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Adaptation accentuates responses of fly motion-sensitive visual neurons to sudden stimulus changes

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Adaptation in sensory and neuronal systems usually leads to reduced responses to persistent or frequently presented stimuli. In contrast to simple fatigue, adapted neurons often retain their ability to encode changes in stimulus intensity and to respond when novel stimuli appear. We investigated how the level of adaptation of a fly visual motion-sensitive neuron affects its responses to discontinuities in the stimulus, i.e. sudden brief changes in one of the stimulus parameters (velocity, contrast, grating orientation and spatial frequency). Although the neuron's overall response decreased gradually during ongoing motion stimulation, the response transients elicited by stimulus discontinuities were preserved or even enhanced with adaptation. Moreover, the enhanced sensitivity to velocity changes by adaptation was not restricted to a certain velocity range, but was present regardless of whether the neuron was adapted to a baseline velocity below or above its steady-state velocity optimum. Our results suggest that motion adaptation helps motion-sensitive neurons to preserve their sensitivity to novel stimuli even in the presence of strong tonic stimulation, for example during self-motion.

Keywords: fly; motion velocity; neuronal adaptation; novelty detection; vision

1. INTRODUCTION

The ability of receptor cells and neurons to adapt to persistent stimuli is a ubiquitous feature across species and sensory modalities (reviewed by Fettiplace & Ricci 2003; Dunn & Rieke 2006; Krekelberg et al. 2006). Adaptive mechanisms are thought to adjust the operating range of neurons to a currently prevailing stimulus level. This adjustment is often reflected by a shift of the neuronal response function along the stimulus intensity axis (see, e.g. Matic & Laughlin 1981; Virsu & Lee 1983; Benda et al. 2005; Garcia-Lazaro et al. 2007). As a functional benefit of such a shift, a neuron gets more sensitive to small changes of stimulus intensity. Without adaptation, small intensity changes might remain undetected either because the neuronal gain is too low or because ambient stimulus intensities already drive the neuronal responses close to their saturation limit.

The functional consequences of adaptation are well documented for photoreceptors, which are able to respond to a large range of light intensities (reviewed by Laughlin 1994; Fain et al. 2001). However, whereas photoreceptors adapt to a single stimulus parameter, namely light intensity, the situation is often more complicated in higher order neurons. The response of visual motion-sensitive neurons (reviewed by Clifford & Ibbotson 2002), for example, is determined by at least four different stimulus parameters: motion velocity, pattern orientation, pattern contrast and the spatial frequency content of the pattern. To cope with variable stimulus conditions, these neurons must adjust their operating range for multiple stimulus parameters. Thus, it is not

surprising that adaptation-induced changes in contrast gain as well as in orientation tuning have been demonstrated in motion-sensitive neurons of animals as diverse as primates and flies (Harris et al. 2000; Kohn & Movshon 2003, 2004; Neri 2007; Kalb et al. 2008a).

Three of the relevant stimulus parameters of motion-sensitive neurons, namely velocity, pattern orientation and spatial frequency, are characterized by either bell-shaped or sinusoidal, but not by sigmoid response functions (Tolhurst & Movshon 1975; Eckert 1980; Hausen 1982; Maunsell & Van Essen 1983). This feature casts doubt upon the usefulness of a pure shift of the response function along the stimulus intensity axis in the course of adaptation. Whereas the slope of a sigmoid function is steepest in a single region, such that adaptation could shift this region of the curve to the currently prevailing stimulus level, there are two such regions on a bell-shaped curve. Thus, given the momentary neuronal response, it is not *per se* clear whether a rightward or a leftward shift of the response function would improve neuronal coding.

Visual motion-sensitive neurons in the third visual neuropil of the blowfly (*Calliphora vicina*), called tangential neurons, present an ideal model system to study the consequences of motion adaptation. About 60 tangential neurons have been individually identified and are thought to perform important tasks in the context of optomotor flight stabilization, collision avoidance and figure–ground discrimination (reviewed by Krapp 2000; Borst & Haag 2002; Egelhaaf et al. 2005). Tangential neurons respond to visual motion in a large area of the visual field in a direction-selective way, being excited by motion in their preferred direction and inhibited by motion in the opposite direction (their so-called null direction).

In flies, motion adaptation was first demonstrated in the tangential neuron H1 (Maddess & Laughlin 1985). H1 gathers horizontal motion signals from a large part of one visual hemifield and transmits this motion information in the form of spike trains to post-synaptic targets in the contralateral brain hemisphere (Eckert 1980). During adaptation with sustained pattern motion in the preferred direction, the response of H1 decreased (Maddess & Laughlin 1985). Nonetheless, the responses to transient deviations from the baseline velocity became more pronounced. This result is in accordance with the view that adaptation improves neuronal sensitivity to changes in stimulus intensity around the current level, leading to a representation of 'velocity contrast' rather than absolute velocity. An adaptive rescaling of the velocity–response function and thus, optimization of information transmission, was also concluded to become effective when H1 was adapted to random velocity modulations that differed in their modulation depth (Brenner *et al.* 2000; Borst *et al.* 2005).

In this paper, we build on the findings of Maddess & Laughlin (1985), and we address two questions. First, is enhanced sensitivity to velocity changes in the course of motion adaptation restricted to a certain velocity range? Second, are the responses to discontinuities in stimulus parameters other than velocity also affected by adaptation?

