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Pretectal neurons responding to slow wide-field retinal motion: could they compensate for slow drift during fixation?

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Abstract

The visual response properties are described of a group of retinal slip neurons in the wallaby pretectum, referred to as slow cells. Their responses to motion are direction-selective: tempero-nasal and naso-temporal motion over the contralateral eye increase and decrease, respectively, the firing rate relative to the spontaneous level. Slow cells are maximally sensitive to image velocities from 0.08 to 10°/s. The present study focuses on slow cells that are maximally sensitive to image velocities below 1°/s. An interesting characteristic of 82% of slow cells is that once motion stops, the firing rate exhibits a same-sign after-response. This is characterized by a slow exponential return from the firing rate during motion to the spontaneous rate. The time constants of the after-responses are independent of the temporal frequency, velocity, duration and direction of the motion stimulus. It is proposed that the neurons may assist the stabilization of eye position during fixation.

Key words: direction-selective, fixation, motion detector, oculomotor system.

Introduction

Motion-sensitive retinal slip cells in the pretectal nucleus of the optic tract (NOT) are sensitive to wide-field motion of the retinal image. Temporal-to-nasal (preferred) motion over the contralateral eye typically increases the firing rate above the spontaneous level while nasal-to-temporal (antipreferred) motion decreases the firing rate. In vertebrates, retinal wide-field slip cells in the oculomotor centres of the midbrain are maximally sensitive to speeds from below 1°/s to over 60°/s,[1–7] and are known to drive ocular stabilizing responses such as the slow phases of optokinetic nystagmus (OKN).[8,9] During head movements and OKN, slip velocities below 1°/s rarely occur,[10] suggesting that retinal slip cells maximally tuned to these slow speeds may not only be involved in producing stabilizing eye movements during head motion.

During fixation in rats, cats, rabbits and primates, the eyes are not perfectly stabilized and small drifting eye movements displace the retinal image with velocities below 1°/s.[11] For example, in fixating cats, 'slow control' is observed, characterized by small, slow, random drifts of the eyes corrected by opposing slow eye movements.[11] The cat has forward-looking eyes and an area of high ganglion cell density in the centre of each retina, called the area centralis. During fixation, objects of interest are projected onto the area centralis. Wallabies have eyes that diverge by approximately 40° from the midline and the retina has a visual streak. However, on the temporal side of the retina, which points directly in front of the animal, there is a particularly high-density region of ganglion cells, which is regarded as a displaced version of the cat's area centralis.[12] A high proportion of ganglion cells in this region project to the lateral geniculate nucleus[13] and the retinotopic projection of visual space onto the superior colliculus shows a region of high magnification in that area.[14] Behavioural experiments show that wallabies actively fixate objects of interest by directing the gaze of both eyes towards the objects.[15] The eye movements are coordinated with head movements, so objects fall on each eye's vertical meridian. It is presumed from these observations that the wallabies are moving their eyes such that objects of interest fall on the forward-looking area of high spatial resolution in the retina. It is therefore plausible that retinal slip cells sensitive to wide-field image motion with very low velocities may help stabilize eye position during fixation in the wallaby. This proposed role of the NOT in assisting fixation would complement its established role in stabilizing the retinal image during head movements as both tasks require detection of wide-field retinal slip and the production of compensatory eye movements.

Retinal slip cells in the wallaby NOT have been classified as fast and slow cells, distinguished by their preference for wide-field motion with velocities above and below 10°/s,

