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Impact of visual motion adaptation on neural responses to objects and its dependence on the temporal characteristics of optic flow

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Liang P, Kern R, Kurtz R, Egelhaaf M. Impact of visual motion adaptation on neural responses to objects and its dependence on the temporal characteristics of optic flow. *J Neurophysiol* 105: 1825–1834, 2011. First published February 9, 2011; doi:10.1152/jn.00359.2010.—It is still unclear how sensory systems efficiently encode signals with statistics as experienced by animals in the real world and what role adaptation plays during normal behavior. Therefore, we studied the performance of visual motion-sensitive neurons of blowflies, the horizontal system neurons, with optic flow that was reconstructed from the head trajectories of semi-free-flying flies. To test how motion adaptation is affected by optic flow dynamics, we manipulated the seminatural optic flow by targeted modifications of the flight trajectories and assessed to what extent neuronal responses to an object located close to the flight trajectory depend on adaptation dynamics. For all types of adapting optic flow object-induced response increments were stronger in the adapted compared with the nonadapted state. Adaptation with optic flow characterized by the typical alternation between translational and rotational segments produced this effect but also adaptation with optic flow that lacked these distinguishing features and even pure rotation at a constant angular velocity. The enhancement of object-induced response increments had a direction-selective component because preferred-direction rotation and natural optic flow were more efficient adaptors than null-direction rotation. These results indicate that natural dynamics of optic flow is not a basic requirement to adapt neurons in a specific, presumably functionally beneficial way. Our findings are discussed in the light of adaptation mechanisms proposed on the basis of experiments previously done with conventional experimenter-defined stimuli.

fly; object detection

THE FUNCTIONAL PROPERTIES of sensory neurons may change during prolonged stimulation. Such changes are thought to be adaptive and have been analyzed in a variety of systems ranging from receptor cells to high-level sensory neurons (reviews in Clifford and Ibbotson 2002; Kohn 2007). At the level of photoreceptors, adaptation to the mean light level adjusts their operating range to the huge variation of light intensities that may be encountered in a natural environment, maintaining sensitivity to fluctuations around this mean (Laughlin 1994; van Hateren 1997; Smirnakis et al. 1997; Fain et al. 2001). An adjustment of neuronal properties to the presently prevailing stimulus characteristics takes place, not only at peripheral levels in sensory systems, but also at higher-level processing stages. For the auditory system in the mid-brain of cats and barn owls, adaptive processes were shown to increase neuronal responses to rare stimuli and to decrease those to frequent stimuli (Ulanovsky et al. 2003; Reches and Gutfreund 2008). In a similar way, motion-sensitive neurons in

the visual system of flies increase their sensitivity to sudden stimulus changes during prolonged motion stimulation, whereas the overall responses decrease (Maddess and Laughlin 1985; Liang et al. 2008; Kurtz et al. 2009b).

In most previous studies on adaptation in higher order sensory neurons, adaptation has been elicited by constant stimuli or stimuli with a simple temporal structure. However, it is still not clear how sensory systems efficiently encode signals with real-world statistics as experienced by animals during normal behavior and what role adaptation plays under such conditions (Rieke and Rudd 2009). This issue will be addressed in the present paper for visual motion adaptation in the fly.

Flies are widely used as a model system to investigate visual information processing and, in particular, the neural control underlying visually guided orientation behavior (Frye and Dickinson 2001; Egelhaaf et al. 2002; Borst and Haag 2002; Kurtz and Egelhaaf 2003; Egelhaaf 2006; 2009). Motion adaptation is one important topic in this context and has been analyzed with a wide range of stimulus paradigms mainly at the level of wide-field, motion-sensitive neurons, the lobula-plate tangential cells (LPTCs) in the third visual neuropile (for reviews see Clifford and Ibbotson 2002; Egelhaaf 2006; 2009; Kurtz 2009). Although it is generally agreed that many features of LPTC responses depend on stimulus history and, thus, may be regarded as adaptive, neither the underlying mechanisms nor the functional significance of motion adaptation have been fully clarified. Nonetheless, a number of mechanisms have been demonstrated to be involved in visual motion adaptation. Some of these operate locally and, thus, presynaptic to the LPTCs and were concluded to be, to some extent, independent of the direction of motion. Other mechanisms, mainly those that depend on the direction of motion, originate after spatial pooling of local motion signals at the level of LPTCs. 1) The time constants involved at different computational stages of peripheral visual information processing and/or local movement detection were proposed to change in the context of motion adaptation (Borst and Egelhaaf 1987; Borst et al. 2003; Maddess and Laughlin 1985; de Ruyter van Steveninck et al. 1986; Safran et al. 2007; see, however, Harris et al. 1999). 2) The gain of signal processing at one or several stages in the peripheral motion pathway and potentially at the level of LPTCs has been concluded to be adjusted depending on the contrast of the motion pattern (Harris et al. 2000). 3) Excitation of an LPTC causes adaptation that shifts the membrane potential of the cell to a less depolarized state and leads to a prolonged hyperpolarization after stimulus offset, probably by opening of potassium channels (Harris et al. 2000; Kurtz 2007;

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Kurtz et al. 2000; Kurtz et al. 2009a). All these mechanisms lead to changes in the operating range of the system.

How do these mechanisms affect motion adaptation under the complex time-varying naturalistic stimulus conditions? Motion adaptation elicited by white-noise velocity fluctuations rescales, on a wide range of timescales, the relationship between the motion input and the neural responses (Brenner et al. 2000; Fairhall et al. 2001). Although the motion stimuli used in these studies varied dramatically over time, the statistics of their dynamical properties deviate much from the dynamics of the retinal motion patterns experienced by the animal in behavioral situations. From responses to artificial stimuli, it is not easy to infer the significance of adaptation under natural operating conditions. To overcome this limitation, we use optic flow that is reconstructed from the head trajectories of virtually free-flying animals as well as targeted modifications of this optic flow. Such reconstructed motion sequences are as close as is presently possible to what the fly has seen during flight.