2. MATERIAL AND METHODS

(a) *Animal preparation and electrophysiology*

Female blowflies (*C. vicina*), taken from our laboratory stock, were briefly sedated with CO_2 to fix them with bee's wax at the dorsal thorax to a small glass plate. The legs were removed and the wounds were covered with wax. The head was pitched downwards and the proboscis was extended, both being fixed in place with wax. The right lobula plate was exposed by opening the head capsule and by removing fat tissue and some main tracheae, if necessary. Ringer's solution (composition in mM: NaCl 128.3, KCl 5.4, glucose 13.9, $NaHCO_3$ 4.8, KH_2PO_4 3.4, $CaCl_2$ 1.9, pH 7.0; all chemicals from Merck, Darmstadt, Germany) was used to prevent desiccation of the brain and to fill a glass pipette that served as indifferent electrode. All experiments were performed at temperatures ranging from 20 to 30°C.

The H1 cell receiving visual input from the left visual field was recorded in its output arborization in the right lobula plate. H1 was identified by its large receptive field in which it responds with high spike rates to back-to-front motion (Eckert 1980; Krapp *et al.* 2001). Spikes were registered by extracellular electrodes pulled from borosilicate glass (GC100TF-10, Clark Electromedical, Edenbridge, UK) with a Brown–Flaming electrode puller (P97, Sutter Instruments, San Rafael, CA, USA) and filled with 1 M KCl. Electrical signals were amplified and filtered by custom-built equipment. Action potentials were detected by adjusting a voltage threshold and transformed into pulses, which were sampled at a rate of 10 (data shown in figures 1 and 2) or 5 kHz (data shown in figures 3 and 4) by an I/O card (DT 3001, Data Translation, Marlboro, MA, USA).

(b) *Visual stimulation*

Drifting sine-wave gratings (data shown in figure 4c,d) or square-wave gratings (all other data) were generated by a PC-controlled image synthesizer (Picasso, Innisfree,

Cambridge, MA, USA) and displayed on a cathode ray tube (Tektronix 608, Wilsonville, OR, USA) at a frame rate of 183 Hz. Pattern motion was always perpendicular to the stripe orientation of the grating. The orientation of the fly's head was aligned with the set-up by adjusting it according to the symmetrical deep pseudopupil in the frontal region of both eyes (Franceschini 1975). The monitor was centred at an azimuth/elevation of 30°/0° with an azimuth of zero degrees corresponding to the frontal midline of the animal and an elevation of zero degrees corresponding to the equatorial plane of the eye. The monitor covered $82° \times 85°$ (horizontal × vertical extent) in the visual field of the fly. In the experiments where pattern orientation was changed (shown in figure 3), the rim of the monitor was shielded by an aperture, resulting in a circular pattern with a horizontal and vertical extent of 78°. If not stated otherwise the spatial wavelength as seen by the fly in the centre of the monitor was 19°. The mean luminance of the grating was 16 cd m^{-2}. The luminance contrast of the pattern and the velocity of pattern motion varied across stimulus paradigms and are given in §3. Although for convenience we use the term 'velocity' whenever general statements are made, pattern motion is quantified by the temporal frequency (velocity multiplied by spatial frequency, given in Hz) instead of the angular velocity (in units of degrees s^{-1}). Note that both measures are linearly related because pattern wavelength remained constant in our experiments. The stimulus sequence consisted of a 6 s period during which a uniformly grey monitor screen with mean luminance (data shown in figures 1 and 2) or the static grating (data shown in figures 3 and 4) was presented. Next, pattern motion was presented for a period of 7 s, followed by a 0.5 s period with a grey screen at medium luminance (data shown in figures 1 and 2) or the static pattern (data shown in figures 3 and 4). The direction of pattern motion was the preferred direction of H1 (i.e. back-to-front) in all experiments, apart from the experiments shown in figure 3, in which the response to changes in motion direction was tested. To characterize neuronal responses to stimulus discontinuities, smooth pattern motion was interspersed with brief periods during which one of the stimulus parameters, motion velocity, pattern contrast or grating orientation, was transiently switched to a value above or below the baseline value. The duration of these stimulus discontinuities was 50 (data shown in figures 1 and 2) or 100 ms (data shown in figures 3 and 4). Further details on the increment or decrement in one of the parameters characterizing the discontinuities are given in §3. Stimulus discontinuities were presented every 780 ms, resulting in eight events per trial. Trials with increments and decrements of a stimulus parameter during the discontinuities were presented in a pseudorandom order. To avoid the accumulation of adaptation effects, individual trials were separated by intervals of at least 5 s, during which a grey screen at mean luminance (data shown in figures 1 and 2) or the static grating (data shown in figures 3 and 4) was shown.