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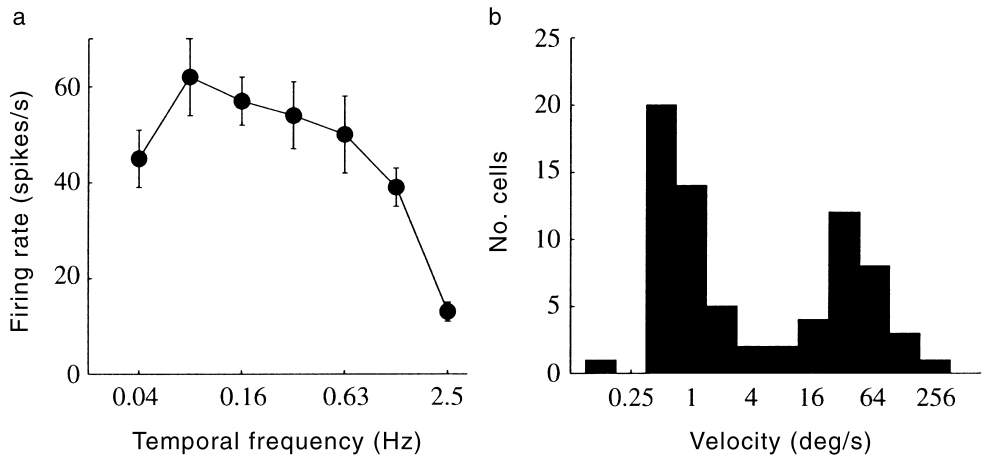

Figure 1. Velocity, temporal and spatial frequency tuning properties. (a) Mean firing rates (minus the spontaneous activity) during motion stimulation at a range of velocities plotted for a slow cell. The grating spatial frequency was 1.25 cpd. Responses were calculated by taking the mean responses in windows spanning 5 s motion periods. (b) The preferred velocities of 72 neurons in the wallaby NOT. These peak velocity values were calculated by dividing the peak temporal frequency by the peak spatial frequency for each neuron. The peak firing rates were measured using a 2–5-s period of motion.

respectively.[2,16] The present study investigates the properties of slow cells, with a particular focus on the cells sensitive to low drift velocities ($\leq 1°/s$) and on the novel after-responses of slow cells following the cessation of motion.

Methods

Extracellular recordings using tungsten-in-glass microelectrodes were made from direction-selective cells in the NOT of anaesthetized, paralysed wallabies (*Macropus eugenii*) weighing 5.0–7.5 kg. All procedures were approved by the animal experimentation ethics committee of the Australian National University and followed the guidelines of the National Health and Medical Research Council of Australia. Methods of anaesthesia, surgery and extracellular recording have been described in detail previously.[2] Action potential arrival times were recorded with 1 kHz resolution and grouped in 10–50 msec bins for presentation as a peristimulus time histogram. This showed the frequency of spike arrival times throughout a stimulus.

Computer-generated visual stimuli (AT Vista; True Vision, Indianapolis, IN, USA) were presented on a display monitor with 480 lines at 512 pixels/line and a refresh rate of 100.8 Hz (CCID7551; Barco Industries, Reading, PA, USA). The monitor was centred within the receptive field of the cell being studied and placed 30–65 cm from the contralateral eye, subtending $65° \times 50°$ or $33° \times 25°$. Stimuli comprised sine-wave modulated contrast gratings that could be presented in any orientation and in rectangular or circular apertures. Gratings were initially stationary for at least 1 s and subsequently moved for 0.16–10 s. A recovery period in which a stationary grating was presented for at least a further 1 s followed the motion period. The stimulus contrast, grating spatial frequency and temporal frequency of motion could also be controlled. The mean luminance of the stimulus and background was 42 cd/m^2. Averages of 8–32 repetitions of each stimulus were used to assess responses.

A Nelder–Meade simplex algorithm was used to fit an exponential to the recovery period of the peristimulus time histogram that followed the period of motion stimulation. The algorithm determined the rate of decay and the asymptote of an exponential that best fitted the change in firing rate during this period. To allow for the latency in the response, the exponential was fitted from 40 msec after motion cessation.

