19. Typically, pairs of stacks of images of secondary and tertiary dendritic branches (test and control sites) were collected at ~15-min intervals. Images were stored digitally and analyzed offline essentially unprocessed. The numbers and lengths of protrusions (lower limit, 0.54 μm) in a field of view (45 μm by 45 μm) containing 69 ± 22 μm of dendritic length were measured, keeping track of the fates of individual structures in optical sections. The limited *z*-resolution of our microscope (~1.5 μm) did not allow us to reliably detect and analyze protrusions that did not project laterally from the dendritic shaft, resulting in an underestimate of the densities of protrusions. Measurements were done in two-dimensional projections, resulting in an underestimate of the lengths of protrusions. To calculate the error resulting from projections, let r be the dendritic radius and l the length of spiny protrusions. Then the length of the projection of the protrusion—the measured length l'—is given by $l' = [(l + r)\cos\theta - r]$, where θ is the angle with respect to the horizontal. Assuming that spines are distributed isotropically, we can compute the average length as

$$\langle l' \rangle = (1/\theta_0) \int_0^{\theta_0} l' d\theta$$

where θ_0 is the largest angle for which protrusions are measured ($<\pi/4$). To estimate an upper bound for the error, we assume $l' = 2.75$ μm and $r = 0.5$ μm, and solve for l. This calculation suggests that we might underestimate the true length of protrusions by up to 13%. Only one set of experiments was performed per neuron (n refers to the number of neurons). Changes in the number of protrusions after tetanus were distributed in a non-Gaussian manner. In particular, our data probably included some experiments where the stimulating electrode failed to evoke synaptic responses on the target dendrite. We therefore used nonparametric statistics to test for differences in changes in morphometric distributions (*30*). Significance levels were computed with the WMPSR test and in all cases agreed with the highly restrictive sign test. Measurements are given as mean ± SD unless otherwise indicated.
20. T. V. P. Bliss and G. L. Collingridge, *Nature* **361**, 31 (1993); A. Kirkwood, H.-K. Lee, M. F. Bear, *ibid.* **375**, 328 (1995); M. C. Crair and R. C. Malenka, *ibid.*, p. 325; K. D. Miller, *Neural Comput.* **10**, 529 (1998).
21. Z. A. Bortolotto, Z. I. Bashir, C. H. Davies, G. L. Collingridge, *Nature* **368**, 740 (1994).
22. G. L. Collingridge, C. E. Herron, R. A. Lester, *J. Physiol.* **399**, 301 (1988).
23. These findings differ from previous studies designed to search for structural correlates of LTP (*4*, *5*). One reason could be that we used developing tissue; another reason could be the fact that we limited our structural analysis to regions of the dendrites that contained most of the activated synapses, thus improving the signal-to-noise ratio; a third factor could be that filopodia may be difficult to detect with EM.
24. K. M. Harris and J. K. Stevens, *J. Neurosci.* **9**, 2982 (1989).
25. C. Collin, K. Miyaguchi, M. Segal, *J. Neurophysiol.* **77**, 1614 (1997).
26. L. Stoppini, P. A. Buchs, D. A. Muller, *J. Neurosci. Methods* **37**, 173 (1991).
27. R. Malinow *et al.*, in *Imaging Living Cells*, R. Yuste, F. Lanni, A. Konnerth, Eds. (Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY, in press).
28. S. H. Shi *et al.*, data not shown.
29. K. Svoboda, D. W. Tank, W. Denk, *Science* **272**, 716 (1996).
30. S. Siegel, *Nonparametric Statistics* (McGraw-Hill, New York, ed. 1, 1956).
31. Supported by NIH (M.M.-S., R.M., and K.S.), the Mathers Foundation (R.M.), the Human Frontiers Science Program, and the Pew and Whitaker Foundations (K.S.). We thank B. Lendvai and E. Nimchinsky for helpful suggestions and B. Burbach, N. Dawkins, and S. Shi for technical assistance.

