

Response latency of a motion-sensitive neuron in the fly visual system: dependence on stimulus parameters and physiological conditions

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Received 29 February 2000; received in revised form 15 May 2000

Abstract

The response latency of an identified motion-sensitive neuron in the blowfly visual system strongly depends on stimulus parameters. The latency decreases with increasing contrast and temporal frequency of a moving pattern, but changes only little when the pattern size and thus the number of activated inputs is increased. The latency does not only depend on visual stimuli, but is also affected by temperature changes and the age of the fly. Since response latencies cover a range of one order of magnitude, the latency changes are expected to be of relevance in visually guided orientation behaviour.

Keywords: Motion vision; Latency; Insect; Motion-sensitive neuron

1. Introduction

Information processing in the nervous system of animals and humans takes time before any reactions can be executed. The latency, i.e. the time which passes between the onset of a stimulus and the onset of the corresponding response, may take between some tens and some hundreds of milliseconds depending on the complexity of the task and the sensory modality involved. A large part of the behavioural latency is often due to muscular contraction. Nonetheless information processing by the neuronal machinery is time consuming. In the case of vision, the transduction of luminance changes into neuronal activity may already take more than 10 ms, depending on the brightness of the retinal image (e.g. Smola and Gemperlein, 1972; Laughlin, 1981; Aho, Donner, Helenius, Olesen Larsen & Reuter, 1993). Moreover, signal conduction, synaptic transmission and dendritic information processing inevitably take some time. Independent of their origin, the neural delays involved in sensory information processing

should have a pronounced influence on the behavioural performance, in particular, of fast moving animals.

It is often implicitly assumed that the latency mainly depends on the number of stages in a processing pathway, i.e. on the number of consecutive neuronal elements between the sensory input and the observed response. This view is supported, for instance, by the finding that in the visual system of monkeys the latencies of neuronal responses elicited by flashing visual stimuli were shortest in the lateral geniculate nucleus and responses occurred in the primary visual cortex before any other cortical area (Raiguel, Lagae, Gulyas & Orban, 1989; Schmolesky, Wang, Hanes, Thompson, Leutgeb, Schall et al., 1998). Even within the primary visual cortex, response latencies were found to increase monotonically from the input layer towards the surface of the cortex (Maunsell & Gibson, 1992). Despite the significance of the level of information processing for the response latency, the hierarchy of information processing is not its sole determinant. There is both behavioural (Miles, Kawano & Optican, 1986) and electrophysiological evidence (e.g. Järvilehto & Zettler, 1971; Bolz, Rosner & Wässle, 1982; Gawne, Kjaer & Richmond, 1996; Carandini, Heeger & Movshon, 1997; Kawano, 1999; Lisberger & Movshon, 1999; Maunsell,

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Ghose, Assad, McAdams, Boudreau & Noerager, 1999) that the latency of visual information processing may depend on stimulus parameters, such as luminance, contrast or velocity. Here we investigate the stimulus-dependence of the response latency in an identified visual interneuron in the motion pathway of the blowfly. The fly and, in particular, the analysed interneuron, the so-called H1-cell, are often used as a model system for investigating the neuronal mechanisms underlying the processing of visual motion information and its reliability (for review see Hausen, 1981; Egelhaaf & Borst, 1993; Egelhaaf & Warzecha, 1999). The H1-neuron is a spiking neuron which receives its input from a large array of retinotopically organised local motion-sensitive elements. As a consequence of this input, it responds directionally selective to motion and has a receptive field which covers almost one visual hemisphere. The H1-neuron connects the two halves of the visual system and transmits information about motion in the contralateral visual field to other neurons which play a role in optomotor course control as well as in object-background discrimination (Hausen, 1981; Egelhaaf, Borst, Warzecha, Flecks & Wildemann, 1993; Horstmann, Egelhaaf & Warzecha, 2000). We will show that the response latency of the H1-neuron depends in a dramatic way on various visual stimulus parameters as well as on the temperature and the age of the animal.

2. Materials and methods

All experiments were done on blowflies of the genus *Calliphora* which were bred in our laboratory stocks. If not specified otherwise, the age of the animals was between 4 and 9 days after eclosion. Animals were dissected as described previously (Warzecha & Egelhaaf, 1997). Extracellular recordings of the activity of the H1-neuron were performed with electrolytically sharpened tungsten electrodes. Recordings were done with standard electrophysiological equipment. The electrical signals were sampled at a rate of 960 Hz (Figs. 3, 5 and 6) or 1000 Hz (Figs. 2 and 4). The data were evaluated by programs written in ASYST (Keithley Instruments). The H1-cell was recorded in its output region which is located in the third visual neuropil in that half of the brain that is contralateral to its input region. The H1-cell was identified on the basis of its receptive field properties and preferred direction of motion. Animals were adjusted within the stimulus setup according to the symmetry of their eyes.

2.1. Visual stimulation

Three different stimulus setups (A–C) were used which varied with respect to the exact position and generation of stimuli. In all setups the motion stimulus

consisted of a squarewave grating moving at a constant velocity in the preferred direction of the H1-cell. The stimulus was always presented within the most sensitive region of the receptive field of the H1-cell.

In stimulus setups A and B visual motion was presented on a CRT screen (Tektronix 608). The stimulus pattern was generated at a frame rate of 183 Hz by an image synthesiser (Picasso, Innisfree).

