
1991; Gardner and Fuchs 1975; Siebold et al. 1997; 1999; Shaikh, 2004; Shaikh et al. 2005a; Zhou et al. 2001). With the exception of Chen-Huang and Peterson (2006), characterization of these responses to translation was limited to horizontal plane translation. Responsiveness to rotation and translation in these earlier studies was taken as the signature of otolith/canal convergence. More recently, however, it has become increasingly clear that the two types of convergence are not necessarily identical. In particular, there is little argument that responses to both yaw rotational and translational motion suggest otolith/canal convergence. However, modulation to translational but not rotational stimuli does not necessarily exclude semicircular canal inputs to the cell. This occurs because otolith afferents respond during both translation and rotation (e.g., roll and pitch from an upright orientation). Thus, the only way for central neurons to respond exclusively to translation is by canal signals canceling out otolith activation during tilt movements relative to gravity (Angelaki et al. 2004; Shaikh et al. 2005b; Yakusheva et al. 2007; 2008).

In contrast to vestibular stimulation, studies testing the responses of central vestibular neurons during visual or optokinetic stimulation (OKS) have been limited. Waespe and colleagues (Waespe and Henn 1977a, b; 1978; 1979) were the first to show modulation of macaque VN neurons during constant velocity yaw optokinetic nystagmus (OKN) and optokinetic after-nystagmus (OKAN). These results were generally in agreement to those in the goldfish (Allum et al. 1976; Dichgans et al. 1973), rabbit (Dichgans and Brandt 1972), rat (Precht 1981), cat (Precht 1981) and guinea pig (Azzena et al. 1974). Using sinusoidal stimulation, Boyle et al. (1985) showed that yaw OKS modulation of VN neurons was limited to low frequencies. Although not quantified
in detail, rostral FN neurons also modulate during OKS (Büttner et al. 1991). Most OKS studies were limited to a single axis of stimulation and characterized neural responses while the animals elicited an optokinetic nystagmus. As a result, the retinal stimulus was continuously varying, thus preventing quantification of the true visual responsiveness of the neurons.

Here we have evaluated the responsiveness of macaque VN and FN neurons to three-dimensional (3D) optokinetic stimulation at two frequencies, 0.5 and 0.02 Hz (one above and the other within the frequency range of the velocity storage mechanism; Cohen et al. 1977). In contrast to previous studies, we have characterized neural responses during OKS cancellation (i.e., while monkeys fixated a head-fixed target), thus providing a controlled retinal stimulus. In addition, we have tested VN and FN responses during OKS and vestibular stimulation in 3D, allowing for the first time a comparison between preferred vestibular and OKS responsiveness.

Materials and Methods

Experiments were performed on three juvenile macaque monkeys (Macaca mulatta), weighing 5 to 7 kg. Our general experimental procedures were similar to previous studies (Angelaki and Dickman 2000; Angelaki et al. 2001; Meng et al. 2005; Gu et al. 2006). Briefly, animals were chronically implanted with a circular, delrin ring and scleral search coils for measuring horizontal and vertical eye movements using a 3-field magnetic search coil system (Robinson 1963). All surgical and experimental procedures were performed under sterile conditions, in accordance with the Institutional
Animal Care and Use Committee at Washington University and National Institutes of Health guidelines.

Sinusoidal 3D motion was delivered using a six degrees of freedom motion platform (MOOG 6DOF2000E; East Aurora, NY). In all experiments, the head was positioned such that the horizontal stereotaxic plane was earth-horizontal, with the axis of rotation always centered at the center of the head. Because we did not have access to a 3D optokinetic sphere, the visual stimuli used here were generated by a 3-chip DLP projector (Christie Digital Mirage 2000, Christie Digital systems, Cypress, CA) that was mounted on top of the motion platform and rear-projected images onto a 60 × 60 cm tangent screen that was viewed by the monkey from a distance of 30 cm (thus subtending 90 × 90° of visual angle; see Gu et al. 2006 for details). The tangent screen was mounted on the front of the field coil frame. The sides, top and back of the coil frame were covered with black enclosures such that the monkey’s field of view was restricted to visual stimuli presented on the screen.