11 September 1998; accepted 8 February 1999

Variability in Spike Trains During Constant and Dynamic Stimulation

Anne-Kathrin Warzecha* and Martin Egelhaaf

In a recent study, it was concluded that natural time-varying stimuli are represented more reliably in the brain than constant stimuli are. The results presented here disagree with this conclusion, although they were obtained from the same identified neuron (H1) in the fly's visual system. For large parts of the neuron's activity range, the variability of the responses was very similar for constant and time-varying stimuli and was considerably smaller than that in many visual interneurons of vertebrates.

The reliability of behavioral responses to external events is limited by neuronal variability. Neuronal variability is commonly quantified by the variance in the number of spikes in response to repetitive presentations of identical stimuli. Variances across trials have often been found to be on the order of the mean spike count (*1–7*). Recently, the idea has been put forward (*1, 8*) that neuronal variability is only as large as the mean spike count if the responses are elicited by more or less constant stimuli. In contrast, it was concluded that more naturalistic dynamic stimuli elicit spike trains that are much more reproducible and thus have considerably smaller variances. Although it is thought that the reliability of neural coding is especially adapted to stimuli encountered by an animal in its natural behavioral context (*1*), our study does not support this hypothesis. Our experimental analysis was carried out on an identified neuron in the fly visual system, the H1 neuron, which has often been used to analyze the reliability of processing visual motion (*1, 9–16*).

The H1 neuron responds selectively to the direction of motion in large parts of the visual field by integrating the output signals of many local motion-sensitive elements. It increases its spike rate above the resting level during back-to-front motion (preferred direction) and decreases the spike rate during motion in the opposite direction (null direction). Because the spontaneous activity of the H1 cell is low, it usually stops firing when the pattern moves in the null direction (*9, 16*). Examples of how visual motion is represented by the H1 neuron are shown in Fig. 1 (*17*). The fly was stimulated by motion with different dynamical properties, that is, either by a pattern moving at a constant velocity or by random velocity fluctuations (*18*). At the onset of constant-velocity stimulation, the spike activity of the H1 neuron increased and, after a transient phase, reached a more or less constant level. During dynamic stimulation, the spike activity fluctuated strongly, following (to some extent) the time course of pattern velocity (Fig. 1D) (*11, 15, 19*). The timing of spikes was not entirely determined by the motion stimulus. It was also controlled by stimulus-independent sources, which becomes obvious when comparing individual response traces that were elicited by identical motion stimuli (Fig. 1, E and F). The variability was quantified by determining the variance in the number of spikes within a given time window in relation to the stimulus onset. For constant- and dynamic-velocity stimulation, the variance across trials was determined for a range of window sizes and was plotted as a function of the mean spike count. Because the stimulus-induced response to constant-velocity motion did not modulate much over time, only a small range of activities was elicited by a given stimulus (Fig. 1C). Therefore, the stimulus strength was altered by changing the vertical extent of the pattern. In contrast, during dynamic stimulation, the spike frequency was strongly modulated over the entire activity range of the H1 neuron (Fig. 1D). The variances obtained within 10-ms time windows were very similar for the two different stimulus dynamics. For constant as well as for dynamic stimulation, the plot of variance versus mean spike count was scalloped (Fig. 2). The variance was very small when the mean spike count was close to an integer number, and the variance was largest for intermediate spike counts. The scalloped distribution of data points is due to the discreteness of spikes [for a detailed explanation, see (*1*)]. The scallops closely followed the minimal variance that could be obtained in a spiking neuron (dotted lines in Fig. 2, A and B). The qualitative features of the single-cell example (Fig. 2, A and B) were corroborated by the mean variance averaged over several cells (Fig. 2, C and D). Hence, the variability of responses of the H1 cell was not influenced by the stimulus dynamics when it was evaluated within

Lehrstuhl für Neurobiologie, Fakultät für Biologie, Universität Bielefeld, Postfach 10 01 31, D-33501 Bielefeld, Germany.

