Encoding of motion in real time by the fly visual system

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Direction-selective cells in the fly visual system that have large receptive fields play a decisive role in encoding the time-dependent optic flow the animal encounters during locomotion. Recent experiments on the computations performed by these cells have highlighted the significance of dendritic integration and have addressed the role of spikes versus graded membrane potential changes in encoding optic flow information. It is becoming increasingly clear that the way optic flow is encoded in real time is constrained both by the computational needs of the animal in visually guided behaviour as well as by the specific properties of the underlying neuronal hardware.

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Introduction

Images of the surrounding environment on the retina often change rapidly. Retinal image changes are partly attributable to changes in the outside world, such as when a moving object crosses the visual field. Even if the outside world is stationary, however, there is a continuous image flow on the retina when the observer, be it humans or other animals, moves about in the environment. This so-called optic flow is a rich source of information about both the outside world and the path and speed of locomotion. Before this information can be used to control visually guided orientating behaviour, it needs to be extracted from the activity profile of the array of photoreceptors and processed by the nervous system.

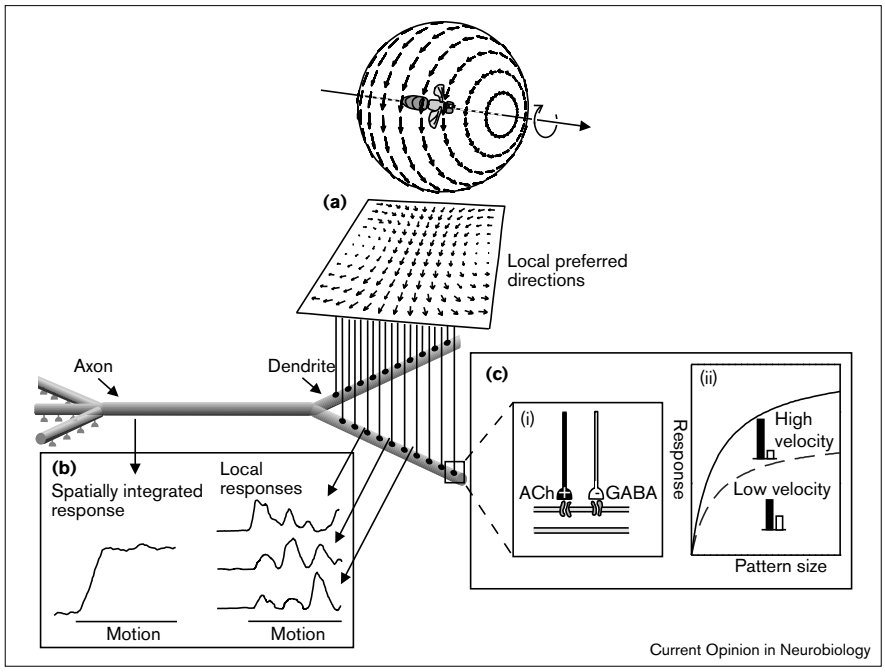
Although humans and other animals usually seem to solve this task without much effort, the ability to process complex, time-dependent sensory signals is by no means trivial given the properties of the neuronal hardware. In particular, when fast reactions are required, unreliable neuronal computations may become a major problem. The indeterminacy of neuronal responses is reflected in their often large variability. When a given stimulus is presented repeatedly to a neuron, the responses are not identical and may vary substantially. Often the variance of neuronal responses is on the order of the average response amplitude (see e.g. [1,2]). Hence, just by looking at the activity of a neuron, say in a sequence of action potentials, it is hardly possible to tell without additional information whether fluctuations in the interspike intervals are induced by a sensory stimulus or result from noise.

By what mechanisms, and how reliably, time-dependent stimuli are encoded by the nervous system is currently being investigated intensively in the context of optic flow processing in the visual systems of various animals, such as monkeys, pigeons and flies. The fly is highly specialised to evaluate time-dependent optic flow to control its often virtuosic visually guided orientation behaviour. In the fly, it is possible to track motion information processing physiologically from the retina to visual orientation behaviour [3].