The optokinetic stimuli simulated yaw, pitch and roll rotation inside a sphere (70 cm radius) whose inner surface consisted of spots of varying sizes (density of 0.01 dots/cm² and dot sizes randomly chosen from a Gaussian distribution centered at 7° with standard deviation of 1.5°). This was achieved by generating stereoscopic images of the simulated sphere (using an OpenGL accelerator board; nVidia Quadro FX 3000G), which were projected onto the flat screen and were viewed binocularly through Kodak written filters (#29 & #61, Kodak, Rochester, NY) mounted on custom made goggles. Two OpenGL cameras were required for accurate rendering of sphere rotation, binocular disparity, and texture cues (for details see Gu et al. 2006). This provided an
effective optokinetic stimulus that generated a robust nystagmus during both low and high frequencies.

Behavioral control and data acquisition were controlled by Spike2 scripts and the CED system (Cambridge Electronic Design, Cambridge UK). During all neural recordings, animals suppressed their OKN/VOR by fixating on a central target that was front-projected onto the screen using a head-fixed laser. The behavioral performance of the animal was continuously monitored using electronic windows, which ensured that right and/or left eye positions were maintained within $2.5^\circ$ of ideal target fixation. This “eye-in-window” signal was monitored by the CED for on-line juice reward delivery and was saved for off-line analyses. Juice rewards were typically given at a frequency of once every ~3 s, as long as eye position was within the specified behavioral windows. To ensure that these stimuli were adequate to generate optokinetic nystagmus, horizontal and vertical eye movements were also collected in the absence of any behavioral control.

Extracellular recordings were obtained using epoxy-coated, etched tungsten microelectrodes using standard electrophysiological techniques. We recorded from vestibular only (VO) cells in the rostral FN and rostral VN (mostly rostral medial and caudal superior nuclei), as identified by the absence of eye movement-related activity during 0.5 Hz $\pm 10^\circ$ horizontal and vertical pursuit eye movements. Once a VO-cell was identified, we tested its responsiveness during the following protocols: (1) 0.5 Hz, $\pm 7^\circ$ yaw, pitch and roll rotation; (2) 0.5 Hz $\pm 10$cm lateral, fore-aft and vertical translation; (3) yaw, pitch and roll OKS at two frequencies: 0.5 Hz ($\pm 7^\circ$) and 0.02 Hz ($\pm 175^\circ$). For both frequencies, peak velocity was kept constant at 22°/s, a stimulus sufficient to elicit
robust OKN and OKAN (Cohen et al. 1977; Waespe and Henn 1977a). Note that, because we wanted to characterize neural responses during OKN cancellation (i.e., in the absence of reflexive eye movements, for a consistent retinal stimulus), constant velocity OKN and OKAN were not used in the present experiments.

The data were analyzed offline using custom-written MATLAB scripts (MathWorks, Natick, MA). Eye position was calibrated and slow phase eye velocity computed by filtered differentiation after removal of fast phases of nystagmus through a semi-automated computer algorithm (see Angelaki 1998; Angelaki and Hess 1994 for details). Neural activity was expressed as instantaneous firing rate (IFR), calculated as 1/interspike interval and assigned to the middle of the interval. IFRs from multiple stimulus cycles were then folded in time into a single cycle instantaneous frequency response for each stimulus condition. This procedure provides no averaging, as all spike occurrences are represented in time (Fig. 1; see Meng et al. 2005 for details). For OKN/VOR cancellation tasks, only portions of data in which the eye position was within 2.5° of the target were included in the folding and further analyses.

Gain and phase were computed by fitting a sine function (1st and 2nd harmonics, and a DC offset) using a non-linear least-squares algorithm (see Dickman & Angelaki, 2002; Meng et al. 2005; Shaikh et al, 2005a for details). To assign a statistical significance in the response modulation for each neuron, we also computed average binned histograms (40 bins per cycle) and a ‘Fourier Ratio (FR)’, defined as the ratio of the fundamental over the maximum of the first 20 harmonics. The statistical significance of FR was then based on a permutation analysis. Briefly, the 40 response bins were shuffled randomly, thus destroying the systematic modulation in the data but
maintaining the inherent variability of the responses. The FR was then computed from those randomly permuted histograms, and the randomization process was repeated 1,000 times. If the FR for the original data exceeded that for 99% of the permuted data sets, we considered the temporal modulation to be statistically significant (p<0.01).