*To whom correspondence should be addressed. E-mail: ak.warzecha@biologie.uni-bielefeld.de

such small time windows (*20*). Moreover, for constant-velocity stimuli, the variance did not equal the mean spike count, in contrast to a previous conclusion on the H1 cell (*1*), but remained markedly smaller. The variance was also not equal to the mean spike count for constant-velocity stimuli when the responses were evaluated within 100-ms time windows (Fig. 3, A and C). Instead, with increasing mean activity, the variance first decreased slightly and then increased again. A decrease in variance with an increasing mean spike count was also obtained in another set of experiments where the pattern moved at different constant velocities (*21*). For dynamic stimuli, the variance within 100-ms time windows somewhat increased with an increasing spike count. Regardless of stimulus dynamics, scallops were hardly visible (*20*). Moreover, for spike counts above about five spikes per time window, the variances of responses elicited by both types of stimulus dynamics did not differ much (Fig. 3, C and D). Only in the low-activity range of the cell was the variance of responses to constant-velocity stimuli larger than that of responses to dynamic stimuli. In any case, the variances of the responses to the tested dynamic- and constant-velocity stimuli were considerably smaller than the mean spike count.

This conclusion generally applies to a wide range of time windows and all dynamic- and constant-stimulus conditions that we tested. In Fig. 4, the Fano factor (the ratio of the variance and the mean spike count) is plotted as a function of the size of the time window that was used for counting spikes. For all constant-velocity stimuli and for the dynamic stimulus, the Fano factor first slightly decreased with an increasing time window, reached a minimum for intermediate windows, and then slightly increased again [for analysis with small time windows, see (*20*)]. Yet, the Fano factor was considerably less than 1 for all constant and dynamic stimuli and for all time windows that we tested. Thus, the variance was smaller than the mean spike count for both types of stimulus dynamics and for all window sizes tested.

These findings disagree with (*1*), which concluded (i) that, for constant-velocity but not for dynamical-velocity stimuli, the variance is on the order of the mean spike count and (ii) that dynamic stimuli result in a much smaller neuronal variability than constant stimuli. These conclusions are at least partly the consequence of a misleading presentation of the experimental data. In diagrams showing the variance of re-

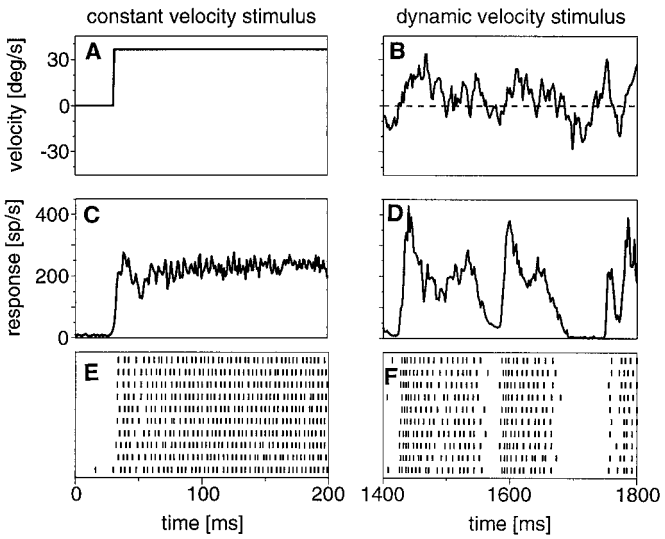

Fig. 1. Responses of the H1 cell to constant- and dynamic-velocity stimuli. (**A** and **B**) Velocity profile of a section of the stimuli used in the experiments. Positive (negative) velocities denote motion in the cell's preferred (null) direction. deg/s, degrees per second. (**C** and **D**) Spike frequency histogram obtained from the responses of five H1 cells to repetitive presentation of the motion trace shown in (A) and (B). For each of the five neurons, between 140 and 300 responses were averaged. The responses were shifted by 30 ms to compensate for the latency. Temporal resolution, 1 ms; vertical extent of the pattern, 76.6°; sp/s, spikes per second. (**E** and **F**) Subsequent sample traces of individual responses to repetitive presentation of the same motion trace. Vertical lines indicate the occurrence of spikes. The section of the responses shown in (E) and (F) corresponds to the section of the spike frequency histogram shown in (C) and (D), respectively.