Results

Retinal slip cells in the wallaby NOT have high spontaneous activities (20–100 spikes/s) and preferred stimulus velocities ranging from below 1°/s up to over 100°/s. A classification of 'slow' and 'fast' cells has previously been made,[2] based broadly on whether a cell's preferred velocity is above or below 10°/s. The temporal frequency tuning of a slow cell stimulated with sine-wave grating motion with velocities from 0.04°/s to 2.5°/s (spatial frequency 1.25 cpd) is shown in Fig. 1a. Sustained responses calculated as the mean firing rate during 5 s of motion indicate a preferred velocity of 0.08°/s (velocity = peak temporal frequency/peak spatial frequency). The preferred velocities of 72 retinal slip cells are shown in Fig. 1b, highlighting the distinct categories of slow and fast cells. The distribution of slow and fast cells shows a clear trough at velocities close to 10°/s, confirming the velocity used previously as the division between fast and slow cells.[2] The entire spatiotemporal tuning of a slow cell for preferred and antipreferred motion is shown in Fig. 2. The peak responses occur at the same range of temporal and spatial frequencies for both preferred and antipreferred motion. Interestingly, this was not found to be the case in similar directional neurons in the oculomotor system of the pigeon.[7] The difference may arise from the lower spontaneous firing rates found in the pigeon neurons. Thus, in the pigeon, the antipreferred responses may saturate more easily, broadening the peak antipreferred velocity tuning.

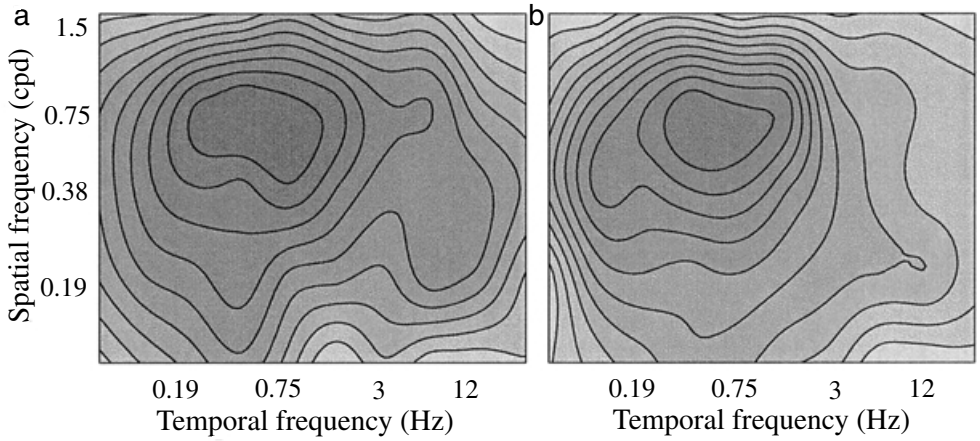

Figure 2. Examples of spatio-temporal frequency tuning plots of the responses to (a) preferred and (b) antipreferred motion. The lightest areas in both plots represent responses close to zero. Maximum excitation (a: dark grey) was 42 spikes/s, while maximum inhibition (b: dark grey) was 27 spikes/s below the spontaneous rate.

