

## Neurotransmitter dynamics in a model of a movement detecting visual system

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**Abstract.** In the visual system of the fly movement sensitive neurons show an amazing flexibility in their processing performance. This flexibility is modelled by introducing in the sequence of processing steps in the parallel input channels of these neurons the dynamics of synaptical functioning. This is done in such a way that the transmitter regeneration rate is a function of the on-going state of the stimulus generated activity in the input circuitry of these neurons. Model simulations fit experimental results in a convincing way.

### 1. Introduction

In the highest order ganglion of the fly visual system, movement sensitive neurons are found with visual fields which equal the visual field of the whole eye. These neurons perform a spatial summation of the activity present in the retinotopically ordered columns of their ganglion and transform this activity into a train of action potentials (spikes). One of these wide-field neurons, the H1, is horizontally selective in its movement detection performance: rates up to 400 spikes/s can be recorded in the case of visual stimuli which move horizontally inward (i.e. from back to front, the so-called preferred direction) in the visual field, whereas movement horizontally outward (null direction) suppresses the spontaneous activity of the element.

It is relatively easy to make extracellular recordings of this neural element which means that the information processing properties of H1 and, in part, up to H1 in this visual system, can be studied without damaging any part of it. A wide variety of precise and systematic experiments revealed the interesting property that the time-resolution of this visual system at this level is set by stimulus properties in such a way that the resolution increases (time constants becoming smaller) with increasing velocity of the moving visual stimulus (Mastebroek et al., 1982; Maddess and Laughlin, 1985; de Ruyter van Steveninck et al., 1986). It has been shown that the temporal resolution of movement detecting elements at this level of the fly system also is affected by temporal modulation of the visual stimulus, but to a much smaller extent (Borst and Egelhaaf, 1987).

In this contribution we present experimental results and model simulations concerning this stimulus-tuned temporal behaviour in the processing of moving

patterns by this visual system. Our basic idea in the description and understanding of this adaptive strategy is that the level of activity in the columns of the input circuitry of the H1 movement detector can regulate the excitable properties of these elements via the biosynthesis of neurotransmitters (Changeux and Heidmann, 1987; Shepherd, 1988; Kuno, 1995) in such a way that the system as a whole is equipped with flexible processing properties in an optimal way. Grossberg and Gutowski (1987) used properties of neural dynamics in their study on decision making under risk. Carpenter and Grossberg (1990) embedded the dynamics of synaptical processes like transmitter accumulation, release, inactivation and modulation in the computational properties of their well known Adaptive Resonance Theory III neural network in order to construct a self-organizing pattern recognition architecture. Ogmen and Gagné (1990) implemented signal transmission via depletable neurotransmitters to obtain temporal adaptation properties in their model for motion perception in the fly visual system.

## 2. Experimental results

The stimulus pattern was a square-wave grating of about  $30^\circ \times 30^\circ$  with a spatial wavelength of  $10^\circ$  (which is about 8 times the interommatidial angle of the fly eye) and with a moderate modulation depth. The pattern was presented in the region of maximum sensitivity of the H1 neuron, i.e. about  $20^\circ$  laterally around the equator of the eye. The time-course of a single stimulus presentation consisted of an adaptation period  $T_{ad}$  of 3 s during which the pattern moved continuously with a constant speed  $V$ , at the end of which the pattern was stopped and kept in a fixed

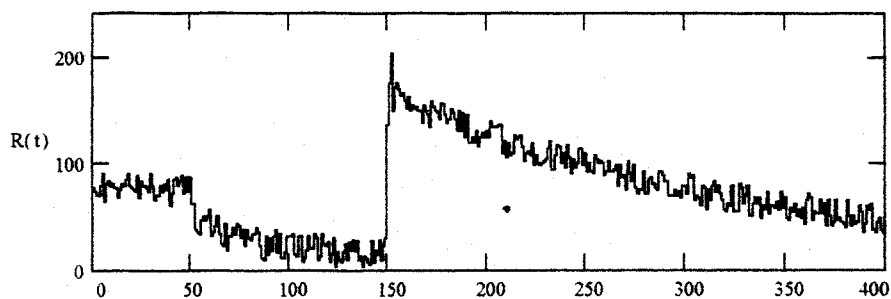


Fig.1. Horizontal axis: time in units (bins) of 2 ms. Vertical axis: spikes/s. The figure shows the averaged H1 spike activity during the last 100 ms (up to bin 50) of the adaptation period, the recovery from this level of activity (bins 51-149) and the onset of the response  $R(t)$  to the test-step of the pattern, beginning 200 ms after the end of the adaptation period (bin 150). During the adaptation period, the pattern velocity was  $V = 0.36^\circ/s$ . The time constant of the exponential decay of  $R(t)$  is  $\tau = 330$  ms. (After de Ruyter van Steveninck et al. (1986)).