The dynamics of the retinal motion patterns of blowflies is actively shaped by saccadic rotations of body and head, while keeping their gaze virtually constant during translational locomotion between the saccades (Schilstra and van Hateren 1999; van Hateren and Schilstra 1999; Braun et al. 2010; see also Fig. 1). In this way rotational and translational components of retinal image motion are kept largely separate, a strategy thought to facilitate the processing of spatial information by the nervous system. Although the neural responses to these characteristic retinal motion patterns have been studied in some detail (Boeddeker et al. 2005; Kern et al. 2005; 2006; van Hateren et al. 2005; Karameier et al. 2006), it is not yet known whether the dynamics of these patterns has a distinct impact on motion adaptation.

We performed our experiments on a specific class of LPTCs, the horizontal-system (HS) neurons (Hausen 1982a; 1982b; Krapp et al. 2001). These neurons have been shown to encode information about the spatial layout of the environment during the intersaccadic intervals (Boeddeker et al. 2005; Kern et al. 2005; 2006; Karameier et al. 2006) although they are conventionally thought to act as rotation sensors (e.g., Hausen 1982a; 1982b; Krapp et al. 2001; Farrow et al. 2006; Nordström et al. 2008). Additionally, it has been shown that motion adaptation affects the responses of HS neurons during the intersaccadic intervals to suddenly appearing objects (Liang et al. 2008). In this study a brief sequence of naturalistic optic flow with an embedded object was shown repeatedly. The object-induced increment in the neuronal response was significantly enhanced after several repetitions of the optic flow sequence. Thus HS neurons serve as a good model to study the consequences of motion adaptation and its stimulus dependence. Here we address the following questions: Does the intricate dynamics of natural optic flow play a crucial role in motion adaptation? Does, in particular, the temporal fine structure of optic flow, mainly caused by the succession of translations and fast rotations, influence the consequences of motion adaptation? If not, what else might be essential stimulus parameters contributing to motion adaptation?

MATERIALS AND METHODS

Stimulation. A flight trajectory (duration 3.45 s) was chosen from a large data set provided by Dr. J.H. van Hateren (University of Groningen, Groningen, the Netherlands). The data were obtained from

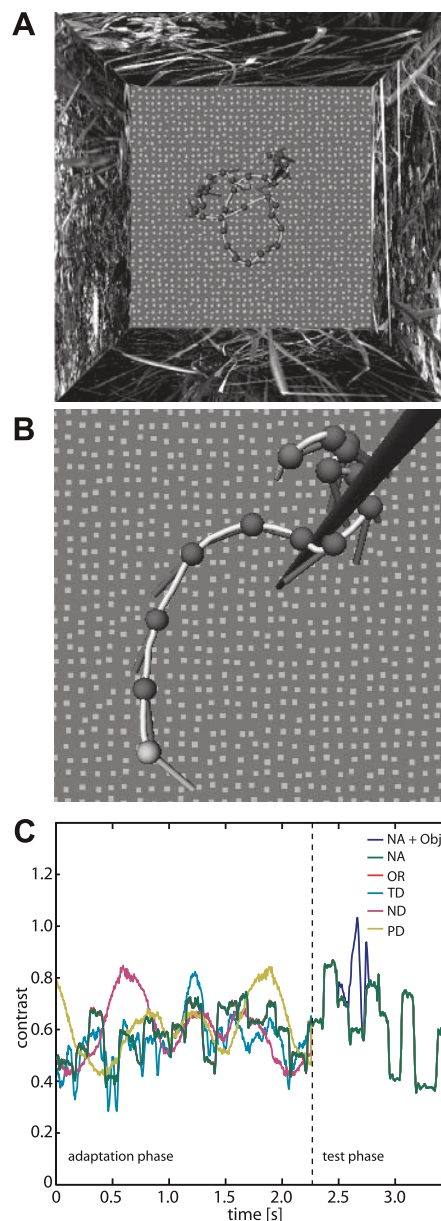


Fig. 1. Top view of the flight trajectory of a blowfly in a cubic arena used for the generation of naturalistic optic flow and contrast changes within a spatial window approximating the receptive field of the horizontal system (HS) cell. The track of the fly is indicated by the white line; the gray dots and short dashes indicate the position of the fly's head and its orientation, respectively; the slightly lighter gray dot indicates the start of the trajectory. The length of one arena wall is 0.4 m, the fly's position is shown every 100 ms. **A:** complete trajectory in the arena. **B:** magnified part of the trajectory constituting the reference/test phase; an inserted object (black cylinder) is located very close to the trajectory. **C:** time-dependent contrast fluctuations within a window approximating the receptive field of an equatorial HS (HSE) cell. The window has a horizontal extent from -10° in the cells contralateral visual field to $+50^\circ$ in the ipsilateral field and a vertical extent of 60° , i.e., $\pm 30^\circ$ about the eye equator. Contrast has been calculated for the original and different adapting motion sequences (NA, natural dynamics; NA + Obj, natural dynamics with object present during test phase; OR, only rotation; TD, track direction; PD, preferred-direction rotation; ND, null-direction rotation).

blowflies flying in a cubic arena (edge length 0.4 m; walls covered with photographs of herbage). To monitor the fly trajectories the arena was placed in a Helmholtz coil; the position and orientation of the blowfly's head were monitored by means of magnetic coils that were mounted on it (van Hateren and Schilstra 1999). The semi-free-flight

sequences recorded in this way do not differ in their saccadic structure from free-flight maneuvers monitored with high-speed cameras under outdoor conditions (Boeddeker et al. 2005). All trajectories reveal the saccadic flight and gaze strategy characteristic of blowflies. The particular trajectory selected for the present study was selected because 1) both preferred direction (PD) and null direction (ND) saccades occur and 2) within the last second of the trajectory a translational segment could be found where an object could be inserted that induced a stronger depolarization compared with the situation without object.

