THE PHYSIOLOGICAL FINE STRUCTURE OF MOTION SENSITIVE NEURONS IN THE PIGEON'S TECTUM OPTICUM

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1 INTRODUCTION

A growing body of evidence suggests that the tectofugal pathway of birds is involved in processing object motion. The optic tectum, which receives monosynaptic input from retinal ganglion cells, contains several classes of motion sensitive units. Here we report on a cell type with a remarkable electrophysiological fine structure: These cells show bursting activity with very regular, high-frequency (600 Hz) firing during bursts, and varying burst frequencies between 1 and 25 Hz (Fig. 1).□□□□□□□

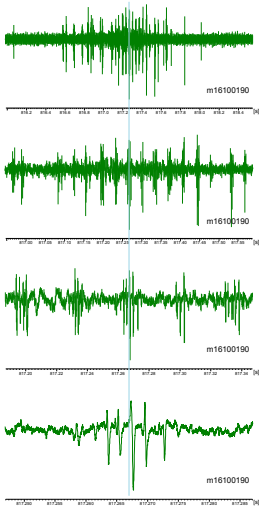

Fig. 1: A typical recording in response to a moving spot is shown in 4 different resolutions.

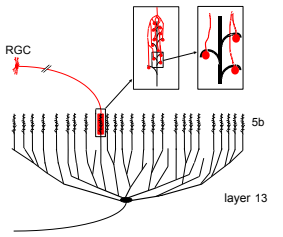

Fig. 2: Schematic drawing of the connectivity and morphology of a tectal SGC neuron. From Luksch et al. 1998.

Recently, Karten et al. (1997) and Luksch et al. (1998) described the anatomical fine structure of tectal neurons from the pigeons' layer 13 (stratum griseum centrale, SGC) that project into the nucleus rotundus. These cells have huge dendritic trees speading out over a field of more than two millimeters and connect in superficial layer 5b with axons from retinal ganglion cells. The dendritic endings show a typical fine structure that the authors called "bottlebrush endings" (Fig. 2).

□Our electrophysiological recordings seem to correlate well with the neuroanatomical fine structure. We hypothesize that we are indeed recording dendritic activity from SGC neurons, and that a single burst corresponds to the output of a single bottlebrush. A prediction arising from this hypothesis would be that burst frequency should depend linearly on the stimlus speed. We tested this prediction by recording from bursting tectum neurons while stimulating with light spots moving vertically at various speeds.

□In particular, we tested the effect of stimulus speed on the following parameters:□

- Peak firing rate
- Spike frequency within bursts
- Total number of bursts and burst frequency

2 METHODS

Pigeons were anaesthetized with a mixture of Kethamine and Rompun and placed in a stereotaxic unit. The dorso-lateral part of the left tectum was exposed by removing the bone at the caudal pole of the forebrain. The tectum was then penetrated with tungsten electrodes (impedence 2 MOhm).

The right eye was exposed to a tangent screen onto which we back-projected a small moving light spot. A slide projector was used to generate the spot and a mirror galvanometer was used to move it across the projection screen.

The size of the moving spot on the screen was 1 cm. Depending of the location of the receptive field of a particular cell this corresponds to about 0.75 deg of visual angle. Up and down movement alternated with a delay of 10 s between single sweeps. The amplitude of the motion was 35 cm (26 deg). Four different speeds were tested in a blocked design with 12 up and 12 down movements in each block. The velocities were 2.7 cm/s, 5.3 cm/s, 10.7 cm/s, and 21.3 cm/s corresponding to about 2 deg/s, 4 deg/s, 8 deg/s, and 16 deg/s.

□We examined 34 cells in 8 different pigeons. □□□□□□□□□□□□□□□

3 RESULTS

1. Qualitative description

- **Directional sensitivity is weak.** Most cells respond best with spots moving vertically downwards.
- **Strong habituation:** An interstimulus intervall of less than 10 s results in reduced responses.
- **Large receptive fields** of about 10 to 20 deg.
- **Broad velocity tuning:** The same cells respond to stimuli as slow as 1 deg/s and stimuli as fast as 30 deg/s.
- **Sensitivity to small spots:** Some cells respond to spots as small as 0.1 deg.
- **Location:** In the dorsal tectum, we get responses with electrodes at depth between 100 mm and 1000 mm below the tectal surface.