(c) *Data acquisition and analysis*

We used custom-written programs in MEASURE FOUNDRY (Data Translation) and MATLAB (The Mathworks, Natick, MA, USA) for control of visual stimuli, data acquisition and data evaluation. The non-parametric rank-based Mann–Kendall test was used for assessing the significance of data trends (Mann 1945). Number of cells and trials per cell are denoted by '*N*' and '*n*', respectively.
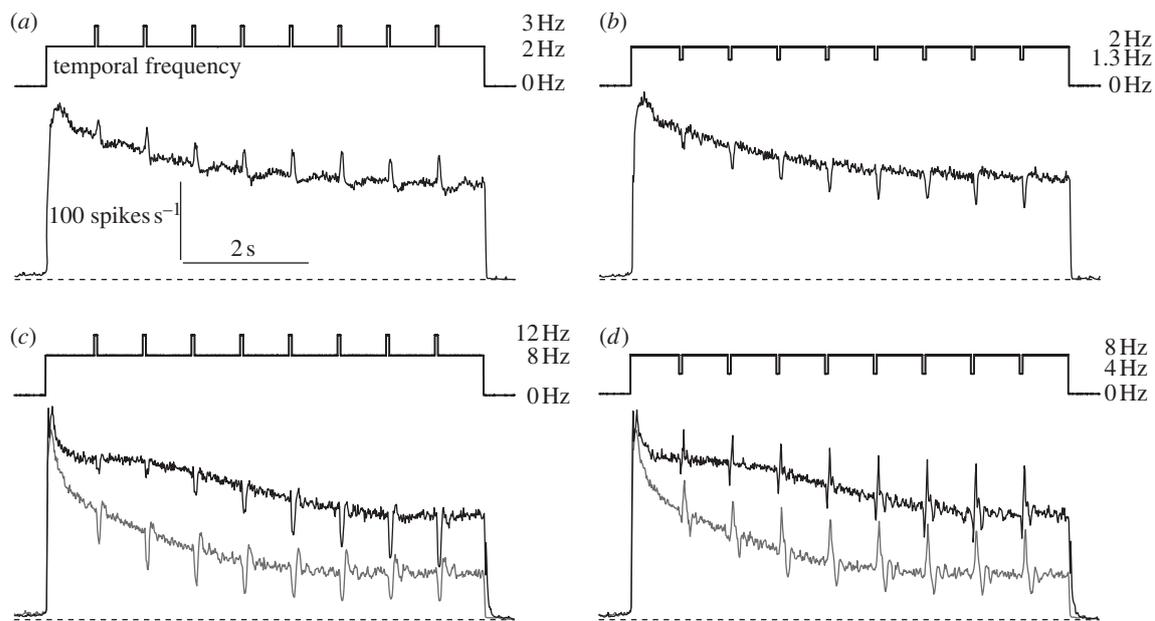
Figure 1. Responses of the fly visual motion-sensitive neuron H1 to (*a,c*) brief increments and (*b,d*) decrements in motion velocity. To analyse the role of adaptation for neuronal sensitivity to these velocity discontinuities, 7 s motion of a grating in the preferred direction with constant velocity was interspersed with eight 50 ms periods, given every 780 ms, during which the temporal frequency of pattern motion differed from the baseline value. (*a,b*) Baseline temporal frequency was 2 Hz. Michelson luminance contrast of the grating was 0.30. (*c,d*) Baseline temporal frequency was 8 Hz. Two conditions varying in luminance contrast of the grating patterns were tested, with 0.88 (black traces) and 0.30 (grey traces) Michelson contrast, respectively. Mean PSTHs were calculated with a temporal binning of 10 ms from spike trains recorded from a single neuron. Number of trials per PSTH: $n = 58$ and $n = 45$ for (*a,b*) and (*c,d*), respectively. Dashed line indicates zero spikes s^{-1}.

3. RESULTS

In the motion-sensitive H1 neuron of the fly, the adaptation to motion with a constant velocity and direction leads to a decline of the neuronal response amplitude (Maddess & Laughlin 1985). We analysed whether this decrease in responsiveness to a persistent stimulus goes along with an equally strong attenuation of responses to stimulus discontinuities, i.e. abrupt changes in one of the stimulus parameters.

(a) *Impact of motion adaptation on neuronal sensitivity to discontinuities in velocity*

Similar to the paradigm used by Maddess & Laughlin (1985), we stimulated H1 by a grating drifting in the preferred direction of the neuron at a constant baseline temporal frequency of 2 Hz, interrupted by eight consecutive brief (duration 50 ms) jumps to a temporal frequency faster than baseline (3 Hz) or to a temporal frequency lower than baseline (1.3 Hz). The example cell responded to the brief velocity increments with corresponding transient increments in its spike rate (figure 1*a*). The amplitudes of these response transients increased with adaptation, although the overall spiking rate of the neuron in the fully adapted state was about one-third smaller than in the unadapted state.

We quantified the upward deflections in spike rate in response to velocity increments by taking the maximum value in a 150 ms time window starting 10 ms after the onset of the velocity increment and subtracting a baseline value averaged over a 50 ms interval preceding the velocity increment. The response increments of H1 increased from 21 spikes s^{-1} for the first velocity increment (starting 780 ms after motion onset) to 34 spikes s^{-1} for the last event (starting 6.23 s after

motion onset). The response decrements to velocity decrements were similarly enhanced during adaptation, with amplitudes (minima relative to baseline determined in the same time windows as given above) of 25 spikes s^{-1} for the first velocity decrement and of 37 spikes s^{-1} for the last decrement (figure 1*b*). Thus, in agreement with Maddess & Laughlin (1985), the sensitivity of H1 to transient changes in velocity was improved by motion adaptation, regardless of whether the change is a velocity increment or a velocity decrement.

(b) *Effect of different baseline velocities and pattern contrasts on motion adaptation*

How general is the adaptation-induced enhancement of response transients to velocity discontinuities? Maddess & Laughlin (1985) only tested responses to velocity changes superimposed on a relatively low baseline velocity. In their experiments, as well as in our experiment shown in figure 1*a*, *b*, brief velocity increments always led to transient increases in the spike rate of H1, whereas velocity decrements always elicited decrements in spike rate. This indicates that the baseline velocity used in Maddess & Laughlin (1985) was below the maximum of the bell-shaped velocity-tuning curve (Eckert 1980). Therefore, we tested H1's sensitivity to velocity discontinuities superimposed on a higher baseline velocity (8 Hz temporal frequency). This was done for two different luminance contrasts of the grating and, thus, in two different activity ranges of the cell (see below).

