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Adaptation changes directional sensitivity in a visual motion-sensitive neuron of the fly

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ABSTRACT

The blowfly visual system is a well-suited model to investigate the functional consequences of adaptation. Similar to cortical motion-sensitive neurons, fly tangential cells are directional selective and adapt during prolonged stimulation. Here we demonstrate in a tangential cell large changes in directionality after adaptation with motion in one direction. Surprisingly, depending on stimulation parameters, sensitivity for motion in the adapted direction relative to the unadapted direction can be either enhanced or attenuated. A simple model reproduces our results. It only incorporates previously identified changes in contrast sensitivity with motion adaptation. Thus, novel forms of motion adaptation seem unnecessary.

1. Introduction

Neuronal adaptation to prolonged sensory stimulation is often accompanied by reduced response magnitudes to subsequently presented stimuli. This phenomenon is commonly thought to adjust a neuron's operating range to the prevailing sensory input by changing the responsiveness of the system (for review see Clifford & Ibbotson, 2002; Ohzawa, Sclar, & Freeman, 1982). Many studies on cortical neurons in the mammalian visual pathway revealed that adaptation involves stimulus-specific effects, which go beyond a simple activity-dependent reduction of neuronal responsiveness (Dragoi, Sharma, & Sur, 2000, 2001, 2002; Hammond, Mouat, & Smith, 1985; Perge, Borghuis, Bours, Lankheet, & van Wezel, 2005; Van Wezel & Britten, 2002). For instance, visual adaptation in orientation selective cells in the primary visual cortex of cats leads to the strongest sensitivity reduction when the test stimulus is aligned with the orientation of the preceding adapting stimulus (Dragoi et al., 2000). As a result, a shift of the peak of the orientation tuning function away from the adapting orientation was elicited. This plasticity of orientation tuning has been proposed to improve the ability to discriminate orientation differences (Dragoi, Sharma, Miller, & Sur, 2002). However, Crowder et al. (2006) demonstrated that most cells in the cat visual cortical areas V1 and V2 strongly adapt even to stimuli with non-optimal orientation. Moreover, stimulus-specific effects of adaptation do not necessarily shift the neuronal sensitivity away from the adapting stimulus. Neurons in the macaque cortical area MT, which are selective for the direction of motion, undergo an adaptation-induced shift of the orientation tuning peak towards the adapting motion direction (Kohn & Movshon, 2004).

Similar to many motion-sensitive mammalian cortical neurons, motion sensitive tangential cells (TCs) in the fly brain reduce their response amplitudes during prolonged exposure to visual motion (see e.g., Harris, O'Carroll, & Laughlin, 2000; Kurtz, Dürr, & Egelhaaf, 2000; Maddess & Laughlin, 1985). Individual TCs are excited most effectively by visual motion in a certain direction, their preferred direction. Motion in the opposite direction, the so-called null-direction, causes inhibition (Borst & Haag, 2002; Egelhaaf et al., 2002). TCs possess large receptive fields in which local preferred directions may deviate from the neurons' overall preferred motion direction. Each TC is endowed with a complex, neuron-specific receptive field, which is established by retinotopic dendritic integration of output signals from many local motion detectors with different preferred direction and/or by inputs from other TCs (Haag & Borst, 2004; Krapp, Hengstenberg, & Hengstenberg, 1998, 2001). Due to their receptive field properties, TCs represent a particularly well-suited model system to investigate whether adaptation has a more specific effect than a pure reduction of overall response magnitudes and, in particular, whether directional sensitivity in TCs is modified by motion adaptation.

Here we focus on the V1-cell (Hausen, 1976; Krapp, Hengstenberg, & Egelhaaf, 2001), a particular type of TC, to investigate whether motion adaptation changes directional sensitivity. The V1-cell is individually identifiable and predominately sensitive to vertical downward motion. We find strong changes in directional sensitivity after motion adaptation in the V1-cell. Response

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attenuation can be stronger either for test stimuli moving in the same direction as the adapting stimulus or for test stimuli moving in a different direction. Unlike cortical neurons both types of changes can be elicited in a single neuron, depending on the parameters of the adaptation protocol. Surprisingly, both types of changes can be largely explained by a simple model incorporating previously described adaptation components that reduce sensitivity to subsequently presented motion in any direction (Harris et al., 2000).