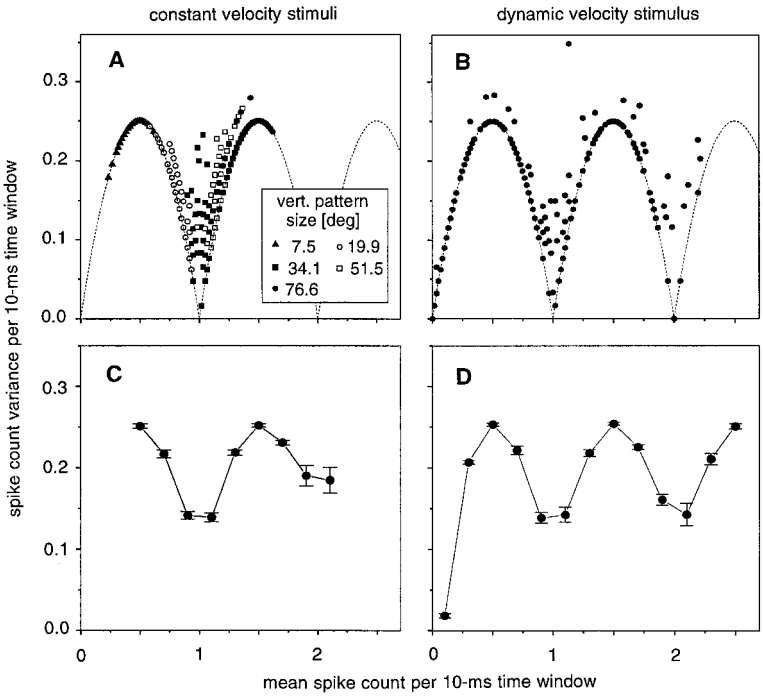

Fig. 2. Variance of the spike count of the H1 cell as a function of the mean count for (**A** and **C**) constant- and (**B** and **D**) dynamic-velocity stimuli. For each of eight cells, 60 individual responses to each stimulus condition were evaluated (*18*). For constant-velocity stimulation, different response levels were obtained by presenting five stimuli that differed in their vertical extent (A and C). The pattern segments with different vertical extent [see symbol legend in (A)] were centered at the equatorial plane of the fly's eye. Mean spike counts and variances were evaluated in 100 consecutive nonoverlapping 10-ms intervals, starting 1.5 s after the motion onset. Because dynamic-velocity stimulation results in pronounced response modulations (see Fig. 1D), the whole activity range of the H1 cell was covered by the motion of a given stimulus pattern (vertical extent, 76.6°) (B and D). Starting 100 ms after the motion onset, we evaluated 490 consecutive nonoverlapping 10-ms intervals. Data of one cell are shown in (A) and (B). Each symbol indicates the mean spike count and corresponding variance within a 10-ms interval that is time-locked to the onset of motion. Dotted lines illustrate the minimal variance that can be obtained in a spiking neuron (*20*). Data, as illustrated in (A) and (B), were combined from eight cells (C and D); the mean spike count was subdivided into activity classes with a width of 0.2 spikes. For each cell, variances were averaged when the corresponding mean spike count was in the same activity class. Thus, for the analysis done for (C), the variances of responses elicited by stimuli of different sizes were averaged. Then the mean variances of up to eight cells were averaged for each activity class. Only those activity classes and corresponding variances to which at least four cells contributed were illustrated. Error bars, SEM from up to eight cells.