Optic flow is initially processed in the first and second visual areas of the fly's brain by successive layers of retinotopically arranged columnar neurons. There is detailed knowledge on the first visual area, the lamina, both at the ultrastructural and functional level. Much attention has been paid in recent years to the strategies for encoding natural, time-dependent input signals by lamina neurons and the functional significance of these strategies (reviewed in [4,5]). Adaptive neural filtering in the lamina is thought to remove spatial and temporal redundancies from the incoming retinal signals and, thus, to maximise the transfer of information about time-dependent retinal images [6]. In contrast to this understanding of information processing in the lamina, little is known about information processing in the second visual area, the medulla. There is a great deal of anatomical knowledge on the medulla [7–10], and electrophysiological recordings are available from an increasing collection of medullar neurons [11–15]. Owing to the small size of these neurons and the difficulty of recording their activity for an adequate interval of time, their functional characterisation is still incomplete; interpretations of their role in motion detection must be regarded as tentative. At least there is evidence that direction selectivity is first computed on a local retinotopic basis in the most proximal layers of the medulla [12–14,16].

In the posterior part of the third visual area, the lobula plate, the local motion information is spatially pooled by the large dendrites of a set of neurons, the so-called tangential cells (TCs) [17,18]. Two types of retinotopic input elements with opposite preferred direction of motion — one inhibitory and one excitatory — converge onto the dendritic tree of the TCs ([19]; for a review, see [20]). As a consequence, the TCs respond selectively to the direction of motion. Owing to the spatial properties of their input organisation and to synaptic interactions with other TCs in the ipsi- and contralateral half of the brain, the TCs are ideally suited to process optic flow. Some TCs respond best to coherent motion in large parts of the visual field, such as when an animal turns about one of its body axes. Other TCs are tuned to relative motion between an object and its background, such as when the fly flies past a nearby object [3,17,18].

Figure 1



Consequences of dendritic integration on the representation of visual motion. Schematic of a fly TC in the third visual area, with two dendritic branches, an axon and an axon terminal. The TC receives retinotopically organised, local motion-sensitive inputs: vertical lines terminating with 'synapses' (black dots) on the dendrites. **(a)** The local input elements do not exhibit the same preferred direction of motion within the entire receptive field of the TC. Instead, the preferred direction of motion changes in a characteristic way (indicated by arrows in the plane above the dendrites). Data courtesy of H Krapp. For the TC shown here, the preferred directions correspond to the directions of motion (indicated by the arrows on the sphere) as experienced by the animal when turning about its long axis. **(b)** Even when the velocity of motion is constant, the activity of the local input elements of the TCs is modulated depending on the texture of the surround in the receptive fields of the local elements. Traces on the right indicate the time-dependent signals of three local input elements of the TC. By dendritic pooling of many local elements, this pattern dependence in the time course of the responses is eliminated to a large extent (left trace). **(c)** Gain control in the TC makes its responses relatively independent of the number of activated input elements and, thus, of pattern size, whereas the response amplitude still depends on pattern velocity. (i) The enlargement illustrates that each point in the visual space is subserved by a pair of input elements of the TCs, one of them being cholinergic (ACh) and excitatory, the other GABAergic and inhibitory [19]. (ii) Even during motion in the local preferred direction of the TC, both types of local input elements are activated, though to a different extent depending on the velocity of motion (black and white columns). As a consequence, the membrane potential approaches different saturation levels for different velocities when the number of activated local input elements increases. GABA, γ-aminobutyric acid.

In the following sections, we concentrate on three specific aspects of real-time motion encoding that have attracted particular attention in recent months: first, the role of dendritic integration by TCs in processing of optic flow; second, the performance of spiking and graded potential neurons in encoding of visual motion; and third, the constraints imposed by the neuronal hardware on the temporal precision with which visual motion can be encoded.