Preferred response directions are described in spherical coordinates, as combinations of azimuth and elevation. A spatio-temporal convergence (STC) function was used to calculate each cell’s preferred direction (Angelaki 1991; 1992; Schor and Angelaki 1992). This was done by first computing the preferred direction in the horizontal plane. The polar angle of this vector defined the azimuth of the 3D preferred response. Then we computed its elevation by applying the spatio-temporal model in a vertical plane defined by the preferred direction in the horizontal plane and the vertical axis. This procedure allows computation of the azimuth and elevation of the 3D preferred direction in spherical coordinates, the gain and phase of the 3D preferred direction, as well as the tuning ratio (i.e., ratio of the minimum over maximum response) in each of the horizontal and vertical planes.

**Results**

*Neural responses to 3D rotation and translation*

We recorded from 53 neurons in the rostral VN (rostral medial and caudal superior nuclei) and 89 neurons in the rostral FN during pitch/roll/yaw rotation and/or lateral/fore-aft/vertical translation at 0.5 Hz. Data were collected exclusively from neurons without any eye movement sensitivity. An example response from a VN neuron
that showed some modulation during motion along all six axes (lateral/fore-aft/vertical translation and yaw/pitch/roll rotation) is shown in Fig. 1A and B. Based on these responses, the cell was classified as a ‘convergent’ neuron. Note that the present classification of VN/FN neurons as ‘convergent’ or ‘non-convergent’ applies to their responsiveness during 3D translation and 3D rotation and not to their presumed canal and otolith inputs. As shown previously, many central neurons that selectively modulate during translation, but not during rotation, receive signals from both otolith and semicircular canals (Angelaki et al. 2004; Shaikh et al. 2005a, b; Yakusheva et al. 2007).

The majority of VN and FN neurons (32/42, 76% and 59/85, 69%, respectively) were significantly modulated for at least one of the three cardinal directions during both translation and rotation, thus they were considered ‘convergent’ cells. In contrast, only 7 (17%) in the VN and 20 (24%) in the FN were only significantly modulated during translation. The remaining 3 (7%) VN and 6 (7%) FN neurons were only modulated during rotation.

Using responses from all three axes, we computed the 3D preferred direction of 47 VN and 82 FN neurons significantly tuned to translation, as well as 38 VN and 66 FN neurons significantly tuned to rotation (Fig. 2A and B, respectively; definitions of azimuth and elevation are shown in Fig. 2C). The corresponding gain distributions along each cell’s preferred direction are illustrated in Fig. 2E and F. Preferred directions, plotted in the form of azimuth and elevation scatter plots, were distributed throughout the 3D space. Translation response preferences were uniformly distributed in both horizontal and vertical planes (uniformity test, p>0.05). Tuning ratios in each of the
horizontal and vertical planes were broadly distributed, with 45% of the VN and 22% of the FN neurons having both tuning ratios less than 0.2. Approximately 19% (VN) and 28% (FN) had tuning ratios larger than 0.2 in both horizontal and vertical planes. For rotational response preferences, there was a weak departure from uniformity for both azimuth and elevation in FN cells (Fig. 2B, red; p=0.03) and for elevation in VN cells (Fig. 2B, blue; p=0.01). When comparing the azimuth of the 3D preferred directions for rotation and translation (Fig. 2D), data points were scattered throughout the range suggesting the absence of tilt-aligned rotation/translation preferences, as previously described in rats (Angelaki et al. 1993; Bush et al. 1993). That is, cells that prefer forward (lateral) motion do not necessarily prefer pitch (roll) rotations and vice-versa.