At the high baseline velocity and high contrast, the example cell responded with decrements in spike rate to velocity increments (corresponding to 12 Hz temporal frequency, figure 1*c*, black trace) and with increments to velocity decrements (corresponding to 4 Hz temporal
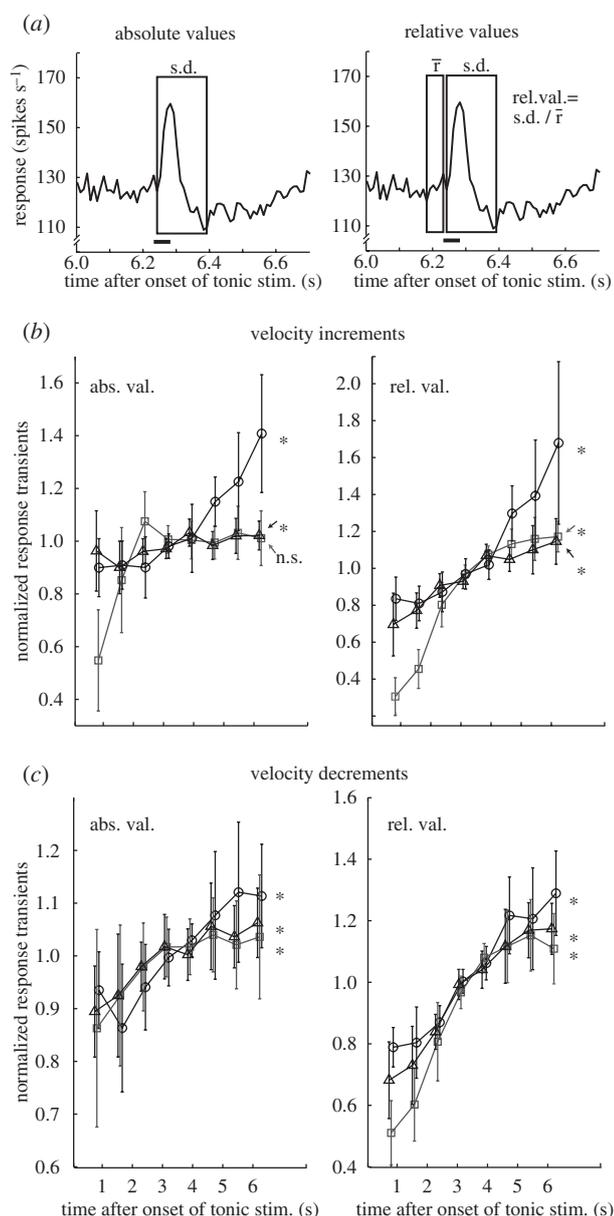
Figure 2. Effect of motion adaptation on sensitivity of H1 to velocity discontinuities. (*a*) Scheme illustrating how the magnitude of the response transients elicited by discontinuities in pattern velocity (indicated by horizontal line) was quantified (see §3 for details). (*b*) Normalized responses to velocity increments based on absolute values (left) and relative values (right), plotted together with the median average deviation (MAD) indicated as error bars. (*c*) Data for velocity decrements. Significant increases are indicated for the different conditions by the asterisks (Mann−Kendall non-parametric trend test, $p < 0.05$). n.s. = not significant. The different symbols depict the following conditions (temporal frequency of baseline motion/Michelson contrast): circle, 8 Hz/0.88; triangle, 2 Hz/0.30; grey square, 8 Hz/0.30. Sample sizes $N = 19/14$ cells for fast and slow baseline velocity, respectively. Median (range) of trials per cell in (*b*): circle, $n = 32$ (13–84); triangle, $n = 36$ (12–88); grey square, $n = 35$ (13–85). Corresponding values in (*c*): circle, $n = 35$ (12–85); triangle, $n = 35$ (12–88); grey square, $n = 33$ (13–85).

frequency, figure 1*d*, black trace). This finding indicates that the baseline velocity was above the cell's velocity optimum. Nevertheless, similar to the results obtained with a suboptimal baseline velocity, the amplitude of the

response transients elicited by velocity discontinuities increased during motion adaptation. To account for the inverted sign of the responses, we then determined baseline-subtracted minima and maxima for velocity increments and decrements, respectively. The response transients increased with adaptation from 37 to 63 spikes s^{-1} for velocity decrements (figure 1*d*, black trace) and from 18 to 66 spikes s^{-1} for velocity increments (figure 1*c*, black trace).

In the previous experiments, the adapting stimulus activated H1 at the onset of motion to very high spike rates (see figures 1*a*, *b* and black traces in figure 1*c*, *d*). Thus, the observed adaptation-induced increase in response transients to velocity discontinuities might be the result of a release from the saturation nonlinearities (resulting from the limit in maximal spike rate) when the overall activity level declines with motion adaptation. To exclude this possibility, we measured the responses of H1 to velocity discontinuities of a grating with a lower luminance contrast (Michelson contrast 0.30). Under this condition, the response of H1 was already lowered to about two-thirds of its maximal spike rate when the first velocity discontinuity occurred (figure 1*c*,*d*, grey traces). Nevertheless, the response transients to velocity discontinuities were enhanced with adaptation in the example cell for the condition with velocity decrements. The response transients increased with adaptation from 35 spikes s^{-1} for the first velocity decrement to 58 spikes s^{-1} for the last velocity decrement. In the condition with velocity increments the response transients first increased slightly (47 and 50 spikes s^{-1} for the first and the second event, respectively), but then dropped to lower values with further adaptation (38 spikes s^{-1} for the last event).