2.1.1. Stimulus setup A

With this setup it was determined how the latency depends on pattern contrast and size. The horizontal extent of the pattern was 91° . The vertical extent was 76.6° , if not specified otherwise as for the experiments with variable pattern size. The centre of the screen was at an azimuth/elevation of $58^\circ/-5^\circ$, with $0^\circ/0^\circ$ referring to the frontal midline of the animal. The front edge of the screen was at an azimuthal position of 4° , the lateral edge was at 95° . The mean spatial wavelength of the grating was 18.2° .

2.1.2. Stimulus setup B

With this setup it was determined how the latency depends on the velocity of the stimulus grating and the head temperature of the flies. The horizontal and vertical extent of the screen were 74° and 59° , respectively. The centre of the screen was at an azimuth/elevation of $42^\circ/0^\circ$. The front edge of the screen was at an azimuthal position of 6° , the lateral edge was at 80° . The mean spatial wavelength of the grating was 10.6° .

The mean luminance, contrast, and the temporal frequency of pattern motion used in stimulus setups A and B will be specified in the respective Result sections and figure legends.

When setups A and B were used for visual stimulation data acquisition was started with the frame synchronisation signal of the image synthesiser. The spontaneous activity was recorded during one second before a motion stimulus was presented. Different data sets were obtained by varying either the contrast of the stimulus pattern (Fig. 2), its velocity and contrast (Fig. 3), its size (Fig. 4) or its velocity and the head temperature of the fly (Fig. 5). While acquiring a given data set, the corresponding visual stimuli were presented in a pseudorandom order, so that each stimulus was presented once before the next sequence started. In each trial the pattern was initially stationary for 1 s. Then it moved for several seconds (Fig. 2 and Fig. 4: 2.5 s; Fig. 3: 2 s; Fig. 5: 8 s) in the cell's preferred direction of motion and then was stationary again for 4–4.5 s.

2.1.3. Stimulus setup C

With this setup it was determined how the latency depends on the body temperature and the age of the fly. Experiments were performed in a climatic chamber, where the temperature could be controlled precisely.

For technical reasons a different visual stimulation device was used as in setups A and B. Stimuli were displayed via an array of light emitting diodes (LEDs) which consisted of 48 columns of 30 quasi rectangular LEDs per column. The horizontal and vertical angular extent of the LED-array amounted to 35 and 42, respectively. The LED-array was placed in the H1-cell's receptive field symmetrically with respect to the equator of the eye. The frontal and the lateral edge of the LED-array were at angular positions of 15 and 50. The stimulus pattern consisted of a squarewave grating with a spatial wavelength of 8.8° a mean luminance of 400 cd/m^2 and a contrast of almost 1. The pattern was displaced stepwise by one LED-column leading to apparent motion stimuli. These motion stimuli elicited pronounced direction-selective responses in the H1-neuron that were virtually indistinguishable from responses elicited by motion stimuli generated on a CRT screen. Apparent motion was presented at a constant temporal frequency of 11 Hz. In each trial the pattern was initially stationary for 1 s. Then it moved for 3 s in the cell's preferred direction and then was stationary again for 5 s before the next trial started.

2.2. Temperature control

The experiments in which the contrast or the pattern size were varied (Figs. 2 and 4), were done at normal room temperature ($21.5\text{--}23.8^\circ\text{C}$). Room temperature has not been measured during the experiments in which the temporal frequency was varied (Fig. 3). In the experiments in which the temperature effects on the latency were addressed explicitly two different temperature regimes were employed (see for details Warzecha, Horstmann & Egelhaaf, 1999). (i) Short-term temperature changes: In these experiments the effects of changes in head temperature were tested. Experiments were performed either at room temperature ($18\text{--}20^\circ\text{C}$) or at a high temperature ($26\text{--}28^\circ\text{C}$). In order to control the head temperature, the sensor of an electronic thermometer (precision: 1°C ; Conrad Electronics, Germany) was placed into the hemolymph of the head. To increase the temperature from room temperature to $26\text{--}28^\circ\text{C}$ the head was illuminated through a small aperture by a lamp (halogen projection bulb, 12 V, 50 W). The aperture was covered by two red filters (Schott RG8 and RG10 with 50% transmission at 695 and 715 nm, and a transmission coefficient of less than 0.001% for wavelengths below 640 and 660 nm, respectively) to prevent visual stimulation of the eyes. The results displayed in Fig. 5 were obtained in this way. (ii) Long-term temperature exposure: The results shown in Fig. 6 were obtained in a climatic chamber, the temperature of which was held either at $19\text{--}20^\circ\text{C}$ or at $29\text{--}30^\circ\text{C}$. The animals were transferred from the normal breeding room into the climatic chamber after pupation and

were kept there for their entire life until they were used in an experiment. Note, that we did not perform electrophysiological recordings from the same animal for several days. Instead we used different animals every day. Five different samples of flies were analysed in these experiments. Animals of one sample originated from eggs which were layed at the same date.