sponses to constant velocities as a function of the mean spike count, the mean spike count has been mainly increased by increasing the time window used for counting spikes [figure 1E in (*1*)], whereas for dynamic stimuli, the spike count has been increased by altering the stimulus strength only [figure 2, E and F, in (*1*)]. The different ways of evaluating the variances elicited by constant and dynamic stimuli result in different dependences of the variance on the mean spike count. These differences cannot demonstrate a difference in the reliabilities with which constant and dynamic stimuli are represented. A potential difference can only be revealed when the data are evaluated in exactly the same way. However, we did not find a principal difference when we evaluated our data, which were obtained for constant and dynamical stimuli, in an identical manner. When scrutinizing the constant-velocity data shown in (*1*), it can be inferred that, for all time windows other than the 3-ms window (*20*), the variances of responses to constant stimuli evaluated within a given time window do not lie along the line of "variance = mean" but increase with a much shallower slope than that line [see figure 1E in (*1*)]. In fact, the variance of the responses then depends on the mean spike count in a manner that is similar to the dependence of the variance that has been obtained for dynamic stimuli and the variances that were determined in our study. Moreover, for the 10-ms time window, the variances obtained in (*1*) for constant-velocity stimuli quantitatively agree with those obtained for the other experiments [that is, for dynamic stimuli in (*1*) and for constant and dynamic stimuli in our study]. However, the variances obtained in (*1*) for constant-velocity stimuli with window sizes of 100 ms are somewhat larger than those determined in the other experiments. Various explanations for this quantitative difference are possible. The responses elicited by constant-velocity stimuli in (*1*) covered only about the lower one-third of the cell's activity range, whereas the responses elicited in the other experiments more or less covered the entire activity range of the cell. Because the variance depends on the activity of the cell, the different activity ranges might be a reason for the quantitative deviations in the variances obtained in the different experiments (*22*). Another reason for the quantitative deviations might be that the previous study (*1*) was based on the responses of only one cell for constant and one cell for dynamic stimuli. Although none of the eight cells analyzed in our study had a mean variance (within a 100-ms window) as large as that of the H1 cell analyzed in (*1*) for constant stimuli, the difference does not seem to be more than what can be expected on the basis of interindividual variability (*23*). In addition, we related only responses to constant and dynamic stimuli to each other, which were obtained from the same cells by presenting the different stimuli in a pseudorandom order, and we excluded nonstationary data (*18*). Both measures reduced the possibility that differences in the variances occurred for the two different stimulus dynamics because of processes that were not induced by visual stimulation.

There is no good evidence to assume that, in general, dynamic-velocity stimuli are processed in the fly's motion pathway more reliably than constant-velocity stimuli. Our data demonstrate that the variability of responses to constant and dynamic stimuli are basically the same when evaluated in exactly the same way. This finding might be surprising because, as is known from cellular neurophysiology, spikes are generated with greater reliability if the membrane potential at the spike initiation zone changes rapidly rather than slowly. Indeed, the occurrence of spikes was found to be tightly time locked to fluctuations of intracellularly injected current if this current contained frequencies above ~30 Hz (*24–26*). However, the motion-induced mem-

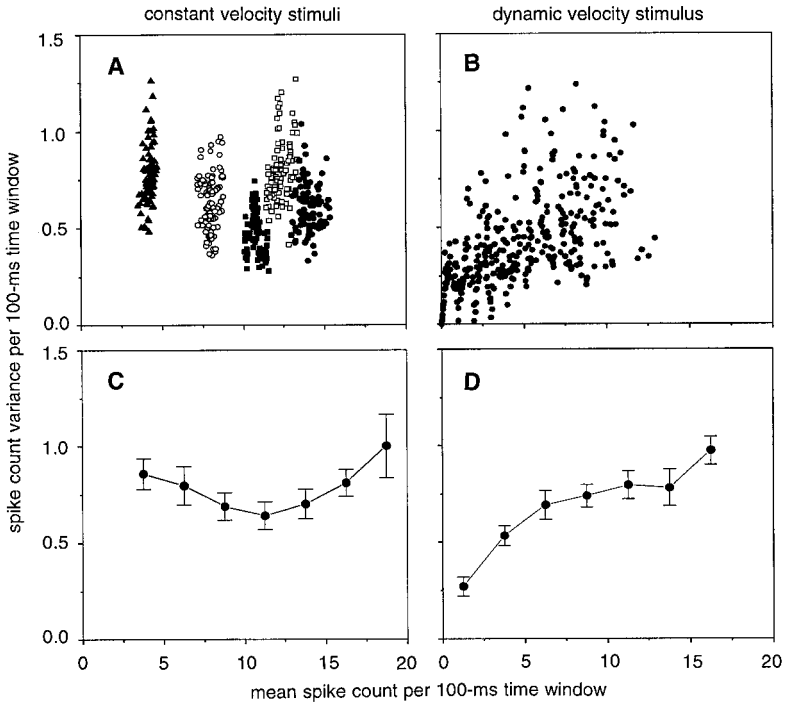

Fig. 3. Variance of the spike count of the H1 cell as a function of the mean count for time windows of 100 ms. (**A** and **C**) Mean responses and variances elicited by constant-velocity motion were evaluated in 91 consecutive time windows starting 1.5 s after the motion onset. Consecutive time windows overlapped by 90 ms. (**B** and **D**) Mean responses and variances elicited by dynamic stimulation were evaluated in 481 time windows with the same overlap and starting 100 ms after the motion onset. The same data set and conventions as in Fig. 2 were used. Data of one cell are shown in (A) and (B). Average variance of up to eight cells for constant-and dynamic-velocity stimuli was determined within activity classes with a width of 2.5 spikes [(C) and (D)]. Averages were obtained as described in the caption of Fig. 2. Error bars, SEM from up to eight cells.