With known gaze direction and visual interior of the cage, the visual stimuli could be reconstructed and presented in a panoramic display instrument, the so-called FliMax (Lindemann et al. 2003). The present version of FliMax equipped with ultrabright light-emitting diodes (WU-14-752GC, 525 nm, 5 mm diameter; Vossloh-Wustlich Opto, Kamp-Lintfort, Germany) has the following characteristics: 1) maximum luminance averaged over the whole array is more than 12,000 cd/m², which is about 30-fold relative to the old version of FliMax used in our previous study (Liang et al. 2008); 2) 190 different levels of light intensities can be displayed; 3) almost panoramic motion can be presented at a rate of 354 Hz, which is sufficiently high to account for the temporal resolution of the fly's visual system.

The time constant of major components of motion adaptation has been shown in previous studies to be in the range of 2–4 s (Maddess and Laughlin 1985; Harris et al. 2000; Fairhall et al. 2001; Wark et al. 2009; Liang et al. 2008). The chosen flight sequence (3.45 s) was divided into two parts, the first part termed adaptation phase lasts 2.26 s, and the second part, the test stimulus, 1.19 s. Presenting the second part in isolation delivered the reference neuronal responses. They were compared with test responses, i.e., responses to the identical stimulus following a motion adaptation stimulus. To create spatial discontinuities in the reference/test stimuli, a virtual object, a homogeneously black vertical cylinder (diameter: 0.01 m; height: 0.8 m), was inserted close to the flight trajectory (Fig. 1). Additionally, to induce large spatial discontinuities, and thus clear object-induced response increments relative to the corresponding background responses, the edge length of the reconstructed virtual flight arena (0.8 m) was doubled relative to the original arena. The wall pattern was scaled accordingly. The angular size of the texture elements, thus, did not change if seen from the center of the flight arena. The root-mean-square contrast of the background pattern was ~0.6. However, it fluctuated considerably when determined within spatial windows in the range of the receptive field size of the equatorial HS (HSE) cell (see below) (see Fig. 1C for a 60° wide window), with the fluctuations being the larger, the smaller the window size. The object led to a contrast increase, depending in magnitude, again, on the window size (dark blue curve in Fig. 1C corresponds to contrast fluctuations resulting from the object).

We analyzed the object and background responses before and after motion adaptation and took changes in the object-induced response increment as an indicator of motion adaptation (Liang et al. 2008). A set of five different adaptation stimuli covering a broad range of dynamics was used to test the consequences of motion adaptation. Details of the various stimuli are described in RESULTS. Different stimulus pairs (i.e., the same dynamic stimuli with and without the object during the test phase after motion adaptation) were presented in pseudorandom order, and the order of stimulation with and without object within a stimulus pair was also randomized. Between two stimuli (intra- and interstimulus pairs), all light-emitting diodes of FliMax were set to the mean luminance (about 4,000 cd/m²) of the whole movie for 20 s to allow the fly's visual system to return to its preadaptation state.

Electrophysiological experiments. One- to three-day-old female blowflies (*Calliphora vicina*) were dissected as described by Dürr and Egelhaaf (1999). Temperatures during experiments, measured close to the animal, amounted to 24–34°C. Voltage responses were recorded intracellularly with glass electrodes (GC100TF-10; Clark Electro-

medical Instruments, Pangbourne Reading, UK) from the axon of HS neurons (Hausen 1982a) in the right brain hemisphere. The responses of the left HS neurons were mimicked by presenting a mirrored version of the reconstructed image sequences. This was done because the object appeared mostly in the receptive field of the left HSE, but not much in that of the right one. The resistance of the electrodes, filled with 1 M KCl, was 20–50 M Ω . Ringer solution (Kurtz et al. 2000) was used to prevent desiccation of the brain. Recordings were sampled at 8 kHz (DT 3001; Data Translation, Marlboro, MA).

Data analysis. Recordings from nine HSE neurons were analyzed with Matlab 7.0.1 (The Math-Works, Natick, MA). For each trial the responses were firstly offset by the resting potential (–40 to –60 mV), which was obtained by averaging the membrane potential over 500 ms before stimulation. As a consequence of recording quality and differences in cellular properties, some recordings contain action potentials of variable amplitude (“spikelets”) in addition to graded voltage changes. To focus on the graded potential signals, we used a low-pass filter ($\sigma = 3.7$ ms) to smooth out the spikelets. The stimuli were displayed pairwise, i.e., the corresponding stimuli with and without object were always displayed in direct succession. Thus there was no large time lag between the two stimulus presentations, and both responses should ideally be identical in the time interval before the object moved into the receptive field of the neuron. We used this similarity in the responses to compensate for potential small drifts in the resting potential of the cell between subsequent recordings by shifting the corresponding response traces to the same mean level. This shift was determined from the average membrane potential over a 330-ms interval before the appearance of the object.

The object-induced response increment could be easily seen from the difference of the time-dependent responses during the reference movie with and without object (Fig. 2, *r6*). The differences between object and background responses were analyzed within two groups of time intervals. These were defined by the following criteria. 1) At least one edge of the retinal image of the object had to be within a spatial window. We tested two window sizes, covering the receptive field of the right HSE to a different extent: *spatial window A* reached from –10° in azimuth (i.e., from approximately the left edge of the right eye) to +50°; *spatial window B* was larger and reached from –10° to 110°. In elevation, both windows covered –30° to 30° relative to the equator of the eyes. Note that it is not possible to delineate the exact borders of the receptive field of the HSE cell because the spatial sensitivity drops along the azimuth from its maximum at around 20° toward lateral positions in the visual field (see Hausen 1982b; Krapp et al. 2001). A comparison of the results obtained for both windows revealed that the exact window size does not affect our conclusions. 2) The object had to move within the spatial window in the PD of the HSE cell and thus induce depolarizations. The same windows were used for all different stimulus conditions to compare object and background responses. 3) Because we were interested in the representation of spatial information, only responses during intersaccadic intervals were taken into the further quantitative analysis. The time windows of data analysis for *spatial window A* are indicated in black, and the time windows for *spatial window B* are in gray in Fig. 2 (*bottom, left*) A pair-wise *t*-test was used to test the significance of differences in object-induced response increments.