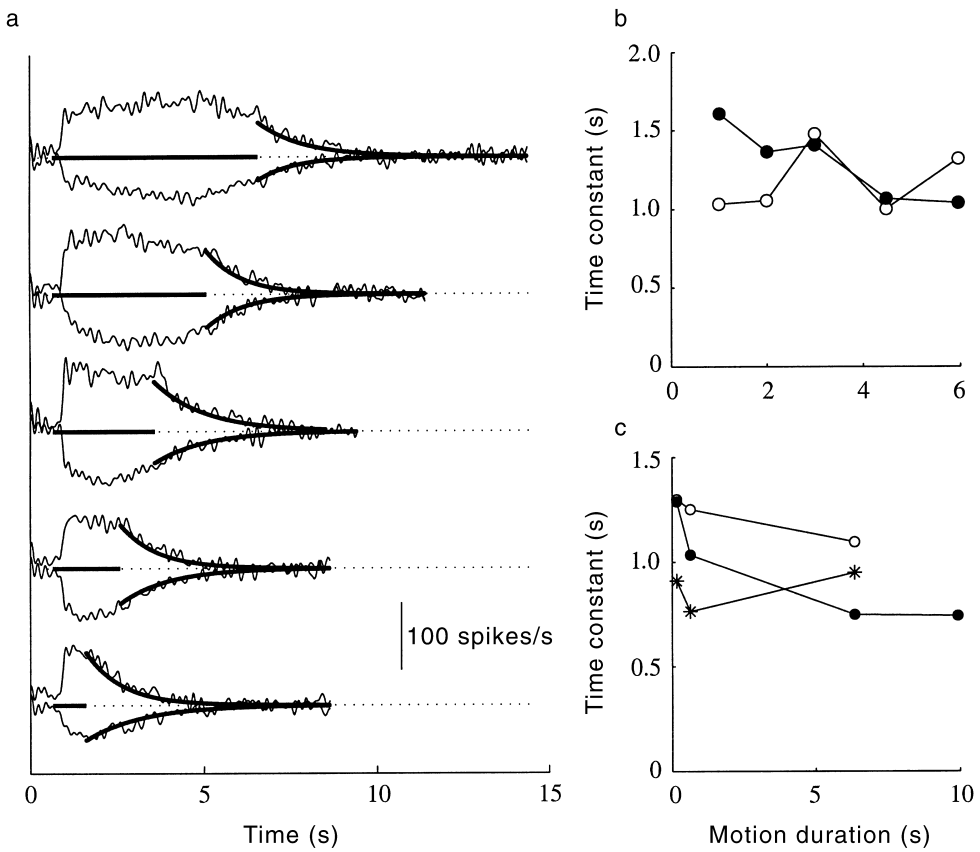

Figure 3. Response decay after motion cessation. (a) Exponential fits (—) to the response decay in one slow cell following preferred and antipreferred motion lasting 1–6 s (0.524°/s; 0.38 cpd). The duration of motion is indicated by the thick horizontal line, which also marks the spontaneous firing rate for each response. For each pair of responses, the upper and lower traces mark the responses to preferred and antipreferred motion, respectively. (b) The time constants of the exponential fits shown in (a) plotted against motion duration: (○) preferred motion; and (●) antipreferred motion. (c) Time constants of exponential fits to the after-response of a different cell stimulated with motion lasting 0.16–10 s and with temporal frequencies of (✻) 0.1 Hz (●) 0.2 Hz; and (○) 0.4 Hz.

Response after motion cessation

After preferred motion stopped, 36 of the 44 (82%) slow cells recorded showed a same-sign decay in firing rate from the sustained level during motion back to the spontaneous rate. A corresponding same-sign increase in firing rate occurred after antipreferred motion ceased (Fig. 3). Thirty-three of the slow cells responded maximally to image velocities at or below 1°/s and also showed same-sign after-responses. For the 11 slow cells with peak responses above 1°/s, three neurons had clear same-sign after-response. It would appear that the higher the peak velocity tuning, the lower the chance of the cell having a same-sign after-response. As previous work has shown, it is clear that all fast cells in the wallaby NOT have opposite-sign after-responses, where the response immediately after the period of motion has the opposite sign to that during the motion.[2,16] It is possible that the slow cells form two functional categories, those with and those without same-sign after-responses. However, it is also possible that there is a cross-over between the fast and slow cells, where cells maximally sensitive to image velocities between 1°/s and 10°/s do not fall precisely into either category (Fig. 1b).

Exponential fits to the after-responses were used to

investigate slow cell dependence on stimulus duration, direction and temporal frequency. Figure 3a shows the response of one cell to motion periods lasting 1–6 s (0.524°/s; 0.38 cpd) and superimposed fits to the after-responses. The responses to periods of preferred and antipreferred motion with the same duration have been plotted together. The asymptote of each exponential fit is the cell's spontaneous firing rate, highlighting the symmetry of responses to preferred and antipreferred motion. Figure 3b shows the time constants of the exponential fits to the data in Fig. 3a, which vary from 1.0 to 1.6 s across the five stimulus durations and two directions. No clear dependence on motion duration is evident and the decay rates following preferred and antipreferred motion were similar.