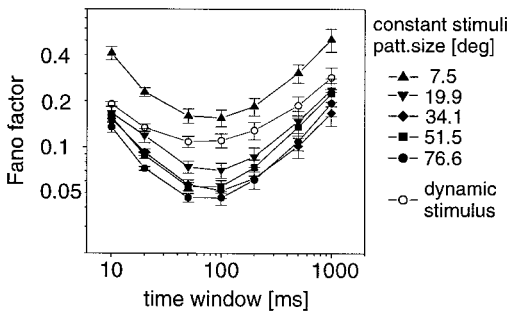

Fig. 4. Dependence of the Fano factor on the size of the time window within which spikes were counted. For each stimulus condition, for each cell, and for each of seven time windows ranging between 10 and 1000 ms, the mean variance and the corresponding mean spike count were determined, and the Fano factor was calculated. Fano factors were averaged over eight cells. Spike counts and corresponding variances were obtained in consecutive time windows that were shifted by 10 ms, irrespective of the size of the time window. The same data set as in Figs. 2 and 3 was used. Error bars, SEM from eight cells.

brane potential fluctuations in fly motion-sensitive neurons have less power at frequencies above 30 to 40 Hz than the stochastic membrane potential fluctuations (*14*). This observation even applies to the very transient dynamic stimuli used in our study. Therefore, it has been concluded that most motion-induced membrane potential changes are not transient enough to elicit spikes with a large reliability (*14*). Hence, there is no reason to expect that dynamic-velocity stimuli result in a smaller spike-count variance than constant-velocity motion. It seems likely that refractoriness plays an important role in regularizing spike generation at high activities (*27*) and thus may reduce, independent of stimulus dynamics, the variance at high spike frequencies as compared to low spike frequencies.

In accordance with our data on the fly H1 neuron, in motion-sensitive neurons in the middle temporal area (MT) of the monkey, the variances of responses to stimuli with different dynamical properties are fairly similar (*7*). However, whereas our study has demonstrated that, in the fly, the variance is smaller than the mean spike count, the variances of neurons in the visual cortex of cats and monkeys were found to be slightly larger than the mean [(*5, 6, 28, 29*); see, however, (*30*)]. Accordingly, the Fano factor in MT neurons has been found to be larger than unity irrespective of the time window and the stimulus conditions (*7*). Thus, the relation between mean spike count and variance of these neurons appears to differ from that found in fly motion-sensitive neurons.