2.3. Evaluation of the latency

Many different methods have been applied previously for estimating the response latency of spiking visual neurons (e.g. Levick, 1973; Bolz et al., 1982; Vogels & Orban, 1990; Kawano, Shidara & Yamane, 1992; Maunsell & Gibson, 1992; Friedman & Priebe, 1999a,b). In general, the latency of responses that do not exhibit a sharp transition from spontaneous activity to stimulus-induced activity is difficult to determine. This difficulty arises because variability of neuronal responses masks the instant of time when the neuronal activity changes. We reduced this uncertainty by averaging over many responses elicited by the onset of constant velocity motion. Moreover, because the H1-cell is individually identifiable from preparation to preparation, we averaged over the mean responses of several cells. To further reduce activity fluctuations that were not induced by visual stimulation, the average spike frequency histograms of all cells were slightly smoothed by a three pixel ($\sim 3 \text{ ms}$) running average. The latency was then determined as the instant of time when the smoothed spike frequency exceeded a threshold for at least the next 6 ms. Since the shape of the spike frequency histograms strongly depends on stimulus conditions (see below), the threshold should be as low as possible so that spike frequency histograms that only differ in the steepness with which the stimulus-induced activity increases but that do not differ with respect to their latency will yield almost the same estimate of their latency. Therefore we did not determine the instant of time when the spike frequency histogram reaches its half peak amplitude as is often done (e.g. Friedman & Priebe, 1999b). The threshold was chosen as the cells' mean resting activity plus two times the standard deviation of the mean spike frequency histogram from its respective time-averaged value when no motion was presented (Fig. 1). It never occurred that this threshold was crossed for more than 4ms during the resting activity of the cell in any of the analysed spike frequency histograms. Since the determination of the latency is inevitably affected by the steepness of the spike frequency histogram after motion onset we will not only plot the values of the response latency but also display a selection of the analysed spike frequency histograms. To show the onset of the responses as clearly as possible, spike frequency histograms of different data sets will be presented at

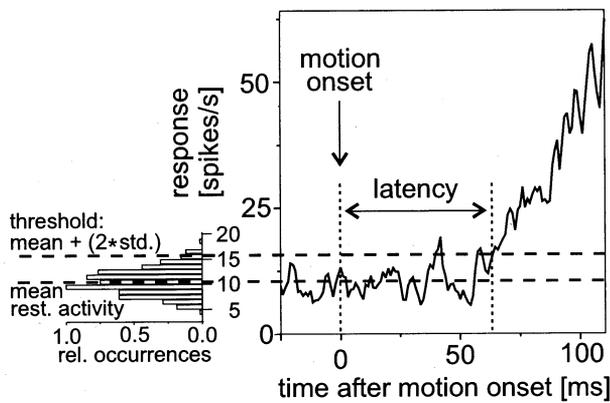


Fig. 1. Method of determining the response latency. Latencies were determined from spike frequency histograms of responses elicited by constant velocity motion in the preferred direction of the H1-cell. Spike frequency histograms were obtained with a 1 ms resolution and smoothed with a 3 ms running average. For most data sets spike frequency histograms were averaged over several cells (see figure legends). The spike frequency histogram shown here was obtained from 19 H1-cells and a total of 553 individual responses. The time instant relative to stimulus onset was taken as latency, when the spike frequency exceeded a threshold for at least 6 ms. The threshold was chosen as the cell's mean resting activity plus two times the standard deviation of the spike frequency histogram from its respective time-averaged value as determined within 375 ms prior to motion onset.

different time scales. Summary plots of the latencies obtained for the different data sets will be drawn to the same scale to facilitate comparisons of the effects of different stimulus parameters on response latency. In addition to inspecting all spike frequency histograms we corroborated our results by using a different method to determine the response latency. For this purpose spike frequency histograms were smoothed using a Blackman filter with a cutoff at 120 Hz (Astheimer, 1989; Blackman & Tukey, 1958) instead of a three-pixel running

average. We then determined a threshold that was never crossed during a 40 ms interval prior to stimulus onset for any of the analysed mean spike frequency histograms. The threshold was found to be the cells' mean resting activity plus four times the standard deviation of the spike frequency histogram from its respective time-averaged value when no motion stimulus was presented. This procedure led to the same qualitative dependencies of the response latency. It was not feasible to determine the latency from the point of intersection between the initial slope of the response and the mean resting activity, because no algorithm could determine the initial slope equally well for all responses obtained under the different stimulus conditions.

3. Results

3.1. Stimulus-dependence of latency

Previous studies have shown in great detail that the response of the H1-neuron as well as of other motion-sensitive neurons in the third visual neuropil of the blowfly depends in a characteristic way on stimulus parameters such as velocity, contrast or pattern size (Eckert & Hamdorf, 1981; Hausen, 1981; Lenting, Mastebroek & Zaagman, 1984; Egelhaaf, 1985; Egelhaaf & Borst, 1989; Haag, Egelhaaf & Borst, 1992). Therefore, these relevant stimulus parameters were varied systematically and the responses inspected at a sufficiently high temporal resolution to test for stimulus-dependent latency changes.