The role of dendritic integration in processing of optic flow

Optic flow information cannot be derived by computations operating on a local basis alone. Rather, motion information from different areas of the visual field must be compared. Here, dendritic integration plays a prominent role. Three functional consequences of dendritic integration will be reviewed below.

Firstly, the preferred directions of the local motion inputs to the TCs are not the same across the entire receptive field, but change in a way characteristic of each cell type. The spatial patterns of local preferred directions of the different TCs form the basis of their specific sensitivity to optic flow [21,22••] (Figure 1a). The sophisticated spatial distributions of preferred directions in the receptive fields of TCs are not modified by visual experience but appear to have resulted from phylogenetic adaptations [23].

Secondly, because the local motion input elements of the TCs have only small receptive fields, their responses are temporally modulated even when the stimulus pattern moves with a constant velocity. Therefore, the signals of these local elements, which 'look' at different areas of the surround, are phase-shifted with respect to each other. Spatial pooling of these local signals by the dendrites of the TCs reduces the temporal response modulations to a large extent [24,25•] (Figure 1b). Hence, dendritic integration produces a signal that is, to some extent, proportional to the time course of pattern velocity.

Thirdly, dendritic integration of the local movement-sensitive elements is a highly nonlinear process. When the signals of an increasing number of input elements are pooled, saturation nonlinearities make the response largely independent of pattern size. As a consequence of the opponent local motion inputs, the response saturates at different levels for different velocities (Figure 1c). Hence, the responses, while still encoding velocity, are almost invariant against changes in pattern size [26,27].

It should be noted that a wealth of active processes have been identified in the dendritic membranes of TCs, such as voltage-dependent sodium, potassium and calcium channels [28–30]. The functional significance of these active processes for encoding the time course of visual motion is still not well understood.

The performance of spiking and graded potential neurons in encoding visual motion

In the TCs, the postsynaptic signals originating from the retinotopic input elements superimpose, and, depending on the direction of motion, the cell either depolarises or hyperpolarises in a graded fashion. In some of the TCs, graded membrane potential changes in the cells' output region are thought to lead to transmitter release. In other TCs, the distance between input and output regions is too large for this mode of signal conduction, and the graded membrane potentials are transformed into spike trains that are actively propagated to the presynaptic terminal. However, there is no clear distinction between these two response modes. In many cells in which graded membrane potential changes reach the presynaptic terminal, they are superimposed and modified by various sorts of active signals [29,31,32]. Whether the different signalling modes differ with respect to information capacity and whether one of them may be superior over the other have been a matter of considerable debate in recent years.