**Neural responses to 3D optokinetic stimulation**

Forty-one (41) of the vestibular-sensitive cells in the VN and FN were also tested with optokinetic stimuli. In the absence of the head-fixed fixation target during yaw and pitch OKS, animals generated a robust horizontal and vertical optokinetic nystagmus (Fig. 3). Fig. 3A and 3B show representative examples of the nystagmus evoked during 0.5 Hz and 0.02 Hz OKS, respectively. Fig. 3C and 3D summarize the distributions of peak horizontal and vertical eye velocities evoked during yaw and pitch OKS, respectively (mean amplitude: 17.7°/s for yaw, 23.3°/s for pitch OKN (0.5 Hz) and 18.9°/s for yaw, 24.0°/s for pitch OKN (0.02 Hz)). To have a greater control over the retinal stimulus, VN/FN neurons were tested while the animal suppressed its optokinetic nystagmus by fixating a head-fixed target. Only a small percentage of VN/FN neurons
were significantly modulated along at least one stimulus direction; VN: 2/12 (17%) at 0.5 Hz and 4/10 (40%) at 0.02 Hz; FN: 2/31 (6%) at 0.5 Hz and 15/31 (48%) at 0.02 Hz.

Even for responsive cells, modulation amplitude was small, as illustrated with the example in Fig. 4A that shows one of the most responsive FN neurons to yaw, pitch and roll OKS at 0.5 Hz (top) and 0.02 Hz (bottom). Like the vestibular responses, we computed the preferred direction and gain of the OKS responses of VN/FN neurons. Fig. 4B compares the respective gains for all cells that were significantly modulated to at least one direction during rotation and optokinetic stimulation (VN: 5 cells; FN: 16 cells). Data at both 0.5 Hz (filled symbols) and 0.02 Hz (open symbols) fall above the unity line, indicating poorer response modulation to OKS than vestibular stimulation. Preferred directions were not matched, as illustrated in Fig. 4C which plots the difference in 3D preferred directions between 0.5 Hz rotation and 0.02 Hz OKS responses (because of the small number of OKS-responsive cells at 0.5 Hz, this comparison is not included). Distributions were not significantly different from uniform (uniformity test, p>0.05).

Discussion

We have characterized vestibular and OKS responsiveness during 3D stimulation in the rostral VN and rostral FN. Unlike previous reports that have implied that all units which were activated by vestibular stimulation could also be activated by moving optokinetic patterns (Buettner and Buttner 1979; Henn et al. 1974; Waespe and Henn 1977a, b), we found that at most half of the vestibular-responsive neurons
modulated during sinusoidal OKS at 0.02 Hz. The fact that this number decreased drastically down to only less than a handful responsive neurons at 0.5 Hz is in agreement with the findings of Boyle et al. (1985) who showed that most VN neurons only modulate during low frequency yaw OKS. In particular, only a few neurons responded at 0.2 Hz and none above 1 Hz (Boyle et al. 1985). The larger proportion of OKS-responding neurons at 0.02 Hz, a frequency that is within the range of velocity storage mechanism (Raphan et al. 1979), suggests that non-eye movement-sensitive VN/FN neurons might mediate the ‘indirect’, ‘slow’ component, but not the ‘direct’, ‘fast’ component of OKN (Cohen et al. 1977).