Fig. 2A shows the spike frequency histograms of responses to pattern motion with a temporal frequency of 2 Hz. The pattern contrast varied between 0.08 and 0.96. Two features of the onset of the responses are

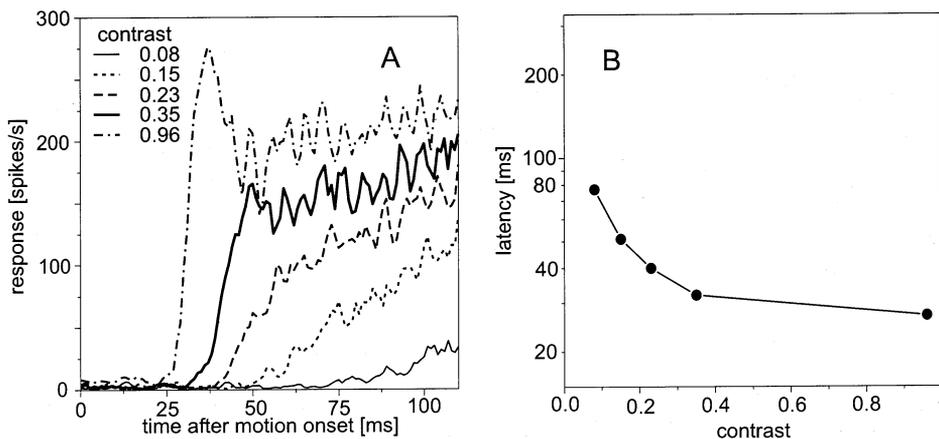


Fig. 2. Contrast dependence of response latency. Data obtained with stimulus setup A. (A) Spike frequency histograms of the H1-cell for the onset of motion stimuli with varying contrast. Both the slope and the final response amplitude increase with increasing pattern contrast. Spike frequency histograms were averaged over six cells each of which contributed between 54 and 90 individual responses to each stimulus condition. Total number of individual responses: 404. Mean luminance: 7.4 cd/m². Temporal frequency: 2 Hz. (B) Latency plotted on a logarithmic scale as a function of pattern contrast.

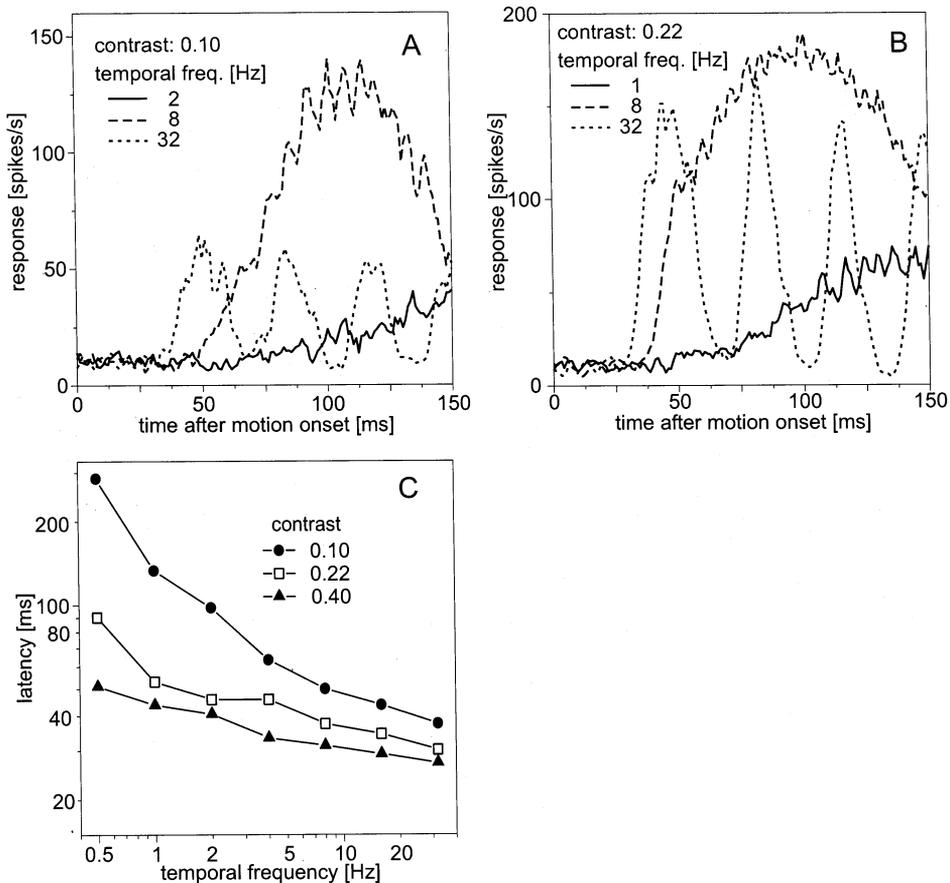


Fig. 3. Temporal frequency dependence of response latency. Data obtained with stimulus setup B. (A,B) Spike frequency histograms of the time-dependent responses elicited by various temporal frequencies at a pattern contrast of either 0.10 (A) or 0.22 (B). Note that the initial response transient shown here modulates with the temporal frequencies of the stimulus pattern. Spike frequency histograms were averaged over 19 cells each of which contributed between 23 and 30 individual responses to each stimulus condition (total number of individual responses: 553). Mean luminance: 3.3 cd/m². (C) Latency plotted for three pattern contrasts as a function of temporal frequency on logarithmic scales.

strongly affected by changing the pattern contrast. The slope of the first response transient decreases considerably with decreasing contrast. For the small contrast the response does not even reach its maximum level within the displayed time window. Moreover, latency increases by a factor of 2–3 when reducing the contrast from 0.96 to 0.08 (Fig. 2B). It should be noted that even at the lowest pattern contrast tested here the steady-state response amplitude reached a relatively high level of 117 spikes/s, though not earlier than 310 ms after the onset of motion.