RESULTS

Natural optic flow on the retina of blowflies is shaped by the succession of flight sections with virtually no rotations and brief sections dominated by fast rotations (Fig. 1; Fig. 2, *left*, first yaw-velocity diagram), which is characteristic of the animals' saccadic flight and gaze strategy. Does the characteristic dynamics of natural optic flow play a critical role in motion adaptation? To answer this question, five different

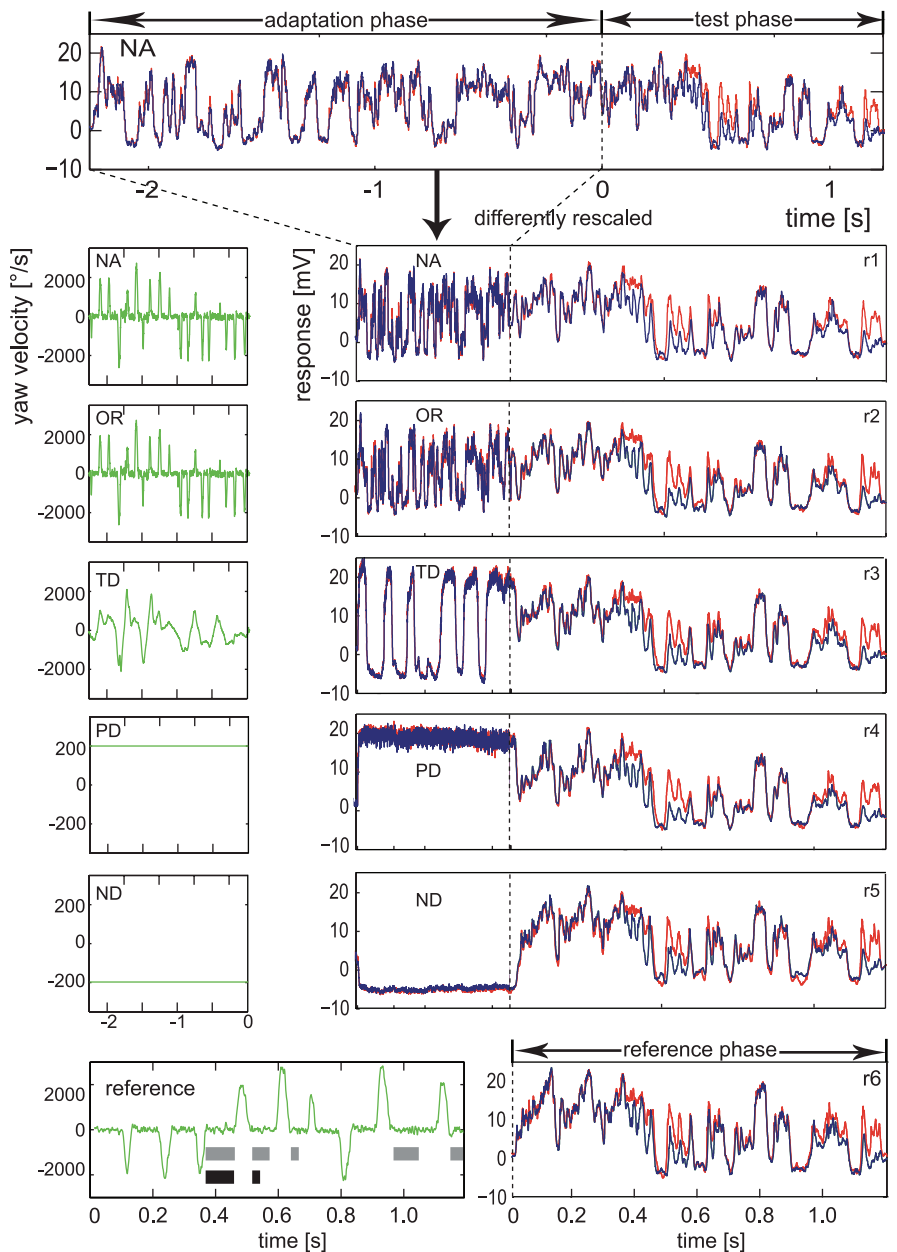


Fig. 2. Yaw velocities related to the stimuli employed and the corresponding responses of a single HSE neuron (averaged from 5–7 trials). *Left*: yaw velocities (green) during the respective motion adaptation stimulus phase: NA, OR, TD, PD, and ND. *Top*: responses to the seminatural dynamic stimuli (NA) obtained in the with-object (red curve) and without-object (blue curve) conditions. The time intervals before and after 0 are defined as adaptation phase and test phase, respectively. The response traces shown in the top diagram are differently rescaled and plotted in *r1*. *r2–r5* present responses to OR, TD, PD, and ND stimuli, temporally rescaled in the same way. Starting from *time point 0* (vertical dashed line) are the responses to the 2 test stimuli (with and without object). Test stimuli are identical for all adaptation conditions. During the reference phase, the responses without preceding motion adaptation are shown in *r6*. The time windows in which the object and background responses were determined are shown as black lines (*spatial window A*) and gray lines (*spatial window B*; for details see MATERIALS AND METHODS). Note different y-axis scaling for PD and ND stimulus trace.

adaptation stimuli, covering a broad range of dynamics, were used to test the consequences of motion adaptation (Fig. 2, *left*): 1) the motion sequence experienced on a semi-free-flight trajectory with its characteristic saccadic structure (naturalistic dynamics, NA); 2) the motion sequence that would have been seen by a fly while rotating with its seminatural dynamics without translating at all in the intersaccadic intervals. To obtain basically the same trajectory of the eye, the intersaccadic translation of the original trajectories was added to the translation during saccades (only rotation, OR; for details of this type of stimulus see Fig. 3B in Kern et al. 2005); note that the resulting additional translational optic flow is negligible during saccades relative to the much larger rotational optic flow; 3) the motion sequence that would have been experienced by a fly with its gaze directed tangentially to the flight trajectory (track direction, TD); this type of optic flow is characterized by smooth rotations superimposed on the translatory

movements; 4) motion sequences encountered during a yaw rotation in the PD of the HS neurons or 5) ND at a constant velocity of 200 degrees/s. A stimulus without preceding motion adaptation was used to obtain the reference responses, i.e., responses affected by only little motion adaptation (Fig. 2, *left*, reference). As indicators of motion adaptation, two response characteristics of HS neurons were used: 1) the decrement of the overall responses after prolonged motion stimulation (Maddess and Laughlin 1985; Harris et al. 2000; Kurtz et al. 2000; Reisenman et al. 2003), 2) the changes in the response increments that are elicited when an object passes the receptive field of the neuron during a translatory intersaccadic phase within a flight sequence (Liang et al. 2008).