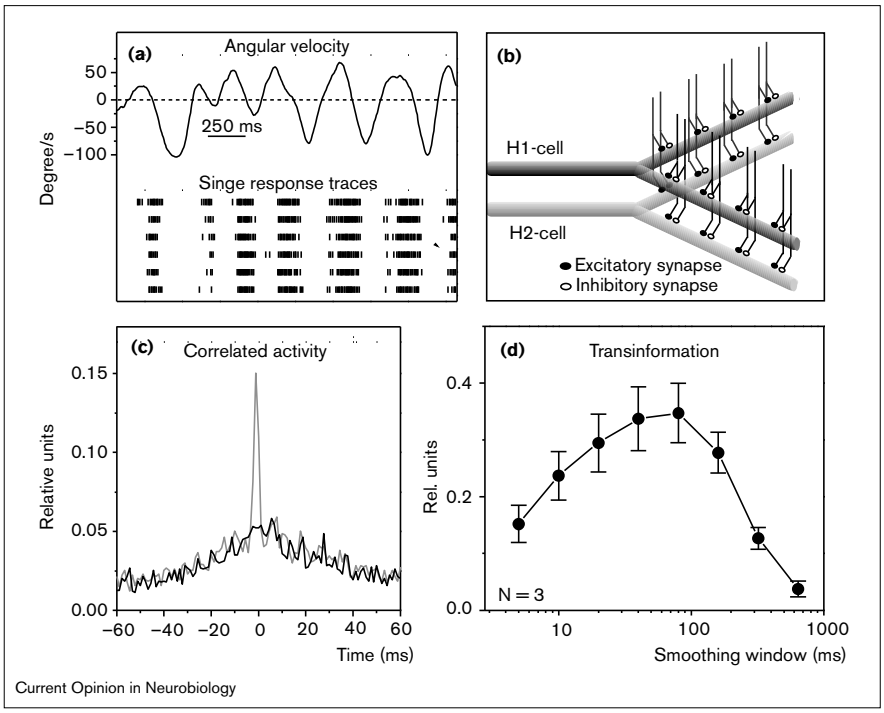
As some TCs differ in their signalling mode but receive basically the same type of retinotopic input, they are well suited for comparing the performance of spiking and graded potential neurons. The reliability with which constant velocity motion can be discriminated from no motion has been found to be basically the same for both response modes [33,34]. The same conclusion has been drawn concerning the time required to detect motion onset as well as for the number of stimuli that can be discriminated reliably [33,34]. Moreover, it has been found that the velocity of a randomly fluctuating motion stimulus is represented by spiking and graded potential TCs similarly well — as long as the pattern moves in the cell's preferred direction. Velocity fluctuations above 10–20 Hz are encoded only poorly by TCs of either signalling mode [35]. This feature is only partly attributable to neuronal noise. It is also the consequence of the fact that the stimulus-induced responses of TCs do not only depend on pattern velocity but also on its higher temporal derivatives [35,36]. In a recent study of a TC that generates both graded potential changes and spike-like events, it was concluded that more information about stimulus velocity is encoded by the graded response than by the spike-like events [37•]. However, one should be cautious about generalising this result to a principal difference in the performance of graded potential cells and spiking neurons. This difference is partly attributable to the relatively low frequency of the spike-like events and partly to the fact that the cell ceases firing spike-like events during null-direction motion [37•]. In contrast, the graded potentials transmit information about the velocity also during null-direction motion, because their membrane potential modulates below its resting level. Apart from this trivial difference, spiking and graded potential TCs perform similarly in encoding motion stimuli. In addition, metabolic costs for information transmission do not seem to favour the graded over the spiking response mode [38••]. Hence, the significance of cells that do not generate action potentials is still open to debate.

Constraints imposed by the neuronal hardware on the temporal precision of encoding of visual motion

The precision with which single neurons can encode information about the outside world is constrained by the variability of neuronal responses (Figure 2a). This is particularly true if time-dependent signals are to be encoded, as is the case in motion vision during normal behavioural situations. Across most of the cells' activity range, response variability (as given by the across-trial variance of the responses of spiking TCs to repetitive presentation of identical motion stimuli) is considerably smaller than the mean response amplitude. This is also true for constant stimuli [39•], despite an earlier claim to the contrary [40]. Although many questions remain regarding the biophysical and neuronal determinants of response variability, fly TCs appear to differ considerably with respect to variability from mammalian cortical neurons, such as in the motion pathway of monkeys [2]. The difference in variability between the different systems might be attributable to a different input organisation. Whereas fly TCs receive most of their input from the peripheral visual system, a considerable portion of synaptic input appears to originate from higher-order processing stages in the mammalian visual system.