To test systematically the effect of motion adaptation on H1's sensitivity to velocity discontinuities, we investigated the responses of a larger sample of neurons. A quantitative comparison was complicated by the fact that the time course of the response transients to velocity discontinuities varied considerably between different stimulus conditions and from neuron to neuron. In particular, a prominent bi- or multi-phasic characteristic was sometimes present in the responses to velocity discontinuities (figure 1*d*, grey trace). Such temporally complex responses are not surprising, because especially under highly transient stimulus conditions, the responses of motion-sensitive neurons are no longer proportional to stimulus velocity, but also depend on acceleration and higher order temporal derivatives of the time-dependent velocity (Egelhaaf & Borst 1989). As a measure of the response transients to velocity discontinuities, which is robust against the strong differences in the response time courses, we determined the modulation in the spike rate of H1 that is elicited by the velocity discontinuity. Modulation was quantified by taking the standard deviation of the response modulation in a time window of 150 ms starting 10 ms after the onset of the velocity discontinuity (figure 2*a*, left). Similar results were obtained with another measure of velocity transients, the difference between the maximum and the minimum in the same time window (data not shown). To facilitate the comparison between different stimulus conditions, which cause largely different overall activities, the response transients to stimulus discontinuities were
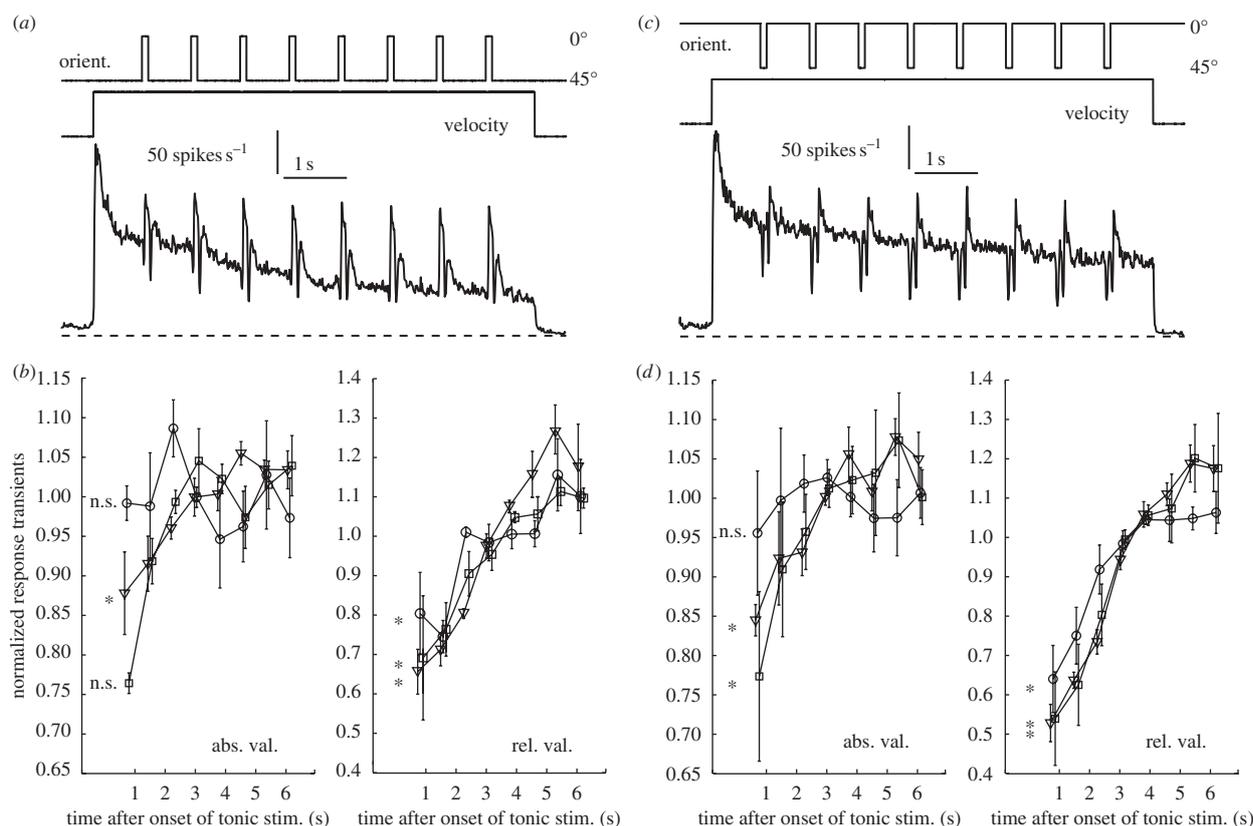
Figure 3. Effect of adaptation on sensitivity of H1 to discontinuities in grating orientation. (a) PSTH ($n = 26$) of a single cell when during motion adaptation the orientation of the grating deviated by 45° from back-to-front motion (0°). During the discontinuities, grating orientation was switched to 0°. Pattern motion was always perpendicular to the orientation of the grating. The grating had a luminance contrast of 0.68 and moved with a temporal frequency of 7 Hz. (b) Quantification of response transients to discontinuities in motion orientation, changing from different baseline orientations (circle, 30°; square, 45°; triangle, 60°) to 0° during the discontinuity. The standard deviations in 200 ms time windows starting 10 ms after the onset of each of the eight discontinuities were calculated and are presented as in figure 2, with normalized absolute (left) and relative (right) values. Sample sizes: $N = 5$, 4 and 5 cells for 30°, 45° and 60° conditions, respectively. Corresponding median (range) of trials per cell: $n = 27$ (22–31), 26 (21–29), 25 (18–33). (c) PSTH ($n = 25$) from the same cell as in (a), now for changes from H1's preferred direction (0°) during adapting baseline motion to an orientation of 45° during the discontinuity. (d) Data shown as in (b) for changes from 0° baseline motion to different orientations during the discontinuity (circle, 30°; square, 45°; triangle, 60°). Sample sizes: $N = 8$, 7 and 8 cells for 30°, 45° and 60° conditions, respectively. Corresponding median (range) of trials per cell: $n = 25$ (17–31), 25 (22–29), 25 (17–32).

