

Population coding of rapid changes in self-motion by the blowfly visual system

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In several sensory systems information is encoded by the activities of a population of neurons where each individual neuron is tuned to a slightly different aspect of the stimulus. Theoretical studies and model simulations demonstrate the accuracy of a population code to depend on the number of cells in the population, the width and form of the tuning curves and the variability of neuronal responses [1, 10]. Our analysis is based on a system of directionally selective motion sensitive interneurons in the blowfly [2, 3, 5, 7]. In the present account we focus on a sub-population of these interneurons, the so-called VS-cells. The receptive field organisation suggests each cell to prefer optic flow induced by the animal's head rotation around a specific horizontally aligned axis [8]. The 10 VS-cells in each half of the brain are output elements to the motor system. VS-cells convey information by graded changes in their membrane potential superimposed by small-amplitude spike-like events [6]. It is under debate whether this graded response mode has advantages over signalling information by trains of spikes [4]. We model individual VS-cell response traces based on experimentally determined responses to large-field stimuli simulating rotations of the fly's head around different horizontal axes. Applying a Bayesian Estimator we investigate the impact of integration time on the population code's accuracy.

VS-cell activity was recorded intracellularly in a panoramic high-speed virtual reality optic flow stimulator [9]. Cells were stimulated with random patterns simulating rotations of the fly around different horizontally aligned body-axes and at different velocities. From these experiments we derived the form and orientation of VS-cells' tuning curves, the time course of the neuronal responses, and the amount of noise for different activity levels (Fig. 1).

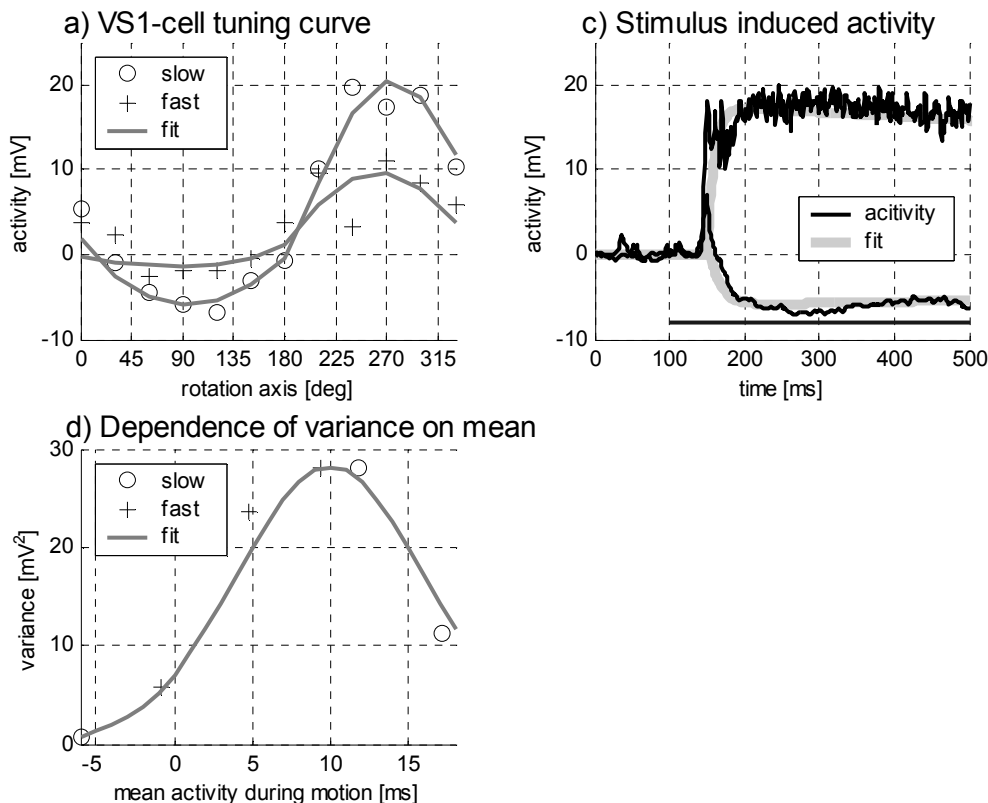


Fig. 1. (a) Tuning curves of VS-cells obtained with low (50°/s) and high (3000°/s) angular velocities are approximated by cosine functions using different amplitude factors for positive and negative half-waves. (b) Mean time course $r(t)$ of the stimulus-induced membrane potential for two rotation-axes. The time course of the response is fitted by band-pass-filtering a step-response scaled to the activity given by the tuning-curve. (c) The dependence of the measured noise on the measured mean activity is approximated by a Gaussian function. The noise is determined as the variance between individual responses and the time-dependent mean response as averaged over many stimulus presentation.

For determining the accuracy of a population code by a Bayesian estimator a much larger number of response traces is required than can be determined in intracellular recordings. Therefore, response traces of the population are modelled after the experimental findings (Fig.1). Individual noise traces are computed as a series of lowpass-filtered, Gaussian distributed random numbers. The noise was scaled according to its experimentally determined dependence on mean activity. Individual response traces ($r_i(t)$) are computed by adding individual noise traces ($n_i(t)$) to the mean time course of the membrane potential ($r(t)$, cf. Fig.1b).:

$$r_i(t) = r(t) + n_i(t).$$

Based on repeated simulations of the population response to a known set of stimuli, we estimate the conditional probability distribution of the responses given a stimulus $p(r|s)$. The distribution of the stimuli given an observed response $p(s|r)$ contains all information about the stimulus present in the response and is derived using Bayes rule:

$$p(s|r) = p(r|s)p(s)/p(r)$$

The stimulus vector maximising $p(s|r)$ is used as an estimate of the stimulus.