position during 1 s except for a "test-step" which consisted of a small ( $0.6^\circ$ ) and

momentaneous displacement presented 200 ms after the moment at which the pattern was stopped. From the system-theoretical point of view, such a test-step can be looked at as an impulse of movement, presented to the system. Averaged responses ("impulse responses") to such test-steps of the stimulus in the preferred direction of the neuron are shown in fig.1. Before the presentation of the test-step the stimulus motion during the adaptation phase was set at  $0.36^\circ/\text{s}$ . The response  $R(t)$  in reaction to the test-step can be described with an exponential decay towards the resting level of the neuron. The time constant of the decay as obtained from a least-squares fit is  $\tau = 330$  ms. From these type of measurements it follows that for adaptation velocities ranging from 0.3 to  $125^\circ/\text{s}$  the time constant of the decay of the response changes from 320 to about 10 ms according to the relation  $\tau = 150 \cdot V^{-0.7}$  with  $V$  the stimulus velocity during the adaptation phase. Further important results are that  $\tau$  is not set by the spike rate of the neuron, and that  $\tau$  is tuned locally which means that spatially separated stimuli with different velocities each tune  $\tau$  according to their own velocity.

When the adaptation phase is followed by a longer period in which there is no stimulus movement, the change of the time constant from the shorter adapted value of the adapted state to the larger value of the unadapted state can be followed in time by presenting a series of test-steps with e.g. interstep-times of 1 s. The results (fig. 2) show that, after adaptation due to stimulus movement, it lasts about

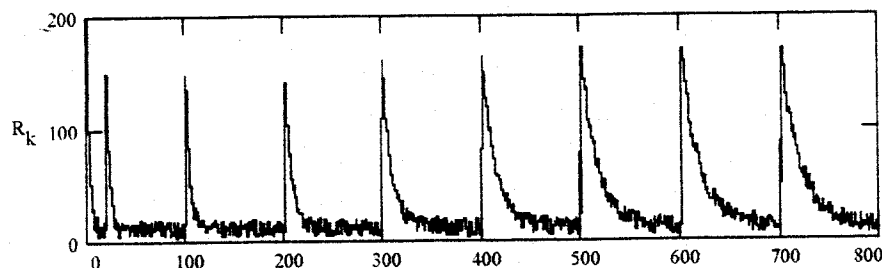


Fig.2. Horizontal axis: time in units of 10 ms. Vertical scale: spikes/s. The figure starts at the end of the adaptation phase of the stimulus and shows responses  $R_k(t)$  ( $k = 1, 2, \dots, 8$ ) to test steps. (After de Ruyter van Steveninck et al. (1986)).

8 to 20 s before  $\tau$  has reached its level of the unadapted state again. For a detailed description of the experiments and an elaborate discussion of the results we refer to de Ruyter van Steveninck et al. (1986).

### 3. Model simulation results

As a first step, we implement a chemical synapse in the sequence of signal processing steps in each of the parallel input channels of the movement detector. Let  $z(t)$  be the amount of transmitter available for release in this synaps and  $B$  the maximal