Despite these general similarities with earlier studies, even responsive cells typically exhibited small modulation during OKS. This observation differs from the robust responses reported previously by Waespe and Henn (1977a, b; 1978; 1979). There are multiple differences between the present experiments and those of previous studies. First, the stimuli are different: We used 0.5 Hz and 0.02 Hz sinusoidal stimulation, whereas the Waespe and Henn studies used constant velocity OKN and OKAN. Second, unlike Waespe and Henn (1977a, b; 1978; 1979), our animals suppressed reflexive eye movements. Indeed, Buettner and Buttner (1979) also reported reduced neuronal responses in the majority of the VN neurons during OKS-suppression. Third, previous studies used actual drum rotation, whereas our optokinetic stimuli were simulated using OpenGL. Although we believe that this is an adequate stimulus (because it elicits robust optokinetic nystagmus; Fig. 3), we cannot exclude the possibility that neural responses were less robust because sphere rotation was not real but simulated. Finally we want to emphasize that our aim for these experiments was to
characterize neural responses during OKN cancellation (i.e., in the absence of reflexive eye movements), as part of a greater effort to characterize the visual motion responses of subcortical neurons. This could not have been possible by recording (like previous studies did) neural activities during OKAN. Perhaps responses are different during sinusoidal stimulation in the absence of reflexive eye movements (present study) and OKAN (Waespe and Henn 1977a, b; 1978; 1979). But the latter does not test for visual (sensory) responsiveness. Neuronal modulation during optokinetic nystagmus and afternystagmus cannot be interpreted as sensory- or motor-driven. Previous studies have instead shown that VN neurons modulate during activation of the velocity storage mechanism. In contrast, the present experiments, where we controlled the retinal motion stimulus by suppressing reflexive eye movements, aimed to test for visual (sensory) responsiveness. Results point out that, unlike a widely-accepted belief in the field, true visual /vestibular interactions might be rather limited in the vestibular and rostral fastigial nuclei.

To our knowledge this is the first study to compare the preferred OKS and rotational preference for VN/FN neurons. We found no relationship between the two, although the number of cells used for this comparison (requiring neurons responsive to both) was small. This result is surprising, given the strong behavioral relationship between the rotational vestibulo-ocular and optokinetic reflexes (Cohen et al. 1977; Raphan et al. 1979). Additional data, with this comparison available for a larger number of neurons, might be necessary to reliably compare these relationships.

Precht (1981) showed that lesions of the nucleus of the optic tract (NOT) or nucleus reticularis tegmental pontis (NRTP) in the cat and rat abolished OKS responses
in the VN. In primates, it is generally thought that descending projections from the nucleus of the optic tract (NOT) and possibly the dorsal terminal nucleus (DTN) project through the central tegmental tract to the ipsilateral vestibular complex, where diffuse terminals are seen in the medial vestibular nucleus (Buettner-Ennever et al. 1996). The lateral terminal nucleus (LTN) is also known to project to the superior and medial VN (Blanks et al. 2000). A similar but smaller projection is also found from the medial terminal nucleus (MTN) to the superior and lateral VN.

Finally, optokinetic signals to the VN/FN can also be carried by Purkinje cell projections from the ipsilateral nodulus and uvula (Carleton and Carpenter 1983; Voogd et al. 1996; Wylie et al. 1994). Although the OKS responses of nodulus/uvula Purkinje cells have yet to be quantified in alert primates, there is evidence that simple spike responses in the anesthetized rabbitmodulate during OKS (Kano et al. 1991a, b). Further experiments are necessary to quantify the properties and origin of optokinetic modulation in vestibular-responsive brainstem and cerebellar areas, as well as potential differences in responses between low frequency sinusoidal versus constant velocity OKN and OKAN.

Acknowledgments

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Figure 1. Responses from a rostral VN neuron during 3D vestibular stimulation. Small dots illustrate instantaneous firing rate during (A) translation and (B) rotation at 0.5 Hz (12-16 cycles superimposed, see Methods). Motion directions are indicated by the cartoon drawings. The solid gray lines illustrate the sinusoidal fits. The stimulus traces (Stim) show linear acceleration (A) or angular velocity (B). Response gains were as follows: A: 209 sp/s/G (p<<0.001, lateral), 55 sp/s/G (p=0.05, fore-aft) and 74 sp/s/G (p=0.01, vertical) and B: 0.75 sp/s/deg/s (p<<0.001, yaw), 0.43 sp/s/deg/s (p<<0.001, pitch) and 1.19 sp/s/deg/s (p<<0.001, roll).