Similar changes in latency are observed when changing the temporal frequency of pattern motion as is illustrated by the spike frequency histograms obtained for three temporal frequencies under low and medium contrast conditions (Fig. 3A,B). It should be noted that not only the latency, but also the timecourse of the responses differs tremendously for the different temporal frequencies. In accordance with previous studies (Maddess, 1986; Egelhaaf & Borst, 1989), the responses tend to modulate with the temporal frequency of pattern motion during their initial transient phase which

may last for several hundreds of milliseconds. Only after this transient phase the responses settle at their steady-state level (not shown in Fig. 3A,B). As is shown in Fig. 3C, the response latency decreases with increasing temporal frequency at all pattern contrasts. This decrease may range over one order of magnitude, at least at low pattern contrast. For high pattern contrasts, the decrease in response latency is less pronounced.

In contrast to pattern contrast and temporal frequency, changes in pattern size and, thus, in the number of stimulated input channels of the H1-neuron affect the latency only little (Fig. 4). The latency decreases by only less than 10 ms for a 10-fold increase of the size of a pattern that has a contrast of 0.99 and moves at a temporal frequency of 2 Hz.

3.2. Temperature and age dependence of latency

The response latency does not only depend on the visual stimulus parameters, but also on the physiological conditions under which the neuron has to operate.

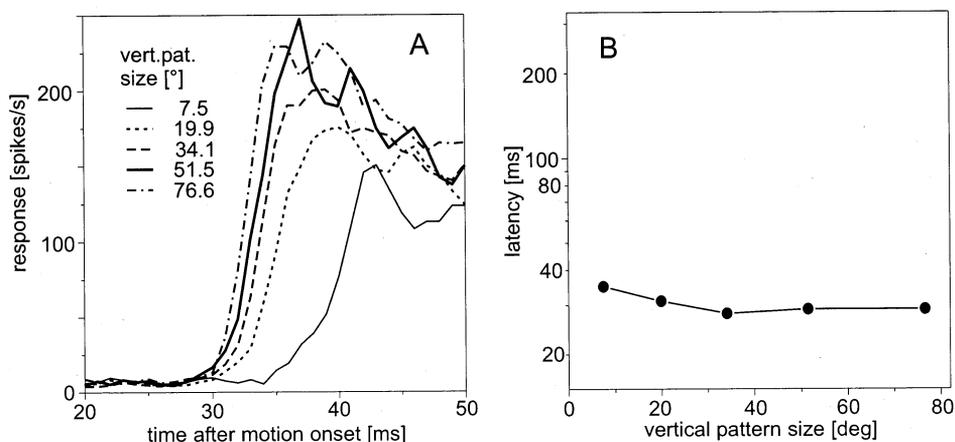


Fig. 4. Dependence of response latency on pattern size. Data obtained with stimulus setup A. (A) Spike frequency histograms for the responses to the onset of constant velocity motion for a range of pattern sizes. Spike frequency histograms were averaged over eight cells each of which contributed 60 individual responses to each stimulus. Mean luminance: 6.8 cd/m². Contrast: 0.99. Temporal frequency: 2 Hz. (B) Latency plotted on a logarithmic scale as a function of pattern size.