HS neurons respond to visual motion with prominent graded de- and hyperpolarizations of their axonal membrane potential, which may be superimposed with action potentials of variable amplitude (which are inconspicuous in average traces) (Hausen

1982b). The time courses of the responses to the different adaptation stimuli differ in most cases dramatically (time intervals preceding time zero in Fig. 2, *right*, named adaptation phase). Only the responses to NA and OR appear to be very similar (Fig. 2, *r1* and *r2*, to the left of the black vertical dashed line). It can be expected from previous studies that upon closer inspection these responses may differ during the intersaccadic intervals because the intersaccadic translational optic flow is present in the naturalistic stimulus (NA) but absent in the OR stimulus variant (Kern et al. 2005). Irrespective of these fairly inconspicuous differences, the membrane potential shows pronounced fast fluctuations both during NA and OR (for details of the time course of HS responses to naturalistic motion stimuli, see Kern et al. 2005; Kern et al. 2006; van Hateren et al. 2005). In contrast, the responses to TD (Fig. 2, *r3*) are much smoother and vary on a much slower timescale. This difference in time course is the consequence of the much slower changes in the direction of the flight track compared with the rapid saccadic changes in head orientation and gaze direction (van Hateren et al. 2005). The responses to PD and ND differ fundamentally from those to the adaptation stimuli discussed so far. Although the adaptation velocities were much smaller than the peak velocities reached under the other adapting stimulus conditions, the response amplitudes reach approximately the same level. However, the neurons show either a relatively constant depolarization (Fig. 2, *r4*) or hyperpolarization (Fig. 2, *r5*) if stimulated with constant velocity motion in PD or ND, respectively. Both during motion in PD and ND the temporal modulations of the responses are weak, as is characteristic of motion-sensitive neurons with large receptive fields when stimulated with panoramic constant motion.

For the reference as well as for the entire set of motion adaptation conditions, we compared the responses to two types of stimuli (test stimuli), presented in the time interval following the adaptation phase (after *time zero* in Fig. 2, *right*). On the one hand, we showed the original image sequence, which is close to what has been experienced by the semi-free-flying fly. On the other hand, an object (a vertical black cylinder) was virtually inserted into the flight arena (object position shown in Fig. 1) and then the image sequence reconstructed. Even in the complex time-dependent responses of the neuron, the displacement of the object in the PD of the neuron leads to an increase in depolarization compared with the corresponding background responses, i.e., when the object was not present (compare red and blue lines in Fig. 2). These object-induced increments in depolarization become more evident when the test stimuli are preceded by one of the adapting stimuli. However, differences in these object-induced response increments between the various adaptation conditions are not immediately obvious. Therefore, the responses had to be further analyzed in detail.

To quantify the object-induced response increments, time intervals were chosen in which the intersaccadic object and background responses were averaged. These time intervals were defined by at least one of the object edges to be present in either *spatial window A* (ranging for -10° to $+50^\circ$ in azimuth) or *spatial window B* (ranging from -10° to 110° ; see MATERIALS AND METHODS) and to move in the PD of the cell. Using the smaller *spatial window A* only time intervals in the first half of the adaptation phase met the criteria listed above. The averaged object and background responses decrease after motion adaptation with NA, OR, TD, and PD stimuli, but not

with the ND stimulus (Fig. 3A). This indicates that there is a strong direction-selective component in the underlying adaptation mechanisms. The amplitudes of both background and object responses after adaptation with NA, OR, or TD were in between those after PD and ND adaptation. However, the decrements resulting from adaptation are stronger in the background responses than in the object responses. Consequently, the object-induced response increments are enhanced by 20% to 26% as a consequence of motion adaptation (Fig. 3B). Differences in the strength of this adaptation effect between the

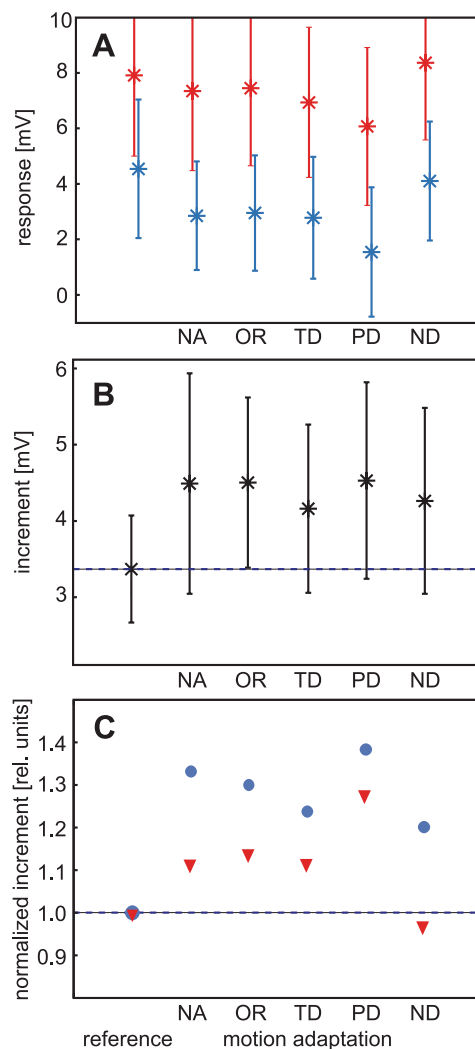


Fig. 3. The averaged object and background responses with and without motion adaptation. **A**: object (red symbols) and background intersaccadic responses (blue symbols) are averaged (9 cells; error bar: SD) while the object moved in the PD of the HS cell within *spatial window A*. The responses are shown for the various tested stimulus conditions (see MATERIALS AND METHODS). **B**: object-induced response increments for the various stimulus conditions. Horizontal line highlights the level reached in the reference condition. The object-induced response increments are significantly enhanced for all motion adaptation conditions. The increment after PD motion is significantly stronger than that after ND. The 1 after NA is also larger than that after ND (pair-wise *t*-test, $P < 0.05$). **C**: comparison of the consequences of motion adaptation for the object-induced response increment during the first and second half of the test stimulus. The responses were determined for *window B* (see MATERIALS AND METHODS) after subdividing the resulting analysis time intervals into an early (blue circles) and a late group (red triangles). The object-induced response increments were normalized to those obtained without preceding adapting stimuli.