2. Materials and methods

2.1. Animal preparation and electrophysiology

We collected data from 17 female blowflies (*Calliphora vicina*), aged 2–4 days and bred in our laboratory culture. The animals were dissected as outlined previously (Karmeier, Krapp, & Egelhaaf, 2003). 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). Spike activity of the V1-cell was recorded extracellularly in its output region in the left brain hemisphere at temperatures ranging from 20 to 25 °C. The V1-cell is unambiguously identifiable by its sensitivity to downward motion in the visual field contralateral to its output region (see Fig. 1a). We used glass electrodes (GC150TF-10, Clarc Electromedical, Edenbridge, UK, electrode resistances 4–8 MΩ when filled with 1 M KCl) pulled on a GMZ-Universal puller (Zeitz, Augsburg, Germany). Spikes were detected by a threshold operation, and resulting pulses sampled at 5 kHz and analog–digital converted (DT 3001, Data Translation, Marlboro, MA, USA).

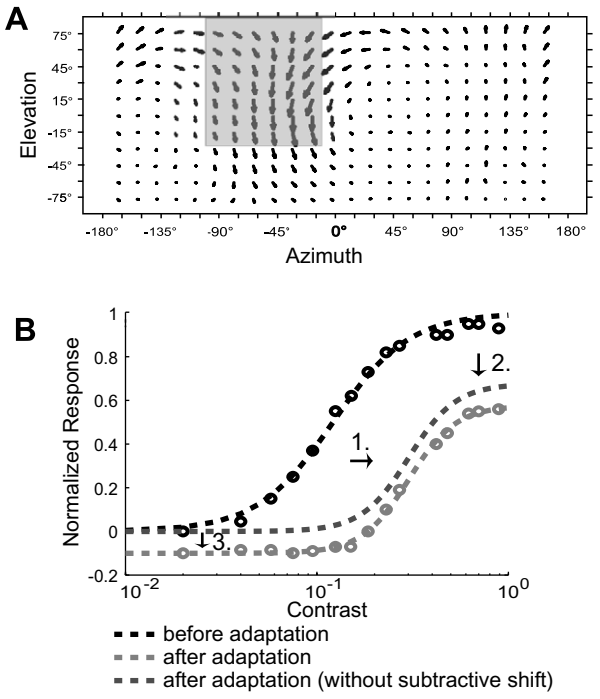

Fig. 1. (A) Reproduction of receptive field profile of the V1-cell determined by the analysis of local visual motion sensitivities by Karmeier et al. (2003). Each arrow indicates the preferred direction of motion at a particular position within the visual field of the fly. Arrow lengths show the normalized response magnitudes to local motion in the direction indicated by each individual arrow. Positive azimuth values correspond to the side where V1's output arborization is located (figure taken and modified from Karmeier et al. (2003)). The shaded area indicates the visual region that was covered by our visual motion stimulus. (B) Illustration of the components underlying the adaptation-induced reduction in contrast sensitivity reported by Harris et al. (2000). The reduced contrast sensitivity can mainly be attributed to a rightward shift of adapted contrast–response functions towards higher contrasts (1), a compression of the output range (2), and a subtractive (downwards) shift (3). Dashed curves show the corresponding sigmoid curves obtained from fitting the contrast–response values with the equation described in Section 2. The dark gray curve corresponds to the adapted curve corrected for by the subtractive shift. Data values taken from Harris et al. (2000).

2.2. Experimental design

We used moving square-wave gratings (24°/s, spatial wavelength: 12°), 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. The monitor was centered at an azimuth/elevation of −55° and 26° with 0° corresponding to the frontal midline of the animal (see Fig. 1a). It covered 90° × 110° (horizontal × vertical extent). A motion adaptation protocol (see Fig. 2) consisted of a 1 s reference (*r*) stimulus, followed by 8 s of adapting (*a*) motion and 1 s of test (*t*) motion. We either adapted the V1-neuron to horizontal back-to-front (*h*) or to vertical downward (*v*) motion. For both conditions, the impact of adaptation on vertical and horizontal motion responses was tested. Our set of adaptation protocols thus included four combinations of adapting and reference/test stimuli: *rh-ah-th*; *rv-ah-tv*; *rh-av-th*; *rv-av-tv*. Between presentation of test and adapting stimuli as well as between adapting and reference stimuli the monitor was homogeneously illuminated at mean luminance (15.6 cd/m^2) for 100 ms. In a first series of experiments, all test and reference stimuli had a luminance contrast of 0.20. The adapting stimuli had a contrast of 0.53. In a second, modified protocol the contrast of the horizontal test and reference stimuli was raised to 0.53, whereas the contrast of the vertical stimuli was reduced to 0.06. We monitored the spike activities of 9 V1-cells using the first stimulus condition and another set of 8 V1-cells with the modified stimulus protocol.