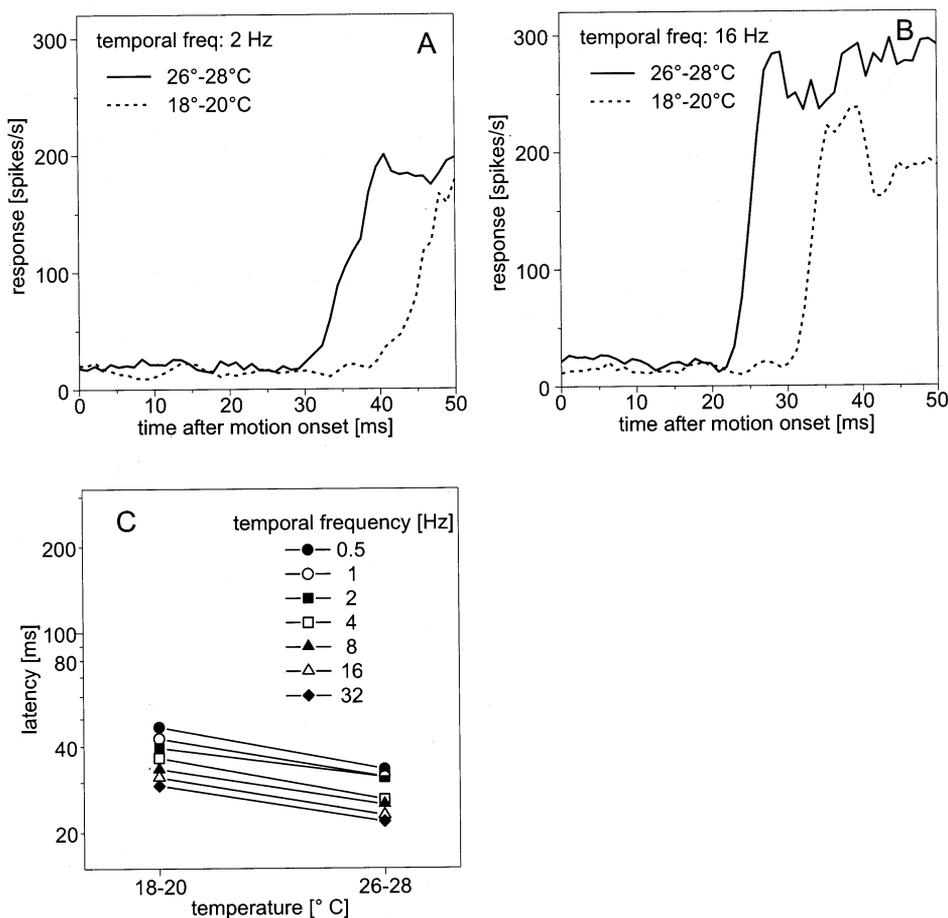


Fig. 5. Temperature dependence of response latency. Data obtained with stimulus setup B. (A,B) Spike frequency histograms of responses to the onset of constant velocity motion at low and high temperatures. The temporal frequency was either 2 Hz (A) or 16 Hz (B). Spike frequency histograms were averaged over 14 cells each of which contributed between ten and 30 individual responses to each stimulus (total number of individual responses for low/high temperature: 411/332). Mean luminance: 1.4 cd/m². Contrast: 0.89. (C) Latency for a variety of temporal frequencies plotted on a logarithmic scale for two temperature ranges.

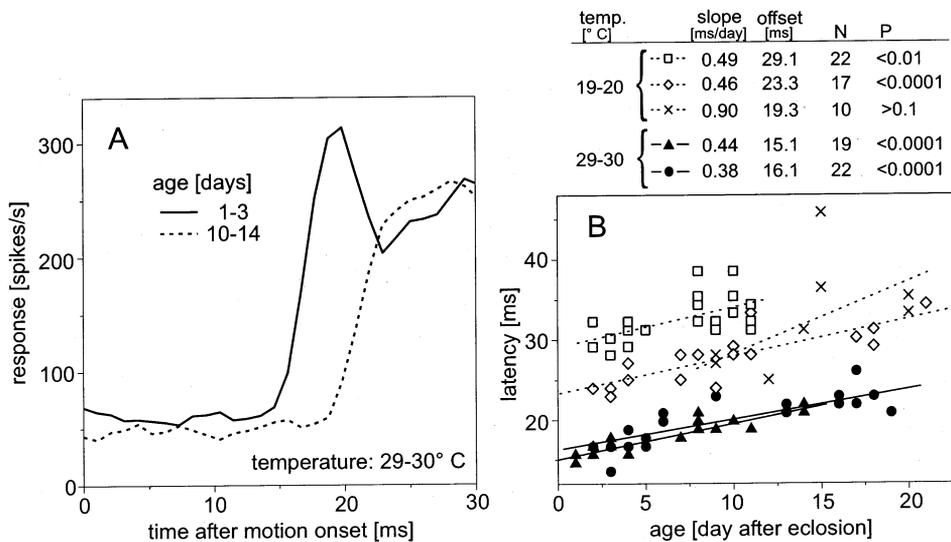


Fig. 6. Age dependence of response latency. The age of the flies is determined in days after eclosion from pupae. Data obtained with stimulus setup C. The data were obtained from five samples of animals (different symbols as explained in the inset). Three samples were kept at the low temperature, two at the high temperature. (A) Spike frequency histograms of responses to the onset of constant velocity motion for six young (1–3 days old) and six old (10–14 days old) animals of one sample of flies (filled triangles in B). Each fly contributed 80 individual responses (total number of individual responses for young/old animals: 480/480). (B) The latency is plotted on a linear scale as a function of the age of the flies. For all samples and irrespective of the temperature at which the flies were kept, the latency slightly increases with the age of the animals. The regression lines are plotted in the figure. For each sample of flies, the slope of the regression line, the number of data points as well as the significance of the deviation of the slope from 0 (*t*-test) are given in the inset. Note, that not all data points are visible because they overlap. For all but one cell per sample 80 individual responses were recorded. For the remaining H1-cell per sample only 40–60 individual responses could be recorded. There was no discernable difference in the latencies of these H1-cells with fewer individual responses and the remaining cells with 80 individual responses.

The spike frequency histograms obtained before and after the flies' heads were heated up by almost 10°C illustrate that the response latency decreases considerably with increasing temperature (Fig. 5A,B). This decrease is found irrespective of the temporal frequency used for motion stimulation. When the head temperature of the experimental animal is changed in a physiological range, the latency decreases by approximately 9 ms irrespective of the temporal frequency and, thus, of the absolute latency level. The H1-cell responses of animals that were exposed to either the low or the high temperature for their entire life exhibit very similar differences in their latency (see below and Warzecha et al., 1999). Hence the effect of the temperature on the latency is neither due to heating up only parts of the animal's body nor does it depend on the duration of exposure to a given temperature.