normalized in the following way: For each neuron, the standard deviations of the response modulation corresponding to the eight consecutive motion discontinuities were calculated from the average peri-stimulus time histograms (PSTHs) as described above. These values of response discontinuities were then divided by the median value of the responses to all eight velocity discontinuities. This procedure relates the individual response transients to the median response transient and allows us to determine error bars for all values. Figure 2 shows the time course of changes in the normalized response transients for all tested conditions, plotted as median values and their corresponding median absolute deviations (MADs) of the cell samples. For most conditions, the response transients of H1 to velocity discontinuities increased with motion adaptation. We found significant enhancements of these response transients both for velocity increments (figure 2b, left) and for velocity decrements (figure 2c, left). In general, adaption enhanced H1's sensitivity to velocity discontinuities, regardless of whether these were superimposed on a low or on a fast baseline

velocity. Only when fast motion of a low-contrast pattern was superimposed by velocity increments, did we find no significant enhancement of the response transients (figure 2b, left, grey squares; see also figure 1c, grey trace). Under none of the tested conditions did the responses to velocity discontinuities decrease, which is in stark contrast to the strong decline of the overall response level during motion adaptation (figure 1).

To account for the time-dependent decrease in spike rate during the course of adaptation, we also took a *relative* instead of an *absolute* measure of H1's response transients: the modulation in spike rate (quantified as explained above) evoked by velocity discontinuities was divided by the baseline spike rate preceding the corresponding response. The baseline spike rate was determined as the mean spike rate in a 50 ms time window that ended with the onset of the velocity discontinuity (figure 2a, right). Over the entire sample of H1 neurons, the relative response transients elicited by brief velocity changes increased significantly with adaptation, regardless of pattern contrast and of baseline velocity (figure 2b,c, right diagrams).
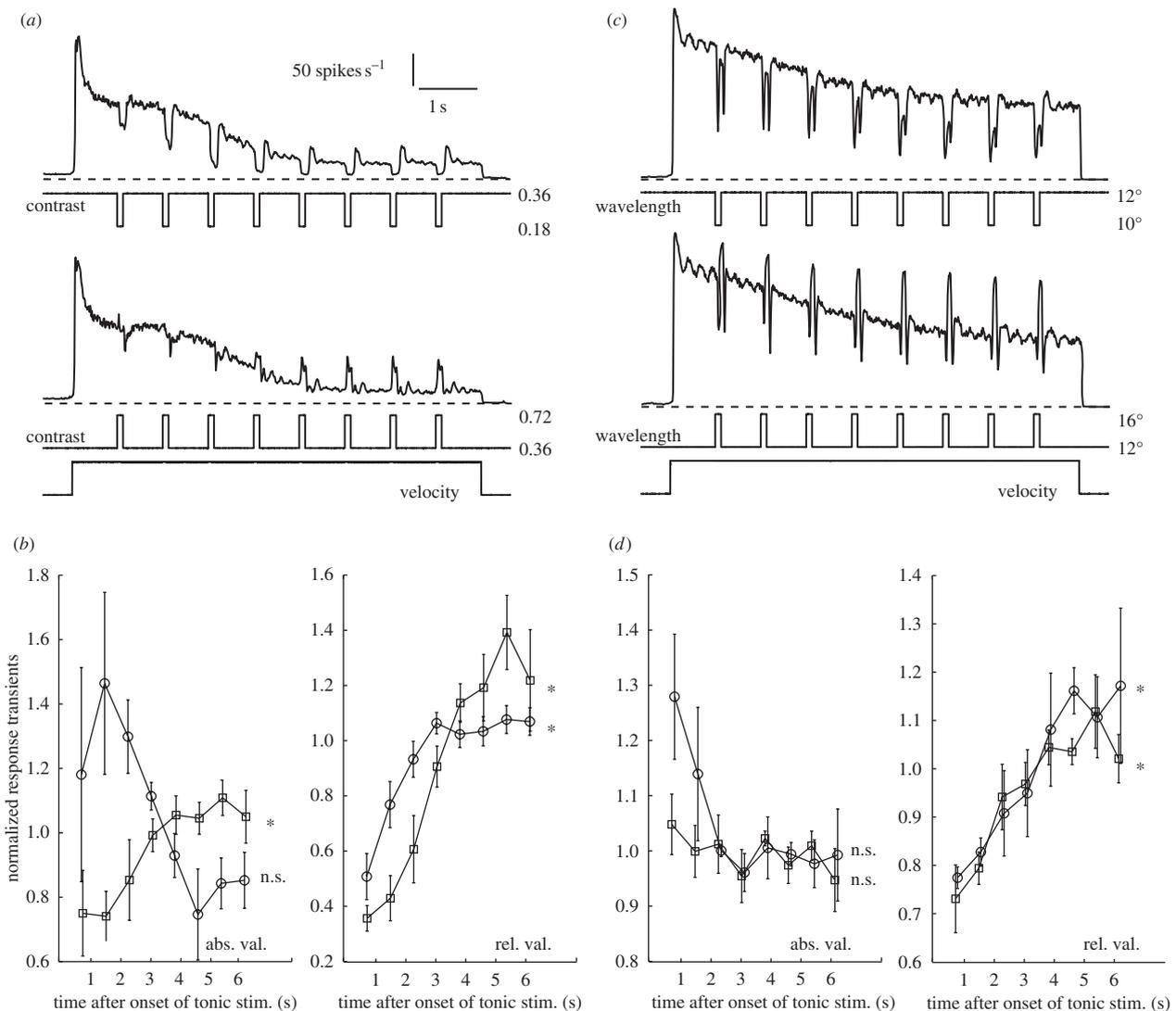
Figure 4. Effect of adaptation on sensitivity of H1 to discontinuities in contrast and pattern wavelength. (*a*) The Michelson luminance contrast of a grating moving in the preferred direction with a temporal frequency of 7 Hz was changed from 0.36 during adapting baseline motion to 0.18 or 0.72 during the contrast decrements (top, $n = 98$) and increments (bottom, $n = 91$), respectively. (*b*) Quantification of sensitivity to discontinuities in pattern contrast as in figure 2 for contrast decrements (circles) and increments (squares). Sample size: $N = 8$ cells. Median (range) of trials per cell: $n = 38$ (10–66) and $n = 60$ (10–182) for decrements and increments, respectively. (*c*) The pattern wavelength was changed during the discontinuities. A grating with sinu-soidal luminance profile moving with a temporal frequency of 5 Hz was used in these experiments. Pattern wavelength was $12°$ during adapting motion and $10°$ (top) or $16°$ (bottom) during the discontinuities. Each PSTH was averaged from 65 trials. (*d*) Quantification of transients in spiking activity in response to decrements (circles) and increments (squares) in pattern wavelength. Sample size: $N = 8$ cells. Median (range) of trials per cell: $n = 38$ (10–66) and $n = 38$ (10–67) for decrements and increments, respectively.