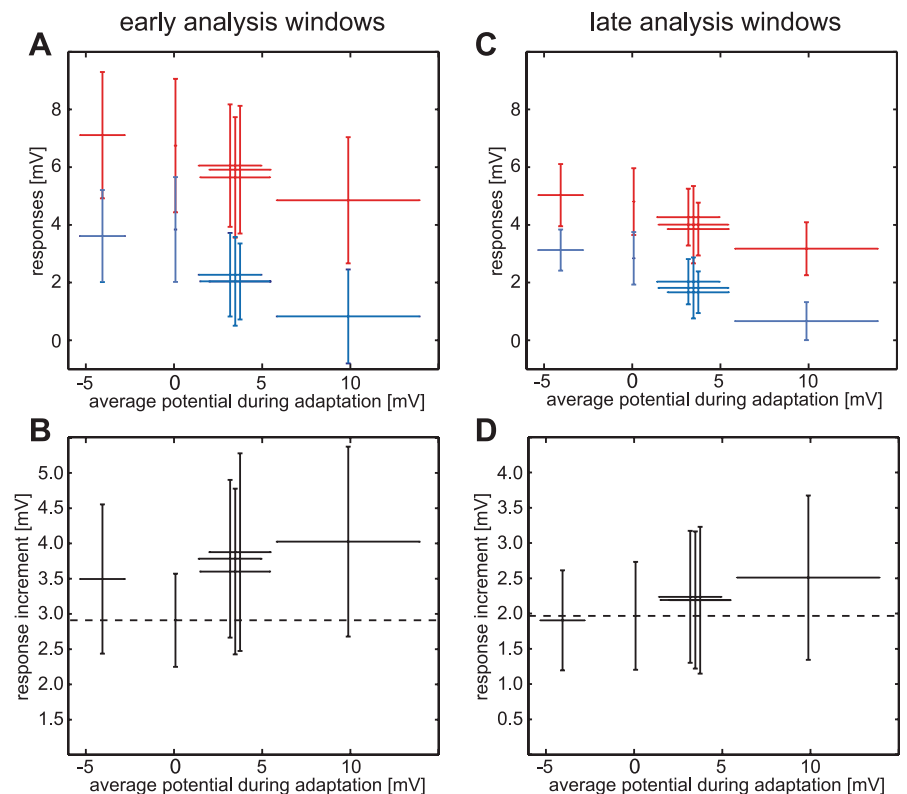
various adaptation conditions are relatively weak; the object-induced response increment increases, not only after an adaptation stimulus with NA, but also after all other tested adaptation stimuli (OR, TD, PD, and ND; Fig. 3B, pair-wise *t*-test, $P < 0.05$). Interestingly, both the adapting PD and ND constant-velocity rotations enhance the object-induced increments significantly, but the increment after PD motion is slightly stronger than that after ND motion. The object-induced response increments after motion adaptation with NA and OR are very similar and slightly larger than those evoked by TD adaptation. These results indicate that there is a consistent increase in object-induced response increments irrespective of the overall dynamics and direction of motion during the adaptation phase. Qualitatively similar results were obtained when the analysis time intervals were set by using a much larger spatial window (*spatial window B*, see MATERIALS AND METHODS) to approximate the receptive field of HSE (data not shown).

To assess whether the adaptive effects last over several hundreds of milliseconds, we compared the consequences of motion adaptation for the object-induced response increment during the first and second half of the test stimulus. This was done by setting the analysis time intervals on the basis of the larger approximation of the receptive field (*spatial window B*, see MATERIALS AND METHODS; Fig. 2, bottom, left). With this larger receptive field approximation, intervals in which the object appeared in the periphery of the receptive field were included, and the resulting analysis time intervals could be subdivided into an early and a late group (see Fig. 2, bottom, left; first three gray time windows belong to the early phase, the last two gray time windows to the late phase). To facilitate comparison, the object-induced response increments were normalized to those obtained without preceding adapting stimuli. In the late phase during the test stimulus, we find a similar

overall dependence of the object-induced response increments on the different adaptation stimuli (Fig. 3C). However, none of the effects of adaptation on the object-induced response increment did reach statistical significance any more. The increments were largest after PD adaptation and entirely vanished after ND adaptation. This observation may indicate that direction-dependent adaptation may last longer than other components of motion adaptation.

Although the dynamical properties of the adaptation stimuli play only a limited role in enhancing object-induced responses, which other parameters might then determine the strength of motion adaptation? The depolarization level of the neuron evoked by constant-velocity stimulation has been suggested to influence the strength of motion adaptation (Kurtz et al. 2000; 2009a; Harris et al. 2000). We therefore investigated whether this finding generalizes across stimuli of various velocity profiles, such as those employed here for motion adaptation. We plotted the averaged object and background responses as a function of the time-averaged membrane potential during the adaptation phase. The results are shown in Fig. 4, A and B, for the analysis using the large *spatial window B* for approximation of the receptive field (see MATERIALS AND METHODS) and the same subdivision of analysis time intervals in an early and a late group as described above; qualitatively the same results were obtained for the small *spatial window A* (data not shown). Despite considerable variability in the responses, there is a clear relationship between the responses and the averaged membrane potentials during the adaptation phase. The relationship was assessed on the basis of Pearson's correlation coefficient determined individually for each of the nine analyzed cells and then averaged over cells. Both the object responses (correlation coefficient: -0.88 ± 0.06 for *window A*; -0.88 ± 0.07 in the early and -0.80 ± 0.21 in the late intervals for

