Some characteristics of the neural activity of directionally selective movement detectors in the visual system of the blowfly

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SUMMARY

This study deals with the properties of directionally selective movement detectors in the visual nervous system of the blowfly Calliphora erythrocephala (M.). These movement detectors are neurons found in the so-called lobula complex. This study is part of a broader research program of the department of Biophysics of the "Laboratorium voor Algemene Natuurkunde", the main theme of which is the relation between brain function and behaviour.

This thesis has two major topics:

1: The way in which neural activity (spikes) is generated by the movement detectors; i.e. the study of the stochastic structure of this activity.

2: The shape of the sensitivity profile of the receptive field of these neurons in relation to the mosaic structure of the compound eye.

Both aspects are essential for understanding the functioning of the visual system as far as it involves the movement detectors at the level of the lobula complex.

Recordings of the neural activity plainly show that the spikes appear very irregularly. With the aid of elementary mathematical methods, the moments of spike occurrence which are unpredictable, but subject to certain probability rules, can be described as a stochastic process.

The directionally selective movement detectors respond with a marked increase of neural activity when movement in a certain direction (the so-called preferred direction) is presented within the receptive field by means of a moving stimulus. Movement in the opposed direction suppresses the neural activity. Apart from the direction of movement, the position of a moving stimulus within the receptive field also determines the magnitude of the response.

Chapter I presents a sketch of the architecture of the visual system in flies. The relation existing between the mosaic structure of the compound eye and the results of optomotor (behavioural) experiments as described in the literature is discussed. A recapitulation of the stochastic structure of the spike activity generated by the movement detectors such as reported in a former study (thesis Mastebroek, 1974) is found at the and of this chapter.

Chapter II deals with some technical details of the investigation: the preparation of the experimental animals, the generation of the stimuli, a review of the stimulus and response parameters and the basic principles of spike registration.

Chapter III forms a continuation of the study of the structure of the stochastic process describing the neural activity and provides an - at least qualitative - final description:

In the case of constant stimuli (no change in time and position) the stochastic structure can be described by a Markov renewal process determined by four parameters of which one is dependent on the stimulus. Therefore, the stochastic structure of this process is invariant, and hence, for this kind of stimulus, a frequency code is involved. In the case of dynamic stimuli (fields modulated in time) more parameters become dependent on the stimulus as a result of which the stimulus invariance is lost. The way in which this happens has been investigated more closely with the aid of moving stimuli. The generation of the spike activity can be strongly influenced by simultaneously presenting in different parts of the receptive field stimuli which each can move in a different direction. It proves that as more and more stimuli move in the preferred direction, the Markov process increasingly resembles the simpler Poisson process. When more and more stimuli move in the opposite direction (suppression of activity) the Markov process becomes ever more pronounced.

Chapter IV reports experimental results regarding the sensitivity profile of the receptive field of the movement detectors. The characteristic response to a small displacement of a stimulus is used to determine the minimally detectable displacement. The value found, 0.06°, is of the same order of magnitude as the values reported for behavioural experiments in the literature. A maximal characteristic reaction is obtained when a pattern is displaced over an angle equalling the effective interommatidial angle of the retinal mosaic. Also it proves that a dark over bright edge influences the reaction more strongly than its complement, a bright over darg edge, does. Experiments in which a small stimulus field is used, show that the sensitivity distribution of the receptive field is modulated spatially with a period (in degrees) equal to the interommatidial angle $\Delta\phi$.

These properties can be largely understood on the basis of an input scheme of the movement detectors as proposed in the literature. In this scheme, based on behavioural experiments, elementary movement detection units correlate visual information which is sampled over an angle of $2\Delta\phi$. Results of experiments regarding the so called "reversed reaction" demand extension of this model with detection units which correlate over an angle $\Delta\phi$. In case of these two systems (probably related to the two types of receptor cells at the retina level) cooperating at the input of the movement detector, one should be able to calculate - as least qualitatively - the responses to sinusoidally modulated moving patterns. Chapter IV ends with this calculation and a comparison of the experimental results and the theoretically predicted course.