Figure 3c shows the time constants of fits to the after-response of a second cell tested with preferred motion lasting 0.16–10 s and three temporal frequencies (0.098, 0.197, 0.394 Hz). Although some variation in the time constants occurred (0.75–1.3 s), no relationship between the decay rate and stimulus duration or temporal frequency was evident. As slow cells give temporal frequency dependent and oscillatory responses to sinusoidal grating motion,[2] it is possible that the decay rate of the after-response may depend on the stimulus phase at motion cessation. However, comparing the decay time constants with the relative spatial phase when motion stopped did not reveal any significant trends.

Discussion

Retinal slip cells in the mammalian NOT are thought to drive optokinetic responses that stabilize the retinal image during head movements.[1,8,9] However, retinal slip velocities during head movements are rarely less than 1°/s in a naturally behaving animal, even during the stabilizing eye movements.[10,17] As 75% (33/44) of the slow cells reported here are maximally sensitive to wide-field retinal slip velocities at or below 1°/s, they would not be optimally stimulated by the retinal slip during head movements or compensatory eye movements. We should stress that it is probable that most of these neurons will respond to some extent during the retinal slip velocities associated with optokinetic nystagmus but they would not be optimally stimulated. In humans, slow drifting eye movements during fixation have peak velocities of up to 0.5°/s.[18,19] Similarly, in cats, slow drift during fixation with a mean velocity of 0.25°/s has been reported.[11] Given the similarity of the retinal slip speeds associated with fixation in primates and cats, and the sensitivity of the slow cells reported here, it is hypothesized that the neurons may have a role in detecting and minimizing slow drift during fixation in the wallaby. Although cells in the NOT are maximally responsive to horizontal motion, their outputs could be combined with those from vertical motion-sensitive units (e.g. in the lateral or medial terminal nuclei of the accessory optic system[20]), to give a vectorized indication of drift direction.

Previous studies of physiological motion detectors have described opposite-sign after-responses following motion cessation.[21] For example, during preferred motion stimulation, the firing rate is raised above the spontaneous level. After motion ceases, the firing rate drops rapidly below the spontaneous level and subsequently increases to the spontaneous rate. This phenomenon was first observed by Barlow and Hill in motion-sensitive units in the rabbit retina and was used to explain the psychophysical phenomenon known as the motion after-effect.[21] Opposite-sign after-responses have also been reported in cat cortical cells,[22,23] fly optic lobes,[24,25] and fast cells in the wallaby NOT.[2,16,26] Computer models of biological motion detectors have been unable to account for the response inversion following motion cessation[27] and show a same-sign after-response in which the firing rate decays exponentially from the response during motion to the spontaneous level, without first inverting. This suggests that the subset of slow cells reported here show similar responses to those predicted by motion detector models. Thus additional physiological mechanisms may be necessary to account for the opposite-sign after-responses observed in previously reported motion detector cells. These mechanisms may involve the opening of Ca^{2+}-sensitive K^{+}-channels as a result of calcium accumulated during a period of motion stimulation.[28]

What role could the same-sign after-responses have? The same-sign after-responses exhibited by most slow cells may provide a 'memory' of any error or change in eye position during fixation. If random slow drift were counteracted, removing the error in the eye position, then the firing rate would return to the spontaneous level. If the eyes stay in a new position after drifting, the firing rate would stay high after motion stopped, continuing to indicate the error. Such a memory may be useful in controlling slow drift during fixation between saccades. It would be worth investigating neurons in the lateral and medial terminal nuclei of the wallaby, which code for vertical image motion, to see if they too contain neurons with same-sign after-responses. If they do, combining the responses of horizontal and vertical sensitive neurons could compensate for all directions of slow drift and provide an error message if the eyes stay in a location displaced from the intended fixation point.

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