Despite the relatively low level of variability of fly TC action potentials, most of their spikes do not lock to velocity fluctuations of a moving pattern on a millisecond timescale, even when these fluctuations contain high frequencies. On the basis of double recordings from pairs of cells with largely overlapping receptive fields, we [41••] concluded that the timing of spikes on such a fine timescale is, to a large extent, the consequence of stochastic membrane potential fluctuations at the cells' spike initiation zone (Figure 2 b,c). Time constants intrinsic to the process of motion computation [20] attenuate high-frequency velocity fluctuations. As a consequence, motion-sensitive neurons do not represent high-frequency velocity fluctuations particularly well. At frequencies above approximately 20 Hz, stochastic membrane potential fluctuations predominate over the motion-induced fluctuations when the cell is stimulated with white-noise velocity fluctuations [35,41••]. As a consequence of the biophysical properties of nerve cells, this frequency range of membrane potential changes, rather than the one in which velocity fluctuations are transmitted especially well, is particularly efficient in eliciting action potentials with a high temporal precision [42–44].

Figure 2



Reliability of encoding of visual motion information. **(a)** Section of a velocity trace that was generated in a flight simulator by a fly by its own actions and reactions, and six single responses of a spiking TC, the H1-neuron, to this motion stimulus. Each vertical line denotes the occurrence of a spike. The H1-neuron responds selectively to the direction of motion. Although the responses are very similar on a coarse timescale, they differ considerably when inspected more closely. **(b)** Schematic of the dendrites of two spiking TCs, the H1- and the H2-neuron, that are thought to receive their input signals from largely the same population of presynaptic elements. **(c)** Cross-correlogram of the responses of the H1- and H2-neuron to random velocity fluctuations. The cross-correlogram displays a pronounced peak when simultaneously recorded responses are evaluated (grey line), indicating that a large proportion of the spikes of the two neurons occurs within the same millisecond. The cross-correlogram is broad when responses elicited by the same motion stimulus are correlated that were not recorded simultaneously (black line). Hence, the synchronicity of the spike responses of both neurons is not induced by the motion stimulus but by stochastic response fluctuations transmitted by common inputs. An ordinate value of '1' would be obtained, if the correlated responses were identical at a timescale of 1.1 ms. (27 individual responses to the same dynamic motion stimulus each lasting 3.1 s; mean spike activity of the H1-cell: 29.2 spikes/s; mean spike activity of the H2-cell: 8.7 spikes/s.) Data from [41••]. **(d)** Information transmitted for each instant of time by the individual responses about the motion-induced response component ('transinformation'). The motion-induced response is obtained by averaging many individual responses to identical motion stimulation, thereby eliminating stochastic signals. Motion stimuli were generated in behavioural experiments by the actions and reactions of tethered flying flies and subsequently replayed to the H1-neuron in electrophysiological experiments [50]. Individual responses were obtained by smoothing the individual spike trains. The smoothing was done by sliding a time window across each spike train and counting the spikes within that window. The width of the time window was varied between 5 ms and 640 ms (abscissa). The transinformation is largest when the individual responses are smoothed with relatively large time windows of about 40–100 ms. With time windows smaller than about 40 ms, the instantaneous motion-induced response cannot be estimated as reliably because the stochastic response component is smoothed out to a lesser extent than with larger windows. With time windows larger than about 100 ms, fast motion-induced response components are smoothed out, thus preventing their reliable estimation. An ordinate value of '1' would be obtained if each individual response was identical to the motion-induced response. Data from [50].

Hence, in contrast to other systems and sensory modalities, in which different computational problems are being solved [45], stimulus-induced membrane potential changes in motion-sensitive neurons are usually not fast enough to elicit spikes with a high temporal precision. This limitation would be disadvantageous only if the fly needed to encode rapid velocity changes. However, velocity changes of the retinal image are attributable either to object motion in the visual field or to self-motion of the animal. In either case, velocity transients are limited by physical constraints such as inertia and friction and thus cannot be arbitrarily fast under natural conditions. With a recently developed magnetic coil technique by Schilstra and van Hateren [46••–48••], the motion transients elicited by body and head rotations of the animal can be estimated for free flight without the dynamical limitations of video analysis. Even the fastest head movements that could be observed take at least 10–15 ms for their execution, whereas the rapid saccade-like turns of the body take even longer. As a consequence, it is not surprising that motion can be decoded best from the instantaneous responses of spiking TCs if the responses are smoothed to some extent, depending on the dynamics of motion (Figure 2d) [34,49,50]. In any case, the timescale of behaviourally relevant motion information can be assessed only if the optic flow experienced by the animal in normal behavioural situations has been reconstructed.