To show the effect of integration time on the accuracy of a population code we simulate the activities of 10 neurons located in one brain-hemisphere. The preferred rotation axis of each neuron is fitted to the experimental data (cf. Fig.2a). The mean responses are estimated by averaging over 1, 2, 5 and 10 ms time windows starting at response onset. The error, i.e. the root-mean-squared difference between true and estimated rotation axis, varies with the rotation axis to some extent (Fig.2b). These modulations of the error with changes in rotation axis decrease at longer integration times.

In general, the error decreases with longer integration time as expected (Fig.2c). But even for an integration time as short as 1 ms the mean error with which a certain rotation axis is encoded is below 2°. This high accuracy of decoding the rotation axis from the activity of only 10 neurons is a consequence of the graded response mode of VS-cells and would hardly be possible for a corresponding population of spiking neurons. This finding has important functional implications for flies: They perform rapid acrobatic flight manoeuvres, which require fast and accurate sensory control signals for visual flight and gaze stabilisation.

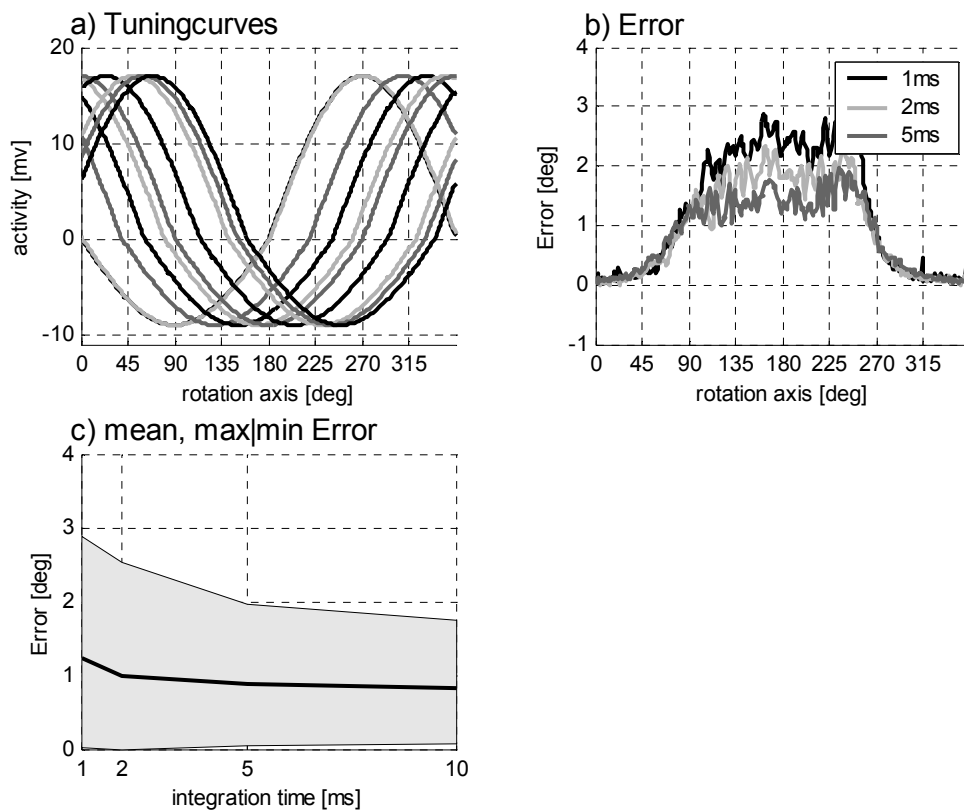


Fig. 2. Error evolution over integration time. a) Tuning curves for 10 simulated VS-cells in one half of the visual system. b) Error as a function of rotation axis computed for different integration times. c) Mean, maximum and minimum error plotted over integration time. Simulations were performed for a noise level with variance 10mV^2 .

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References

- [1] L.F. Abbott, P. Dayan, The effect of correlated variability on the accuracy of a population code, *Neural Comput.* 11 (1999) 91-101
- [2] A. Borst, J. Haag, Neural networks in the cockpit of the fly, *J. Comp. Physiol. A* 188 (2002) 419-437
- [3] M. Egelhaaf, R. Kern, H.G. Krapp, J. Kretzberg, R. Kurtz, A.-K. Warzecha, Neural encoding of behaviourally relevant visual motion information in the fly, *Trends Neurosci.* 25 (2002) 96-102
- [4] M. Egelhaaf, A.-K. Warzecha, Encoding of motion in real time by the fly visual system, *Curr. Opin. Neurobiol.* 9 (1999) 454-460
- [5] K. Hausen, M. Egelhaaf, Neural mechanisms of visual course control in insects, *Facets of Vision* (D.G Stavenga and R.C.Hardie, eds), Springer (1989) 391-424
- [6] R. Hengstenberg, Spike responses of 'non-spiking' visual interneurons, *Nature* 270 (1977) 338-340

- [7] H.G. Krapp, Neural matched filters for optic flow processing in flying insects, *Neural Processing of Optic Flow* (M. Lappe, eds), Academic Press (2000) 93-120
- [8] H.G. Krapp, R. Hengstenberg, Estimation of self-motion by optic flow processing in single visual interneurons, *Nature* 384 (1996) 463-466
- [9] J.P. Lindemann, R. Kern, C. Michaelis, P. Meyer, J.H. van Hateren, M. Egelhaaf, FliMax, a novel stimulus device for panoramic and highspeed presentation of behaviourally generated optic flow, *Vis. Res* 43 (2003) 779-791
- [10] A. Pouget, S. Deneve, J.C. Ducom, P.E. Latham, Narrow versus wide tuning curves: What's best for a population code? *Neural Comput.* 11 (1999) 85-9