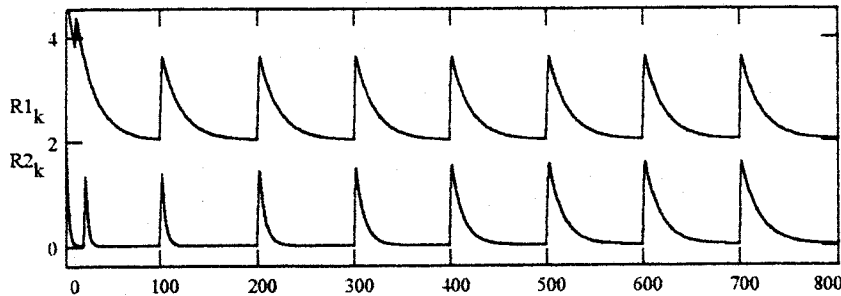


Fig. 3. Horizontal axis: time in units of 10 ms. Vertical scale: arbitrary units. The model responses  $R1_k(t)$  and  $R2_k(t)$  ( $k = 1, 2, \dots, 8$ ) start at the end of the adaptation phase of the stimulus. Upper trace: model response with constant value  $A$  of transmitter regeneration rate, lower trace: model response with  $A$  as a function of the ongoing stimulus generated activity.

amount of transmitter. This means that  $(B-z(t))$  is the amount of depleted transmitter at time  $t$ . This depleted transmitter re-accumulates with a time rate  $A$ . If we denote the stimulus by  $S(t)$  and suppose a gating action of  $z(t)$  on  $S(t)$ , then the amount of transmitter released (inactivated) by the stimulus is proportional to  $S(t) \cdot z(t)$ , e.g.  $C \cdot S(t) \cdot z(t)$  with  $C$  a constant. For the resulting production rate of transmitter we can now write (with for reasons of convenience  $C=1$ ):

$$\frac{dz(t)}{dt} = A(B - z(t)) - S(t) \cdot z(t)$$

Note that, if  $S(t) = 0$ ,  $z(t) = B$  in the stationary state and, when after a stimulus action  $z(t)$  has become smaller than  $B$ , it will return to  $B$  with a time constant  $\tau = 1/A$  as long as  $S(t) = 0$ . This equation, which is an ordinary differential equation from the stiff type, can be solved directly when  $S(t) = S \cdot H(t)$ ,  $H(t)$  being the Heaviside function and  $S$  the stimulus amplitude. It follows that:

$$z(t) = (BS/(A+S)) \cdot \exp(-(A+S)t) + AB/(A+S)$$

which means that, due to the action of the stimulus,  $z(t)$  levels to the value  $AB/(A+S) < B$  with a time constant  $\tau = 1/(A+S)$ . This time constant is set by the stimulus such as the larger the stimulus, the smaller the time constant! Transmitter regeneration dynamics is reflected now in the system behaviour as long as  $S(t) \neq 0$ . This property does not deliver however the movement detector's behaviour as depicted by the experimental results presented in fig. 2. Indeed, after adaptation to a movement stimulus, the system slowly recovers from this adaptation while  $S(t) = 0$ . In order to realize this behaviour in the model we introduce another expression  $A(t)$  for the transmitter regeneration rate  $A$ , equipping the model with a "memory" term (like a moving average) weighted via a kernel function  $k(t)$  with a long time constant. We thus write:

$$A(t) = A_0 + k(t) \otimes RS(t)$$

where  $A_0$  is a constant,  $\otimes$  denotes convolution and  $RS(t)$  is a function which describes the stimulus generated activity in the input channels of the movement detector. In a simple first approximation we take  $RS(t) \approx S(t)$ . For the kernel function we take:  $k(t) = (1/T) \cdot \exp(-t/T)$ , with  $T$  being a large time constant ( $T = 10$  s). Simulation results of the model with  $A$  as a constant and  $A(t)$  as a function of the past are given in fig. 3. The improvement of the model's performance in the case of a stimulus-tuned transmitter regeneration is evident.

#### 4. Conclusions

From the experiments it follows inevitably that the system's time resolution is set by the stimulus generated activity in the parallel input channels of the movement detector and, that -after the stimulus has been taken away- this adaptation phenomenon fades away according to a large time constant. As can be seen immediately from the differential equation, variations of the parameter  $B$ , the maximum amount of transmitter, do not influence  $\tau$  but vary amplitudes. To account for the activity-dependant behaviour of the time constant we have to make the transmitter regeneration rate  $A$  in the modelling of the synaptical properties to be a function of the past. In this way we endow the system with flexibility properties which depend on its on-going state.

We did not produce so far any direct experimental evidence with respect to the basic assumptions which underly our model. In order to do so and to realize a more quantitative comparison between experimental resp. model results, totally different kinds of experiments must be done.

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