Conclusions

The processing of the spatio-temporal retinal brightness changes that are characteristic of optic flow is constrained by the spatial and dynamical nature of the motion stimuli as well as by the biophysical properties of the neuronal hardware. Although this conclusion may appear almost trivial, its implications for further analyses have been explored only recently.

On one hand, much research on motion computation was previously performed under *in vivo* conditions, with electrophysiological, pharmacological and optical recording techniques primarily aimed at elucidating the cellular mechanisms underlying motion computation (for a review, see [3]). Because these studies were focused on the mechanisms themselves, they do not allow us to predict easily how these mechanisms encode the often complex optic flow typical of behavioural situations.

On the other hand, the reliability of motion encoding has now been quantified using data analysis approaches derived from signal detection and information theory [33–35, 39•,40,41••,49–52,53•,54]. Although these approaches have been important for analysing neuronal performance, their limitations have to be kept in mind. In particular, the measures that are used to quantify the performance of neurons are just measures of the variability of neuronal responses or the relationship between the diversity of the stimulus and the variability found in the corresponding responses. These measures, though very useful to quantify the relationship between stimulus-induced neuronal signals and noise, and thus the reliability of an information channel, do not reveal anything about the functional significance of the information being processed.

Because visual systems evolved in specific environments, the functional significance of the information being processed can only be assessed by analysing neuronal performance under conditions that come as close as possible to natural situations. Hence, it will be a most important task for future research on neural computation to take an ecological perspective. This perspective requires, on the one hand, analyses using visual stimuli that the animal encounters in everyday life. On the other hand, the internal state of the animal in different behavioural situations needs to be taken into account. For instance, the motion–vision system of the fly adapts to the prevailing dynamical conditions of the optic flow with which it is confronted [55–58]. These conditions may vary considerably, such as when the animal is walking or flying. Moreover, in poikilothermic animals such as the fly, body temperature depends on the temperature of the environment [59], as well as on the activity of the animal [60]. Indeed, over a range of plausible operating temperatures in the fly (about 20–30°C), the response latency decreases considerably and the signal-to-noise ratio of neuronal responses increases [61]. Hence, the animal's internal state affects the real-time performance in processing optic flow under natural conditions.

With respect to the processing of behaviourally relevant optic flow, two complementary approaches are currently being employed. In an attempt to understand the specific differences in neuronal performance as adaptations to the respective computational needs, O'Carroll *et al.* [62,63] have compared various insect species that differ considerably in their visually guided orientation behaviour. The largest challenge to this type of project will be to assess quantitatively the spatio-temporal properties of the behaviourally relevant stimuli.

Another approach to analyse the encoding of behaviourally relevant motion stimuli is to reconstruct and replay time-dependent optic flow as experienced in behavioural situations to motion-sensitive neurons. This approach has been successful so far in analysing tethered flight in a flight simulator, in which the visual system is confronted with the visual consequences of the animal's behaviour, which is similar to real flight (Figure 2d) [50,64]. In the meantime, sufficiently fast stimulus equipment has been developed to replay to neurons optic flow reconstructed from the trajectories of freely moving animals [65].

In the fly, sophisticated behavioural approaches allowing quantification of natural optic flow can now be combined with *in vivo* electrophysiology and optical recording. Therefore, this model system is exquisitely suited to investigate how behaviourally relevant motion information is encoded in real time. By applying this kind of multidisciplinary approach, it will be possible to understand which neural codes are used by specific neural circuits to solve a given task.

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