Figure 2. Summary of rotation/translation responses in 3D. (A), (B) Distributions of preferred directions (shown in spherical coordinates as azimuth and elevation) during translation and rotation, respectively. Each data point in the scatter plots corresponds to the preferred azimuth (abscissa) and elevation (ordinate) of a single neuron with significant responses along at least one motion direction. The data are plotted on Cartesian axes that represent the Lambert cylindrical equal-area projection of the spherical stimulus space (see Gu et al. 2006 for details). Histograms along the top and right sides of each scatter plot show the marginal distributions. Filled symbols indicate cells with significant modulation along at least one direction during both rotation and translation (‘convergent’). Open symbols show ‘non-convergent’ cells that only modulate during either translation (A) or rotation (B). Cells that were not tested during both rotation and translation are shown with open triangles. (C) Definition of azimuth and
elevation: Top and side view. Straight arrows depict the direction of translation, while curved arrows show the direction of rotation around each of the movement axes (based on the right-hand rule). (D) Scatter plot comparing preferred azimuths for rotation and translation (shown only for convergent cells). For tilt-aligned rotation/translation preferences, data points should fall along the ±90° diagonals (e.g., forward translation is defined with an azimuth of 0°, but a pitch rotation-tilt has an azimuth of 90/270°). (E), (F) Distribution of neural response gains along the 3D preferred direction for translation and rotation, respectively. FN neurons: red symbols/bars; VN neurons: blue symbols/bars.

**Figure 3.** Nystagmus elicited during yaw and pitch optokinetic stimulation (OKS). (A), (B) Examples of horizontal (left) and vertical (right) eye position during yaw and pitch OKS at 0.5Hz and 0.02Hz, respectively. (C), (D) Histograms of peak horizontal and peak vertical slow phase eye velocity elicited during yaw and pitch OKS, respectively. Data are shown separately for 0.5Hz (filled bars) and 0.02Hz (open bars).

**Figure 4.** (A) Examples of neural responses from a FN cell during yaw, pitch and roll OKS at 0.5 Hz (top, ~15 cycles superimposed) and 0.02 Hz (bottom, ~3 cycles superimposed). Response gains were as follows: 0.5 Hz: 0.20 sp/s/deg/s (p=0.6, yaw OKS), 0.12 sp/s/deg/s (p=0.5, pitch OKS) and 0.28 sp/s/deg/s (p=0.3, roll OKS); 0.02 Hz: 0.07 sp/s/deg/s (p=0.09, yaw OKS), 0.34 sp/s/deg/s (p<<0.001, pitch OKS) and 0.33 sp/s/deg/s (p=0.03, roll OKS). (B) Scatter plot comparing 3D neural response gains during rotation and OKS, shown separately for FN (red symbols), VN (blue symbols) at 0.5 Hz (filled symbols) and 0.02 Hz (open symbols). Data are only shown for cells with
significant modulation during both rotation and OKS. (C) Distribution of the difference in 3D preferred directions for responses to 0.5 Hz rotation and 0.02 Hz OKS stimulation. A difference of 180° signifies alignment of preferred directions; 0° represents anti-alignment.
References


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**Shaikh AG, Green AM, Ghasia FF, Newlands SD, Dickman JD, Angelaki DE.**


**Yakusheva TA, Shaikh AG, Green AM, Blazquez PM, Dickman JD, Angelaki DE.**


A Translation Rotation

100 sp/s
22 deg/s
0.1 G
1s

Stim
A  Yaw OKS, 0.5Hz  Pitch OKS, 0.5Hz

Eye Pos

Stim

dashed line: 10 deg

2 s

7 deg

B  Yaw OKS, 0.02Hz  Pitch OKS, 0.02Hz

Eye Pos

Stim

dashed line: 10 deg

50 s

175 deg

C  Yaw OKS

D  Pitch OKS

Number of trials

Eye velocity (deg/s)

- 0.5 Hz
- 0.02 Hz

0 5 10 15 20 25

0 5 10 15 20 25

0 10 20 30 0 10 20 30
A

Yaw OKS 0.5 Hz

Pitch OKS 0.5 Hz

Roll OKS 0.5 Hz

STIM

IFR

B

C

Rotation gain (sp/s/deg/s)

OKS gain (sp/s/deg/s)

Number of pairings

Preferred direction (deg)

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FN VN

0.5 Hz 0.02 Hz

0.5 Hz 0.02 Hz