The latency also increases slightly with the age of the animal. This feature was tested for five samples of flies which were kept in a climatic chamber for their entire post-larval life. Two samples were kept at a high temperature (29–30°C) and three samples at a lower temperature (19–20°C). For one sample kept at the high temperature, mean spike frequency histograms are illustrated as obtained from six 1–3 day old flies and from six 10–14-day old flies (Fig. 6A). In contrast to the procedure used for evaluating the data obtained in all

other experiments, the response latency was determined for the spike frequency histogram of each individual fly. Again, the response latencies are considerably larger for the flies kept at the low temperature (Fig. 6B). Irrespective of the temperature the latency increases by 0.4–0.9 ms per day. This increase is significant for four out of five samples of flies. The age of the sample without a significant increase in the latency ranges only over 11 days and includes only ten flies. The relatively small sample size and age range render it more difficult to establish an age-effect than is the case for the other samples.

4. Discussion

The response latency is one major determinant of how fast an animal or a human can respond to sensory stimuli. Here we could show for a motion-sensitive neuron in the visual pathway of the blowfly that the response latency is affected by visual stimulus parameters as well as by the temperature and the age of the animal. The response latency decreases with increasing pattern contrast and temporal frequency, but is only slightly affected by pattern size. By increasing the temperature within the fly's normal activity range, the latency decreases. Irrespective of the temperature the latency slightly increases with the age of the animal.

Stimulus-induced changes in response latency similar to the ones described here for the H1-cell are found in other motion-sensitive neurons of the fly (Warzecha, unpublished). Hence the latency changes are likely to reflect a general property of the fly's motion pathway, rather than a specific property of the analysed neuron. Since the observed response latencies cover a range of one order of magnitude, they are expected to be of immediate relevance for visually guided orientation behaviour.

These results raise several questions which will be discussed in the following. (i) Are similar changes in latency also found in other systems or are they specific for the fly visual system? (ii) What could be the cellular basis of the observed latency changes?

4.1. Latency changes in different visual systems

Stimulus-dependent latency changes are not specific for fly motion-sensitive cells, but can be found also in other visual systems at both the behavioural and neuronal level. In monkeys a reduction of latency with increasing speed of the stimulus pattern has been described for many motion-sensitive neurons as well as for ocular following responses (Miles et al., 1986; Kawano et al., 1992; Kawano, Shidara, Watanabe & Yamane, 1994; Lagae, Maes, Raiguel, Xiao & Orban, 1994; Lisberger & Movshon, 1999; Raiguel, Xiao, Marcac & Orban, 1999; for review see Kawano, 1999). In some of these neurons latency seems to be mainly determined by the overall response level rather than by the speed as for very large speeds which lead to only relatively small response amplitudes the latency increases again (Raiguel et al., 1999). The influence of the spatio-temporal properties of the visual input on the latency has been analysed systematically for ocular following responses of monkeys (Miles et al., 1986). Quite similar to what we have found on the H1-neuron of the fly, the latency of the ocular following responses was found to decrease with increasing temporal frequency. Interestingly, a slight increase in response latency was found, after reaching a minimum, for very high temporal frequencies (i.e. above 40–50 Hz). Temporal frequencies in this range were not tested in the present study. In humans, the reaction times to the onset of moving textured stimuli decreased considerably with increasing velocity (Hohnsbein & Mateeff, 1992; Tynan & Sekuler, 1982), in accordance with our data on the H1-cell of the fly.

Apart from velocity, also other stimulus parameters influence neuronal responses in a wide range of visual systems. At the input site of the visual system, it is well known that the latency of photoreceptors depends much on the light intensity (e.g. Järvilehto & Zettler, 1971; Smola & Gemperlein, 1972; Baylor, Hodgkin & Lamb, 1974; for review see Laughlin, 1981). Intensity-

dependent changes in the latency are known to exist also at later processing stages (e.g. ganglion cells: Lennie, 1981; Bolz et al., 1982; Donner, 1989; Aho et al., 1993; LGN: Maunsell et al., 1999, visual cortex: Maunsell & Gibson, 1992). However, it has not yet been studied to what extent intensity dependent latency changes are reflected at the level of motion-sensitive neurons. Contrast-dependent latency changes have been analysed at higher processing stages, such as in the visual cortex of cats and monkeys (Maunsell & Gibson, 1992; Gawne et al., 1996; Carandini et al., 1997) as well as for ocular following responses (Miles et al., 1986). It has been found, again in accordance with our H1-cell data, that the response latency decreases with increasing contrast. Whereas we believe that, at least in the H1-cell of the fly, the contrast dependence of the latency may be just an inevitable consequence of the mechanisms underlying visual information processing, similar changes in the monkey visual cortex have been hypothesised to be a functionally significant feature of a neural code and to play a role in feature binding (Gawne et al., 1996).

Although the effect of the size of the stimulus pattern on response latency has been tested in the visual system of cats and monkeys (e.g. Bolz et al., 1982; Allman, Miezin & McGuinness, 1985; Raiguel et al., 1999), a direct comparison of the results of these studies with our H1-cell data is not possible, because the input organisation of the neurons is principally different. In particular, for the fly H1-cell, increasing stimulus size activates an increasing number of input elements so that the response will increase until it saturates (e.g. Hausen, 1984; Egelhaaf, 1985). In contrast, the above mentioned neurons of cats and monkeys exhibit an antagonistic surround. Hence, their responses decline if pattern size is increased above a certain limit. The latencies of the two types of input signals that transmit either the response to the central region or the antagonistic surround have been found to be different. Psychophysical evidence, however, indicates, that pattern size does not much influence reaction time (Tynan & Sekuler, 1982).