References and Notes

1. R. R. de Ruyter van Steveninck, G. D. Lewen, S. P. Strong, R. Koberle, W. Bialek, *Science* **275**, 1805 (1997).
2. D. J. Tolhurst, J. A. Movshon, I. D. Thompson, *Exp. Brain Res.* **41**, 414 (1981).
3. R. Vogels, W. Spileers, G. A. Orban, *ibid.* **77**, 432 (1989).
4. J. P. Miller, G. A. Jacobs, F. E. Theunissen, *J. Neurophysiol.* **66**, 1680 (1991).
5. K. H. Britten, M. N. Shadlen, W. T. Newsome, J. A. Movshon, *Visual Neurosci.* **10**, 1157 (1993).
6. M. N. Shadlen and W. T. Newsome, *J. Neurosci.* **18**, 3870 (1998).
7. G. T. Buracas, A. M. Zador, M. R. DeWeese, T. D. Albright, *Neuron* **20**, 959 (1998).
8. M. J. Berry, D. K. Warland, M. Meister, *Proc. Natl. Acad. Sci. U.S.A.* **94**, 5411 (1997).
9. K. Hausen, *Verh. Dtsch. Zool. Ges.* **74**, 49 (1981).
10. M. Egelhaaf and A. Borst, *J. Neurosci.* **13**, 4563 (1993).
11. W. Bialek, F. Rieke, R. R. de Ruyter van Steveninck, D. Warland, *Science* **252**, 1854 (1991).
12. R. R. de Ruyter van Steveninck and W. Bialek, *Philos. Trans. R. Soc. London Ser. B* **348**, 321 (1995).
13. A.-K. Warzecha and M. Egelhaaf, *Eur. J. Neurosci.* **9**, 1365 (1997).
14. A.-K. Warzecha, J. Kretzberg, M. Egelhaaf, *Curr. Biol.* **8**, 359 (1998).
15. J. Haag and A. Borst, *J. Neurosci.* **17**, 4809 (1997).
16. H. Eckert, *J. Comp. Physiol.* **135**, 29 (1980).
17. All experiments were carried out with female blowflies (*Calliphora erythrocephala*) from our laboratory stock. Animals were dissected for electrophysiological experiments as described previously (*13*). The activity of an identified motion-sensitive neuron in the fly's third visual neuropil, the H1 cell (*9, 16*), was recorded extracellularly by standard electrophysiological techniques. Spikes were transformed into unit pulses and given to a PC at a rate of 1 kHz. Experiments were performed at temperatures between 21.5° and 23.5°C. The age of the animals was between 4 and 10 days after ecdysis. Animal care was in accordance with institutional guidelines.
18. Square-wave gratings were used as stimuli (spatial wavelength, 18.2°; contrast, 0.99; mean luminance, 6.8 cd/m^2) and displayed on a cathode ray tube screen (Tektronix 608) at a frame rate of 183 Hz by a Picasso image synthesizer (Innisfree, Cambridge, MA). The image synthesizer was controlled by a PC. It is unlikely that the finite frame rate influenced the precision in the timing of spikes, because a Fourier analysis of the spike frequency histograms revealed only a very small peak at 183 Hz, which is negligible in comparison to the time-averaged response (that is, the constant term in the Fourier series) and the noise level. Stimulus patterns covered the central part of the cell's receptive field (horizontal extent of the pattern is 91°, and the vertical extent of the different patterns is specified in the figure captions). At the beginning of each trial, data acquisition was triggered by the frame synchronization signal of the image synthesizer. It was ensured that, at the end of each sweep, data acquisition and stimulus control were still synchronized. Two types of motion stimuli were used: constant velocity and dynamic. For constant-velocity stimuli, the pattern was moved in the cell's preferred direction for 2.5 s at a velocity of 36.4°/s. Even constant-velocity stimuli may induce small-amplitude modulations with the temporal frequency of the pattern superimposed on a constant mean response level (*31*). To minimize potential effects due to these modulations, we varied the pattern size instead of the pattern velocity in order to cover different parts of the activity range of the H1 cell. Five patterns that differed with respect to their vertical extent were presented to each cell. In this way, different proportions of the cell's receptive field and thus a varying number of local input elements were stimulated. In order to analyze the steady-state response instead of response transients, as can be observed at the onset of constant-velocity stimuli (compare Fig. 1C), only the last second of the response was evaluated. To obtain a dynamic velocity stimulus, we generated white-noise velocity fluctuations according to a Gaussian distribution with a standard deviation of 0.57°/ms. The resulting velocity trace was low-pass filtered with a cutoff at 80 Hz to avoid aliasing due to the frame rate limit of 183 Hz. The pattern was moved for 5 s; the last 4.9 s of the response were evaluated. In between individual stimulus presentations, there was a pause of 5.2 s. For the data illustrated in Figs. 2 through 4, the six stimulus conditions (five constant-velocity stimuli of different vertical size and one dynamic-velocity stimulus) were presented in a pseudorandom order before the next sequence started. For quantitative analysis, 60 consecutive response traces were selected for each stimulus condition and cell. The variance would be overestimated with nonstationary data that show a trend in their activity over the recording period. Therefore, the mean activity during stimulation with any of the six motion stimuli was not allowed to change by more than 10 spikes per second over 60 trials, as judged from a regression line through the mean activities plotted over the trial number. In this way, 4 of 12 cells were excluded from the analysis.