(c) *Motion adaptation influences neuronal sensitivity to discontinuities in orientation, contrast and spatial frequency of the pattern*

Motion adaptation might affect neuronal sensitivity to stimulus discontinuities in a general way by not only alter-ing the responses to brief changes in velocity, but also in other stimulus parameters. Therefore, we tested whether motion adaptation affects the sensitivity of H1 to other stimulus discontinuities such as brief changes in the orientation, contrast or spatial frequency of the grating pattern.

Discontinuities in grating orientation were presented for two different orientations during baseline motion. (i) Baseline motion was in the preferred direction of H1 (orientation $0°$, denoting back-to-front motion). During

motion discontinuities, grating orientation and, thus, the direction of motion was switched during motion dis-continuities away from the preferred direction of H1 by either $30°$, $45°$ or $60°$ relative to the baseline orientation. Hence, during motion discontinuities, the grating moved from back-top to front-bottom with increasing deviation from the preferred direction. (ii) The grating orientation during baseline motion deviated by either $30°$, $45°$ or $60°$ from the preferred direction of H1. The grating orientation was then switched to produce motion in the preferred direction during the discontinuity (orientation $0°$).

In figure 3, the responses of an example cell to changes in orientation from oblique during baseline ($45°$ relative to the preferred direction) to $0°$, i.e. the preferred direc-tion, during the discontinuity (figure 3*a*) and vice versa

(figure 3*c*) are shown. For both conditions, the response transients evoked by orientation discontinuities increased with motion adaptation. Similar enhancements were observed for the entire sample of neurons for most conditions (figure 3*b*,*d*, left plots). Only for weak changes in grating orientation did the absolute response transients elicited by the discontinuities not increase significantly with adaptation, in particular for the changes from 0° background motion to 30° transient motion and vice versa (figure 3*b*,*d*, left, circles). However, the relative response transients, i.e. responses relative to baseline level before the discontinuity, increased significantly with adaptation in all conditions (figure 3*b*,*d*, right).

We performed similar experiments with discontinuities in pattern contrast (figure 4*a*,*b*) and spatial wavelength (figure 4*c*,*d*). In the first paradigm the luminance contrast was changed during the discontinuities from the background level of 0.36 to a value of 0.18 or 0.72, for contrast decrements or increments, respectively. In the second paradigm the spatial wavelength was changed from 12° to 9° or 16° for decrements and increments, respectively. Consistent enhancements of the absolute response transients elicited by these discontinuities were only present under some of the conditions (figure 4*b*,*d*, left), whereas the relative response transients increased significantly in all the conditions (figure 4*b*,*d*, right).

We can conclude that in spite of a marked decrease in the overall response level with motion adaptation the sensitivity of H1 to changes in several stimulus parameters is maintained or even enhanced. This result implies that adaptation with ongoing visual motion enhances the ability of the H1 neuron to signal sudden changes in the stimulus.

4. DISCUSSION

We presented a constant stimulus to the fly motion-sensitive neuron H1 interspersed with brief periods in which one of the parameters of a drifting grating, velocity, orientation, contrast or wavelength was changed. In spite of a decrease in the overall response level, the response transients elicited by the discontinuities in the stimulus were not attenuated to a similar extent. For most of the stimulation conditions, motion adaptation even led to an enhancement of the evoked absolute response transients. A major reason for the absence of such an enhancement under some conditions appeared to be the strong decline in overall activity with motion adaptation. Spike rate modulations in response to stimulus discontinuities are then constrained by the spike threshold nonlinearity, in particular for discontinuities that elicit decrements in spike rate (figure 4*a*). Nonetheless, when the amplitude of the response transients was related to the immediately preceding spike rate, the sensitivity to stimulus discontinuities with motion adaptation increased consistently for all conditions.

Our results show that motion adaptation enables a neuron to maintain or even enhance its sensitivity to changes in a variety of stimulus parameters. This is not self-evident because the mechanisms underlying changes in sensitivity for the different parameters of the motion stimulus are probably diverse and might result from a variety of cellular processes, either in the motion-sensitive tangential neurons themselves or in their input neuropiles

(Maddess & Laughlin 1985; Harris *et al.* 2000; Borst *et al.* 2005; Neri & Laughlin 2005; Kurtz 2007; Neri 2007; Nordström & O'Carroll 2009).