Latency does not only increase with the age of the fly H1-cell. Also in monkeys the latency of visual interneurons in the lateral geniculate nucleus and the striate cortex increases with the age of the animal. However, for the monkey, it cannot be decided yet, whether the size of the animal or its age are the critical determinants of this latency dependence (Maunsell & Gibson, 1992; Maunsell et al., 1999). There does not seem to be any advantage of increasing response latency with age.

Since the rate of all biochemical reactions depends on temperature, it is not surprising that physiological processes including those operating in the nervous system are considerably affected by temperature. However, ambient temperature is expected to affect only poikilo-

therms under physiologically relevant conditions, because homoiotherms maintain a constant body temperature. Temperature-dependent effects on the response latency in visual systems have therefore been investigated mainly in poikilotherms. In general, the latency of photoreceptors decreases with increasing temperature (Baylor et al., 1974; French & Järvilehto, 1978; Weckström, Järvilehto, Kouvalainen & Järvilehto, 1985; Roebroek, Tjonger & Stavenga, 1990; Tatler, O'Carroll & Laughlin, 2000). The decrease in the latency of light-induced photoreceptor responses in the fly are in the same range as the latency changes observed in the H1-neuron (Roebroek et al., 1990; Tatler et al., 2000; see also Warzecha et al., 1999). Hence, changes of the latency with temperature are likely to be caused by photoreceptor properties. The pronounced decrease of photoreceptor latency with increasing temperature has been concluded to be mainly due to the phototransduction cascade (Roebroek et al., 1990; Tatler et al., 2000).

4.2. Mechanisms underlying stimulus-dependent latency changes

A reduction in response latency with increasing stimulus strength might have a variety of causes. An increasing stimulus strength leads to an increasing synaptic input strength of a neuron. For instance, the input resistance of a neuron might be reduced when it receives massive synaptic input during strong stimulation. A smaller input resistance, apart from changes in the gain of the cell, leads to a reduced time constant of the dendrite. The membrane time constant of a layer V cortical cell has been estimated to vary by a factor of up to 10 depending on the amount of synaptic input (Bernander, Douglas, Martin & Koch, 1991). So at higher input strengths the membrane introduces shorter signal transmission delays within the neuron (Koch, 1999) and thus shorter response latencies. Stronger stimuli might have an additional effect. They may lead to steeper rise times of the postsynaptic potential, and if the cell is equipped with active processes with a threshold nonlinearity, such as spikes, shorter latencies are associated with stronger stimuli.

In principle, these cellular mechanisms could play a role at any processing stage from the photoreceptor to the analysed neuron. In the case of the H1-neuron of the fly several characteristics of the neural responses need to be taken into account when interpreting stimulus-dependent latency changes. In the case of motion-sensitive neurons, it is not straightforward to define 'stimulus strength', because various features of the response are modified by changing the stimuli. For instance, the responses may increase with only a shallow slope, but nevertheless reach a large response ampli-

tude, whereas for other stimulus conditions there might be a steep increase in response amplitude although the peak response stays relatively small. Inspection of our experimental data indicates that the initial slope of the responses at the onset of motion rather than the final response amplitude is a major determinant of the latency. In this regard, the H1-neuron of the fly may differ from motion-sensitive neurons in monkey area MT, where the response latency was found to be correlated with the response strength (Raiguel et al., 1999).

There is one characteristic property of the response which sheds some light on the site in the visual pathway which might be most relevant in determining the response latency. Whereas the latency was shown to depend much on contrast and temporal frequency, it was found to be largely independent of the size of the stimulus pattern. While under the former two stimulus conditions the local motion-sensitive elements which form the input of the H1-neuron are stimulated in a different way by changing the stimulus strength, this is different in the latter case. Here the activity of the individual local input elements is independent of the stimulus strength and only the number of activated input elements is increased by increasing the size of the stimulus pattern. The small effect of pattern size on latency, thus, provides evidence that, at the level of the H1-neuron, changes of the stimulus conditions induce only minor changes in response latency. The more pronounced stimulus-dependent latency changes mainly arise peripherally to the H1-neuron. The slight decrease in latency with increasing pattern size might be due to the convergence of an increasing number of activated inputs (see Carandini et al., 1997).

The dramatic increase of the latency with decreasing contrast and velocity of motion can be expected to interfere considerably with visual course control. The H1-cell is an intrinsic element of neuronal circuits that are thought to mediate optomotor course stabilisation (Hausen, 1981; Horstmann et al., 2000) and object background discrimination (Egelhaaf et al., 1993). For optomotor course stabilisation large latencies entail the risk of instability of the underlying feedback control system (Warzecha & Egelhaaf, 1996). Moreover, if objects cannot be detected fast enough, the animal runs the risk of bumping into them.

Acknowledgements

We thank Judith Eikermann and Monika Mielich for performing most electrophysiological experiments. Thanks are also due to Norbert Böddeker, Roland Kern and Rafael Kurtz for reading the manuscript and helpful discussions. Experiments comply with current laws of Germany.

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