Fig. 4. Average object and background responses plotted against average stimulus-induced membrane potential changes during the adaptation phase (*spatial window B*; 9 cells; error bars: SD). A: object (red) and background responses (blue), which are averaged from the early time windows, decrease when the averaged membrane potential increases. B: object-induced response increment increases when the averaged membrane potential relative to the resting potential (set to 0 mV) gets positive and negative (the neurons are depolarized or hyperpolarized, respectively). C and D: analogous results from the late group of analysis windows.



window B) and the background responses (correlation coefficient: -0.91 ± 0.08 for window A; -0.94 ± 0.06 in the early and -0.87 ± 0.12 in the late intervals for window B) relative to the resting potential decrease when the neuron is more depolarized during adaptation (Fig. 4, A and B). The averaged membrane potential during the adaptation phase with NA, OR, and TD stimuli has almost the same level, and the corresponding object and background responses are, accordingly, very similar. Moreover, the object-induced response increment increases with an increasing positive-average depolarization during the adaptation phase (Fig. 4, C and D). Accordingly, the object-induced response increments are similar after NA, OR, and TD motion stimulation. However, when the neuron is hyperpolarized during the adaptation phase, the averaged object response increases very slightly and the background response remains almost at the same level (Fig. 4A, left). As a consequence, in the early analysis time intervals the object-induced response increment gets larger even if the membrane potential is hyperpolarized (Fig. 4C). The latter finding cannot be explained on the basis of a direction-selective mechanism of motion adaptation.

It has been shown in previous studies with experimenter-defined stimuli that responses to instantaneous displacements of the stimulus pattern are, not only enhanced after adaptation with constant velocity stimuli, but also have more rapid time courses (Maddess and Laughlin 1985; de Ruyter van Steveninck et al. 1986; Borst and Egelhaaf 1987). This effect of adaptation may also be present under NA conditions, and it may be relevant for the responses to objects. This issue cannot easily be resolved because natural image displacements, especially during the intersaccadic intervals, where spatial information may be encoded by HSE cells, are hardly ever as fast as the artificial image displacements employed in the above-mentioned studies. During stimulation with naturalistic optic flow, the most transient responses are evoked by saccades displacing the retinal image into the ND of the cell (Kern et al. 2005). The time course of these responses does not change much under the different adaptation conditions compared with the reference conditions without adaptation. Only the intersaccadic depolarization level is lightly reduced for the different adaptation conditions (Fig. 5). This finding does not suggest any obvious changes in response dynamics owing to motion adaptation, at least not at the time scales that are relevant in the context of naturalistic optic flow.

DISCUSSION

We used naturalistic optic flow to adapt motion-sensitive HS neurons in the visual system of blowflies and tested to what extent responses to an object suddenly entering the receptive field of an HS neuron are enhanced relative to the background responses. By modifying the dynamic characteristics of optic flow in various ways we were able to show that natural dynamics is not indispensable to generate this effect of motion adaptation. The typical enhancement of object-induced responses with adaptation was preserved not only with adapting stimuli that led to a modified fine structure of the neuronal response fluctuations, but even after pure constant-velocity rotation in the PD or ND of the neurons, which led to a maintained de- or hyperpolarization of the neuron, respectively. Moreover, ND rotation differed in two ways from all

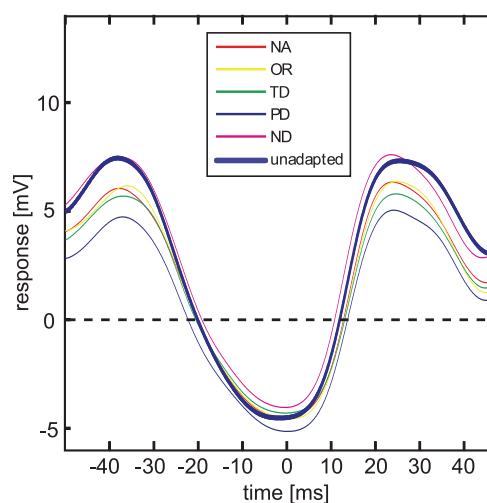


Fig. 5. Saccade-triggered averages of neuronal responses before and during the first 3 saccades during the test stimulus that led to motion in the ND of the HS cells. The test stimulus was preceded by the different adapting stimuli (see inset). The minimum response peak evoked by the saccade was arbitrarily set to time 0, which is delayed with respect to the saccadic peak velocity, on average, by 22.5 ms. The responses to saccades displacing the retinal image into the ND of the cell do not change much as a consequence of the different adapting conditions compared with the reference conditions without adaptation. Only the intersaccadic depolarization level is reduced for the different adaptation conditions.

other stimuli; it produced a net hyperpolarization during the adaptation phase, and it left background responses after adaptation unattenuated. Nevertheless, similar to all other conditions, object responses were enhanced after adaptation with ND rotation.

Potential functional benefits from enhanced object responses after motion adaptation. Improved detectability of novel stimuli has been suggested to be a major functional benefit of adaptation (Kohn 2007). Novelty detection is a crucial task for animals during natural behavior, especially for fast-flying animals. It can be viewed as redundancy reduction by the sensory system, which improves the efficiency of encoding sudden changes in stimulus strength in space or time at the expense of a consistent encoding of absolute intensity levels (Attneave 1954; Barlow 1961). Novelty detection can be accomplished by suppressing responses to frequent or persistent stimuli, thus leading to an enhancement of the relative strength of responses to novel stimuli. Improved novelty detection by adaptation has been proposed to be effective in the nervous system of some vertebrate species (Dragoi et al. 2002; Ulanovsky et al. 2003; Benda et al. 2005; Reches and Gutfreund 2008; Gill et al. 2008) as well as in insects (Maddess and Laughlin 1985; Kurtz et al. 2009b; Ronacher and Hennig 2004). For instance, in the auditory and visual systems, the sensitivity to stimulus discontinuities increases with adaptation (Li et al. 1993; Gill et al. 2008; Maddess and Laughlin 1985; Kurtz et al. 2009b). These discontinuities in the stimulus could be sudden brief changes in one of the stimulus parameters, such as velocity, spatial contrast, or orientation of a drifting visual grating or the frequency in a sound. In monkeys, it has been shown that the movement of the visual scene during a saccade can improve the capacity for the eyes to track the moving scene during postsaccadic image motion (Kawano and Miles 1986). Such transient enhancement in ocular following may be related to rapid-motion adaptation, which is similar in