Many properties of fly tangential neurons are captured by models comprising arrays of correlation-type elementary motion detectors (EMDs) (reviewed by Borst & Egelhaaf 1989). The basic operation performed by an EMD is to multiply the intensity signal from a retinal location with its temporally delayed counterpart from a neighbouring location. The range of image velocities coded by the EMD is determined by the distance between the two retinal sample points and the temporal delay, which is often mathematically implemented as a low-pass filter. Soon after Maddess & Laughlin (1985) demonstrated motion adaptation in H1, it was proposed that the underlying mechanism is an activity-dependent downregulation of the time constant of the EMD low-pass filter. This parameter change would shift velocity tuning towards higher values (de Ruyter van Steveninck *et al.* 1986; Clifford *et al.* 1997). However, with such a mechanism alone, adaptation would enhance sensitivity to velocity discontinuities only for low velocities. At high velocities, response transients evoked by changes in velocity might even become weaker in the adapted than in the non-adapted state. This prediction can be made with regard to the bell-shaped signature of the steady-state velocity-tuning curves, but was not experimentally tested by Maddess & Laughlin (1985). In the present study, we could show that H1 responded strongly to discontinuities in motion velocity regardless of whether it was adapted to a baseline velocity below or above the steady-state velocity optimum. This finding indicates that an adaptation-induced shift of the neuronal velocity tuning towards higher values cannot entirely account for the enhancement of response transients to velocity discontinuities. In accordance with our results, consistent changes in the velocity optima of tangential neurons following adaptation have not been found (Harris *et al.* 1999; Kalb *et al.* 2008*b*). It has been suggested that motion adaptation shortens the time constant of a high-pass filter in the periphery rather than that of the temporal low-pass filter in the EMD (Borst *et al.* 2003; Safran *et al.* 2007). It is hard to predict without extensive modelling what effects such changes might have on velocity response functions and on the responses to discontinuities in motion velocity.

Increased sensitivity to stimulus discontinuities with adaptation appears to be prevalent in higher order processing centres, in particular in the auditory system (Li *et al.* 1993; Gill *et al.* 2008; Reches & Gutfreund 2008). It has been proposed that one of the mechanisms that enable neurons to maintain their sensitivity to novel stimuli during sustained stimulation is stimulus-specific adaptation (Ulanovsky *et al.* 2003). A plausible cellular basis of stimulus-specific adaptation is the selective attenuation of synaptic inputs that are specific for certain stimulus qualities, e.g. distinct frequency bands. However, unlike the auditory system in which different frequencies of sound are processed separately in the periphery, such segregation is likely to exist only for some of the parameters of a visual motion stimulus. There is evidence that H1 receives input from neurons that differ in their preferred motion directions (Krapp *et al.* 2001). If these inputs adapt during ongoing

stimulation with motion, it is likely that adaptation is strongest in those inputs that most closely match with their preferred direction the adapting motion direction. Moreover, it has recently been shown that two input pathways to the fly motion vision system differ in their contrast sensitivity. This was discovered when eliminating distinct types of neurons in the lamina (the neuropil directly following the photoreceptor layer) by genetic tools in the fruitfly *Drosophila* (Rister *et al.* 2007). Thus, at a given contrast level of the motion stimulus, the neurons in the input pathway with a low contrast threshold might be more active than those with a high contrast threshold. Such a differential activation might lead to selective adaptation of low-threshold inputs. On the level of tangential cells, such selective adaptation would manifest itself as a shift of the contrast-response function towards higher values (Harris *et al.* 2000), thus adjusting the neuronal working range to current contrast levels. The concept of stimulus-specific adaptation might thus provide an explanation for why the adapted H1 neuron responds highly sensitively to discontinuities in pattern contrast and grating orientation. In contrast, stimulus-specific adaptation through differential attenuation of distinct classes of inputs is unlikely with respect to discontinuities in motion velocity. The reason for this is that there is in *Calliphora* no evidence for the existence of distinct input channels that differ in their velocity preference. Unlike motion-sensitive neurons in insects that are able to hover during flight (O'Carroll *et al.* 1996), the velocity–response curve of H1 has a single optimum (Eckert 1980; Warzecha *et al.* 1999), consistent with the view that it receives input from motion detectors with uniform velocity preference (Borst & Egelhaaf 1989).

Recently, it was examined by *in vitro* electrophysiology and modelling how neurons in the mammalian visual cortex respond to abrupt changes in the magnitude of their input (Puccini *et al.* 2006). Post-synaptic neurons decreased their activity during tonic activation of the network, but they were still able to respond strongly whenever the input current given to the pre-synaptic neurons was changed abruptly. In a model, this behaviour could be reproduced when pre-synaptic spike-frequency adaptation was combined with synaptic short-term depression. In the fly visual system, the cellular basis of adaptation is largely unknown. However, an activity-dependent conductance that is activated by sustained excitatory stimulation is present in tangential cells (Kurtz 2007). Spike-frequency adaptation, one of the model prerequisites for detection of abrupt input changes, has been shown to be based on similar conductances, e.g. in mammalian visual cortex (Sanchez-Vives *et al.* 2000).

The accentuation of response transients to stimulus discontinuities with adaptation appears to enhance neuronal sensitivity to signals that are novel and, thus, potentially more important than continuing, unchanged signals. During flight, for instance, the visual system of the fly will be exposed to persistent motion stimulation. These stimuli will change abruptly when heading direction is shifted or when changes in the distance to objects in the environment become effective. In a recent study, horizontal-system cells, another type of fly tangential neuron, were stimulated with naturalistic visual motion as perceived by the fly during unrestrained flight in a cubic arena with textured walls. Repeated presentation

of the motion sequence led to a strong reduction in the neuronal response level. However, when a virtual object was placed near to the fly's trajectory, the attenuation of the neuronal response with adaptation was weaker in time segments during which the object moved into the receptive field than in time segments where the object was invisible (Liang *et al.* 2008). These results are consistent with those of the present study, as the appearance of an object in the visual field leads to discontinuities in the motion stimulus. Thus, the detection of novel, behaviourally relevant stimuli might be facilitated in a natural situation if neuronal responses to sudden changes in the stimulus are enhanced with adaptation.

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