Optimisation of movement detection in insects

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Organisms are the outcome of a long evolutionary process. Therefore, they are generally conceived as being adapted to their respective environments by natural selection. This may hold true also for the behaviour of animals and the underlying neuronal machinery. Often it is quite easy to call the specific features of a particular neuronal mechanism an ´adaptation´. However, it is usually much harder or even impossible to demonstrate that these features optimise the behavioural fitness of the animal. To be able to assess the degree of adaptation of a particular neuronal mechanism, it is necessary to know the operating conditions of the neuronal mechanism during the animal´s normal behaviour. For visual information processing, this means that we need to know the complex spatio-temporal characteristics of the retinal images an animal is usually confronted with. However, experiments on neuronal processing of visual information are usually performed with rather artificial stimuli. Moreover, to get rid of the consequences of neuronal noise the responses to many presentations of a given stimulus are averaged in most studies. This approach might be useful to unravel the neuronal mechanisms underlying sensory information processing. However, it does not easily allow to assess the performance of these mechanisms under normal behavioural conditions in real-time and, thus, the extent to which neuronal mechanisms are optimised to solve their tasks.

To analyse how behaviourally relevant information is processed in real time and to assess the adaptiveness of neuronal mechanisms, my co-workers and I employ a novel approach: On the one hand, we started to analyse how the visual system processes stimuli that are seen by an animal during behaviour. On the other hand, we analyse the constraints set by the neuronal hardware on the reliability of information processing in real-time.

Our experiments are done on the visual system of the fly, because here it is possible to investigate visual information processing at all relevant levels. Visually induced orientation behaviour can be analysed both in tethered flight with a flight simulator and under free-flight conditions by using video techniques. Moreover, it is possible to characterise the underlying neuronal mechanisms *in vivo* with electrophysiological, pharmacological and optical recording techniques (Egelhaaf and Borst 1993).

Neuronal processing of optic flow

Locomotion causes continuous displacements of the retinal images of the surroundings. Visual systems have evolved strategies to derive from this ´optic flow´ information, for instance, about ego-motion or the location of objects in the environment. Flies make use of optic flow information to guide their often virtuosic flight manoeuvres. In the fly´s third visual neuropile there are neurons, the so-called tangential cells (TCs), which are tuned to various aspects of optic flow. For instance, there are neurons which respond best to coherent wide-field motion as occurs when the animal performs particular flight manoeuvres. Moreover, there are cells which respond best to relative motion between an object and its background and, thus, may serve the detection of nearby objects during flight (Egelhaaf and Borst 1993, Hausen and Egelhaaf 1989).

The TCs pool with their extended dendritic arborizations the output signals of large numbers of retinotopically organised local motion sensitive elements. The preferred directions of these local motion detectors are not uniform throughout the cells´ receptive fields but vary in a way characteristic of each of the TCs. The local preferred directions of motion correspond to the local velocity vectors of the optic flow generated in certain behavioural situations such as rotations of the fly about a given body axis. As a consequence, the TCs have been concluded to be optimised as neural filters for particular types of optic flow (Krapp *et al.* 1998). Recent experiments by Katja Karmeier and Holger Krapp have shown that these characteristic receptive field properties are not modified by early visual experience. Instead the adaptations to optic flow processing were apparently evolved on a phylogenetic timescale.

However, despite this sophisticated spatial pooling of local motion information the selectivity of the TCs for particular types of optic flow is much increased by synaptic interactions between several TCs in the ipsi- and/or contralateral half of the visual system. One example are the FD-cells. In contrast to other TCs, the FD-cells respond preferentially to small moving objects and are inhibited during wide-field motion in large parts of the visual field. For a particular FD-cell this inhibition was shown to be the consequence of synaptic input from another TC that responds best to wide-field motion (Warzecha *et al.* 1993, Egelhaaf *et al.* 1993).

Cells involved in optic flow processing are usually characterised by relatively simple stimuli designed exclusively by the experimenter. However, in real life optic flow is complex since it depends on both the three-dimensional structure of the environment as well as the animal´s own movements. Employing a novel approach we investigated neuronal performance using optic flow that was induced by the actions and reactions of a behaving fly (Warzecha and Egelhaaf 1997). Bernd Kimmerle recently replayed optic flow to FD-cells which was generated by a tethered fly flying in a flight simulator while fixating an object. The object

could be discriminated from the background by motion information alone. Under the conditions of behaviourally generated optic flow the FD-cell was found to respond very specifically to object motion. Although object selectivity of the FD-cell is due to inhibitory input from TCs tuned to wide-field motion (see above), background motion has little effect on the object response of the FD-cell. This performance of the FD-cell appears to be well adapted to normal behavioural situations. Since optic flow in free-flight may be much more complex than in our flight simulator, it is advisable to be cautious with this conclusion. Before a final assesment on the performance of FD-cells can be made, it is necessary to reconstruct the optic flow as seen by free flying flies and to replay this optic flow to TCs. Roland Kern and Maik Lutterklas have recently started doing just this type of replay experiments (Kern and Warzecha 1998). We hope that these experiments will eventually allow us to assess to what extent the processing of optic flow by the fly visual system is optimised to process the retinal input as is seen by the fly in its normal behavioural context.

Constraints imposed by the neuronal hardware on the reliability of encoding of visual motion

Neuronal mechanisms are not constrained exclusively by the spatio-temporal features of the complex natural stimuli occurring in behavioural situations, but also by the specific characteristics of the neuronal hardware. With respect to the real-time performance and reliability of neuronal mechanisms we need to take into account that neurons are noisy elements. This is a consequence of stochastic cellular processes, such as transmitter release and the opening and closing of ionic channels. Thus the reliability of neuronal information processing and the performance of an animal is limited by a host of noise sources.

As a consequence of inevitable time constants which are intrinsic to any mechanism computing motion information fast motion transients are considerably attenuated in motion sensitive neurons. As a result, membrane potential fluctuations in a frequency range above about 20Hz are dominated by noise and do not represent much information about stimulus motion. Anne-Kathrin Warzecha could show in electrophysiological experiments that the timing of spikes on a millisecond timescale is primarily determined by the noise, whereas spikes are usually time-locked to motion stimuli only on a much coarser time-scale (Warzecha *et al.* 1998). This feature is the consequence of both the dynamical properties of motion-induced responses and the cellular mechanisms underlying spike generation. The probability for eliciting a spike is higher when the membrane at the spike initiating zone of the nerve cell depolarises more rapidly.

It appears unplausible that this limitation of the neuronal machinery represents a severe drawback for biological motion vision systems which are either required to sense ego-motion of the animal or the motion of objects. Because of inertia and friction impeding rapid velocity changes of objects, virtually no behaviourally relevant motion stimuli are likely to change their direction that fast to require a temporal precision of spiking in the millisecond range. Whether this notion is true needs to be elucidated in experiments where the dynamics of the natural motion input is analysed.

Conclusion

Since analyses on the neuronal encoding of the retinal input characteristic of natural behavioural situations have just begun, it is not yet possible to assess to what extent the computation of motion information is optimised to process behaviourally relevant information. Nonetheless, there are various features of the neuronal mechanisms underlying optic flow processing which may turn out as useful adaptations to optimise the visual system's performance given the limitations of the neuronal hardware.

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