our adaptation stimuli involving alternating rotations and translations. Our previous paper (Liang et al. 2008) has indicated that motion adaptation with such a stimulus enhances the response to an object suddenly appearing, whereas the sustained background motion response decreases. Compared with our previous study, which used a sustained optic-flow sequence assembled from several shorter repetitive loop-like trajectories (Liang et al. 2008), our present experiments reproduced this phenomenon for a contiguous trajectory, and thus for optic flow stimuli that are closer to the situation during real flight. Although HS neurons have conventionally been regarded as control elements for optomotor turning responses that compensate for deviations from an intended flight course, the enhancement of object responses with adaptation suggests that these neurons may also be functional in the context of object detection and collision avoidance. Consistent with this notion, it has been shown that HS neurons encode behaviorally relevant information about the spatial structure of the visual surround (Boeddeker et al. 2005; Kern et al. 2005; Karmeier et al. 2006). Nonetheless, the responses of HS neurons depend on various stimulus parameters apart from retinal velocity (e.g., Hausen 1982a; 1982b). Accordingly, from the activity of just a single HS cell, it is not possible, without additional information, to infer the presence of an object in its receptive field.

Role of statistical stimulus properties in motion adaptation. Using random velocity fluctuations and information-theoretic approaches, it has been demonstrated how adaptive processes affect the input/output relation in fly visual motion detection (Brenner et al. 2000; Fairhall et al. 2001). Adaptation was shown to work on different timescales to match the neuronal response range to the dynamic range of the external environment and efficiently transfer information about the input signal. More precisely, the system stretches or compresses its tuning curve to match the range of the incoming modulations in motion velocity. However, our results show that the dynamics of optic flow experienced on a seminatural flight trajectory does not conspicuously contribute to motion adaptation, namely the enhancement of object-induced neural activity. Our results are not directly comparable with those of the previous studies (Brenner et al. 2000; Fairhall et al. 2001), in which white-noise velocity fluctuations of a grating were used, and coding of a single stimulus parameter, velocity, was assessed. Moreover, our results do not exclude that the dynamics of a stimulus is relevant for adaptation because under all conditions tested in the present study strong irregular modulations are expected to be present in the local inputs of the neurons recorded in our study. Only with spatial integration over many of these local inputs, a prominent feature of optic flow-sensitive neurons, these modulations can be integrated into a fairly smooth response, as is the case during constant-velocity rotation (Egelhaaf et al. 1989; Single and Borst 1998).

Putative mechanisms underlying adaptation to naturalistic optic flow. In the present study two effects of motion adaptation were observed: 1) a decrease in the overall response level, and 2) an enhancement of response increments elicited by the appearance of an object in the receptive field. Whereas previous studies provide some evidence concerning the origin and cellular mechanism of the first effect, it is more difficult to unravel the putative cellular origins of the second, more re-

markable effect of adaptation to naturalistic optic flow. In the fly visual system as well as in the visual cortex of cats, a component of adaptation exists, which is selectively elicited by motion in the preferred direction (Carandini and Ferster 1997; Harris et al. 2000). In fly HS neurons, this direction-selective adaptation goes along with an increase in the conductance and becomes visible as a prominent after-hyperpolarization following stimulus offset (Kurtz et al. 2000; Harris et al. 2000; Kurtz 2007). The attenuation of the background response found in the present study may be attributed, at least to some extent, to this form of adaptation. This assumption is plausible because, on the one hand, an after-hyperpolarization can be experimentally evoked in HS neurons by membrane depolarization (Kurtz et al. 2009a), and, on the other hand, we found a correlation between the attenuation of the background response and the average level of depolarization during the preceding adaptation stimulus (Fig. 4).

Although the enhancement of object-induced response increments is likely to be affected by direction-selective adaptation, it cannot result alone from this form of adaptation. This is the case because object responses are also enhanced by previous ND rotation, a stimulus condition that generates net hyperpolarization and, consequently, does not lead to an attenuation of background responses. This finding implies that components of adaptation that are independent from the direction of motion play a role in enhancing object-induced response increments. Harris et al. (2000) described a prominent decrease in contrast gain of HS neurons, elicited by motion adaptation in any direction. An attenuation of contrast gain, which has also been reported for motion adaptation in cat visual cortex (Hitmanen et al. 2007), could enhance responses to an object if its contrast is higher than that of the textures in the background. Nevertheless, previous studies argue against the idea that adaptation of contrast gain alone can explain the enhancement of object-induced responses. When stimulating a fly optic flow-sensitive neuron with a continually drifting grating, interrupted from time to time by brief changes in stimulus parameters, the responses to these discontinuities were enhanced in the course of adaptation. This simple adaptation protocol was effective to enhance the sensitivity for stimulus discontinuities consisting of changes in the velocity (Maddess and Laughlin 1985) as well as changes in other stimulus parameters, e.g., grating orientation, wavelength, and also contrast (Kurtz et al. 2009b). Thus the motion vision system might be equipped with similar adapting properties as the auditory system. Here adaptation is thought to be based on the specific attenuation of those elements within an ensemble of inputs that are strongly activated by the adapting stimulus. Inputs that are only weakly activated by the adapting stimulus thus remain responsive to the sudden appearance of a novel stimulus (Ulanovsky et al. 2003). Assuming that such a type of stimulus-specific adaptation is also present in motion vision would imply that the enhancement of object-induced response increments found in the present study originates not from cellular processes in the optic flow-sensitive neurons themselves but from adaptation at their input synapses or even more in the periphery. As already outlined above, this view is also consistent with the lack of effects of different dynamics of the optic flow on this form of adaptation.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

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