19. M. Egelhaaf and W. Reichardt, *Biol. Cybern.* **56**, 69 (1987).
20. The scalloping is most prominent when the time window for counting spikes is small. If the chosen time window is so small that no more than one spike is ever counted, the variance inevitably lies on the scallop that stretches between the mean spike counts of 0 and 1. If the chosen time window is even smaller so that the mean spike count does not exceed a value of ~0.2, the variance lies on the initial part of the first scallop and thus virtually equals the mean spike count. This becomes evident, for instance, for the variance of the H1 cell as determined in a 3-ms time window [figure 1E in (*1*)]. Hence, for small mean spike counts, the ratio of the variance and the mean spike count approaches unity. These features are independent of whether there is little or much variability in the neural responses. This consideration hints at the limitation of the variance as a measure of variability if the variance is computed within small time windows.
21. The response amplitude of the H1 neuron is not only determined by the size of the stimulus pattern but also by other stimulus parameters such as the velocity of motion. In some experiments with constant-velocity stimuli, we used two different velocities to obtain different activity levels. A stimulus pattern moving at 42.3°/s elicited a mean response (±SEM) of 133 ± 9.6 spikes per second with an across-trial variance within 100-ms time windows of 0.59 ± 0.13, whereas a velocity (211.5°/s) that is higher than the velocity that results in the maximal response elicited a mean response of 30 ± 11 spikes per second with a variance of 1.02 ± 0.16. Data were obtained from three animals. Each animal was confronted with the fast and the slow stimulus alternately. For each of the tested animals, the variance was larger for the fast stimulus, which elicited only a weak response, than for the slow, more effective stimulus. Independent of the velocity, variances were always considerably smaller than the mean spike count. Variances were obtained from 50 trials per animal and stimulus condition. Each trial lasted 3 s, the last second of which was used for this analysis [spatial wavelength, 10.6°; pattern contrast, 0.89; mean luminance, 1.4 cd/m^2; horizontal (vertical) extent of the stimulus pattern, 74° (59°)].
22. Preliminary results suggest that different variances may be obtained for a given mean spike count induced, for instance, by constant-velocity motion of either a small high-contrast pattern or a large low-contrast pattern. At least at small mean spike counts, the variances in the latter case tended to be larger than in the former. When for a given pattern size the contrast was varied to obtain different activity levels, the variance did not increase but rather decreased with the mean spike count.
23. The spike count variance of responses to constant velocity of the most variable H1 cell analyzed in the present study was 1.44 when averaged over the variances determined in 91 consecutive partly overlapping 100-ms time windows. Depending on the size of the stimulus, the variance of the most variable H1 cell differed from that of the most reliable H1 cell by a factor of 2.5 to 3.2 when evaluated in a 100-ms window. This factor suffices to explain the quantitative discrepancies in the different sets of results in (*1*) and those between (*1*) and our study.
24. Z. F. Mainen and T. J. Sejnowski, *Science* **268**, 1503 (1995).
25. J. Haag and A. Borst, *Nature* **379**, 639 (1996).
26. L. G. Nowak, M. V. Sanchez-Vives, D. A. McCormick, *Cereb. Cortex* **7**, 487 (1997).
27. M. J. Berry and M. Meister, *J. Neurosci.* **18**, 2200 (1998).
28. W. S. Geisler and D. G. Albrecht, *Visual Neurosci.* **14**, 897 (1997).
29. E. D. Gershon, M. C. Wiener, P. E. Latham, B. J. Richmond, *J. Neurophysiol.* **79**, 1135 (1998).
30. M. Gur, A. Beylin, D. M. Snodderly, *J. Neurosci.* **17**, 2914 (1997).
31. M. Egelhaaf, A. Borst, W. Reichardt, *J. Opt. Soc. Am. A* **6**, 1070 (1989).

32. We thank J. Eikermann for technical assistance in the experimental part of the study and R. Kern, B. Kimmerle, H. Krapp, J. Kretzberg, and R. Kurtz for critically reading and discussing the paper. Two anonymous referees made many valuable suggestions on the manuscript and thus greatly helped in improving the paper.

24 August 1998; accepted 16 February 1999