2. Peak firing rate

- Peak firing rate increases linearly with stimulus speed (Fig. 3).
- The slope of this relation equals the number of spikes per degree of visual angle. The mean values are 5.53 deg^{-1} for the upward movement and 9.72 deg^{-1} for the downward movement (Fig. 4).

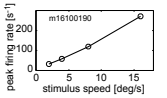

Fig. 3: Peak firing rate as a function of stimulus speed for a typical cell.

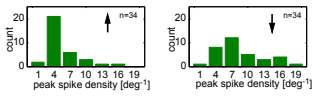

Fig. 4: Distribution of peak firing rate over all recordings for upward (a) and downward (b) motion.

3. Spike frequency within bursts

- Interspike intervals (ISI) showed a sharply peaked distribution (Fig. 5).
- The peak of the ISI histograms corresponds to the spike interval within bursts. Within-burst-ISIs were not effected by stimulus speed (Fig. 6).
- Across cells, within-burst-ISIs varied in a range of about 1.6 ms to 2.0 ms which corresponds to spike frequencies between 500 and 625 Hz (Fig. 7).

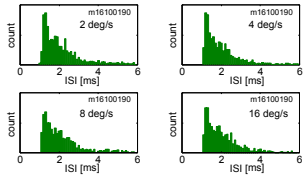

Fig. 5: Interspike interval histograms from a single recording for the four different stimulus speeds.

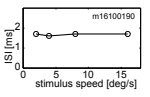

Fig. 6: Summarizing Fig. 5, the interspike interval is plotted against the stimulus speed for the same example cell.

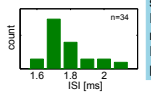

Fig. 7: This diagram shows the distribution of ISI over all 34 recordings. None of the ISI histograms had a peak larger than 2.1 ms.

4. Total number of bursts and burst frequency

- For the majority of the cells, total number of bursts remained constant when stimulus speed increased (Fig. 8a).
- In some cells, the number of bursts decreased with increasing stimulus speed (Fig. 8b).
- Burst frequency linearly increased with stimulus speed. This was the case even in cells, in which the number of bursts was not constant over stimulus speed (Fig. 9).
- The average increase of burst rate with stimulus speed (number of bursts per degree of visual angle) over all cells was 0.68 per degree of visual angle (Fig. 10).

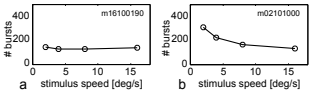

Fig. 8: The total number of bursts for two different example cells illustrating the two different patters that occured.

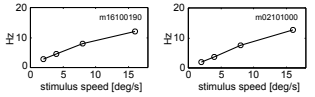

Fig. 9: The increase of burst rate with speed for the same two recordings as in Fig.8.

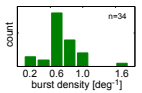

Fig. 10: Distribution of burst densities over all recordings.

4 DISCUSSION

Our results suggest, that the neurons we are recording from are identical with the SGC neurons described by Karten et al. (1997) and Luksch at al. (1998). The depth in which we find the bursting neurons matches the region where the SGC neurons spread their extended dendritic trees. We assume that we are observing dendritic rather than axonal activity.

Evidence for this view is provided by

- The linear relation between burst frequency and stimulus speed fits with the idea of successivly exciting bottlebrush endings, each getting input from a tiny receptive field.
- The exceptionally high spike frequency during bursts and the heterogeneous shape and amplitude of single spikes suggest the involvement of processes that are different from standard axonal Na^+ action potentials.

If a single bottlebrush ending would respond in a totally deterministic way, we would expect nicely lined-up raster plots. A preliminary analysis showed that this was not the case. Possible reasons for the lack of this finding are:

- Small eye movements may result in a mismatch between retinal and visual field coordinates.
- A single bottlebrush ending might respond in a stochastic all-or-nothing manner. Tuning curves of single bottlebrushes might be much narrower than the sensitivity of the whole system with the consequence that the majority of the burst come from bottlebrushes that respond only with a small probability to the current stimulus speed.

5 REFERENCES

Karten H. J., Cox, K., and Jorge M. (1997) Two distinct populations of tectal neurons have unique connections within the retinotectorotundal pathway of the pigeon (Columba livia). The Journal of Comparative Neurology 387:449-465.

Luksch H., Cox, K. and Karten, H. J. (1998) Bottlebrush dendritic endings and large dendritic fields: Motion-detecting neurons in the tectofugal pathway. The Journal of Comparative Neurology 396:399-414.