The different adaptation protocols were presented in pseudo-random order. Each presentation was interleaved with 15 s of mean luminance in order to allow complete recovery from adaptation.

2.3. Adaptation model

In fly TCs, adaptation to sustained motion causes strong reduction in neuronal contrast sensitivity. In graded-potential TCs sensitive to horizontal motion (HS-neurons) of *Eristalis tenax* basically three components were identified to contribute to this decreased sensitivity (Harris et al., 2000) (see Fig. 1B): a rightward shift of the contrast–response function (1), a compression of the output range of the neuron (2), and a subtractive shift of the contrast–response function (3). The subtractive shift is induced by an excitation-dependent after-hyperpolarization of the membrane potential of TCs and is thus elicited mainly by preferred direction motion, whereas the rightward shift of the contrast–response function is induced by motion in any direction. The output range compression is elicited by motion in either preferred or null-direction, but not by motion in a direction orthogonal to the preferred-null-axis (cf. Harris et al., 2000, their Figs. 2 and 5). All these adaptation components are supposed to be reflected in the responses of the neuron to subsequently presented motion independent of its direction. Note that even the subtractive shift, although it is *elicited* primarily by preferred direction motion, would equally *affect* responses to subsequent stimuli in any motion direction.

Based on the three adaptation components, we built a simple adaptation model to test in a phenomenological way whether changes in contrast sensitivity affect the relative sensitivity of the V1-cell to different motion directions. We fitted the mean contrast–response functions obtained from the responses of unadapted and adapted TCs (see Fig. 1B) shown in Harris et al. (2000) by sigmoid curves using the equation:

$$R(c) = (R_{\max} * c^n)/(c^n + C_{50}^n) - s.$$

$R(c)$ is the relative response amplitude at contrast c, s is the subtractive shift of the adapted curve, n is the exponent that determines the steepness of the curve and $R_{\max}$ is the maximum response level. We fitted the curves by using a least square algorithm. The unadapted contrast–response curve was best described by a sigmoid function with $n_{\text{unadapted}} = 2.19$ and $C_{50\ \text{unadapted}} = 0.12$. Since the unadapted curve was fitted to normalized values, $R_{\max}$ was set to 1 and s to zero. The fit to the adapted curve yielded $n_{\text{adapted}} = 3.50$, $C_{50\text{adapted}} = 0.28$, $s_{\text{adapted}} = 0.10$ and $R_{\max\ \text{adapted}} = 0.68$.

Based on this simple adaptation model the responses in the adapted state were estimated by the following procedure: (1) for the specific contrast value c used in the experiment the response reduction coefficient (*rrc*) was calculated from the relation $rrc = R_{\text{unadapted}}(c)/(R_{\text{adapted}}\ (c) + s)$. (Note that $R_{adapted}\ (c) + s$ represents the adapted curve corrected by the subtractive shift, as depicted in dark gray in Fig. 1B.) The mean responses induced by the reference stimuli in each motion direction were multiplied with *rrc*. This procedure accounts for the effects of the first two adaptation components, i.e., the rightward shift and the compression of the response function. (2) The subtractive shift was handled in a different way, because it is assumed to depend on excitation (i.e., depolarization) of the neuron: we determined the mean response during the entire vertical and horizontal adapting period, respectively and multiplied this response with s_{adapted}. The values obtained by this procedure were subtracted from the results of step (1) to predict the horizontally or vertically adapted responses, respectively. We calculated the predictions individually for each recorded V1-cell and used the predicted adaptation-induced changes in directional sensitivities as a reference to our experimentally observed changes in directional sensitivities. To verify the robustness of the modeled effects of response reduction on the change in directional sensitivities, we varied the *rcc* value and the subtractive shift (s_{adapted}) by taking the values obtained from the fit, but also half these values and twice these values.

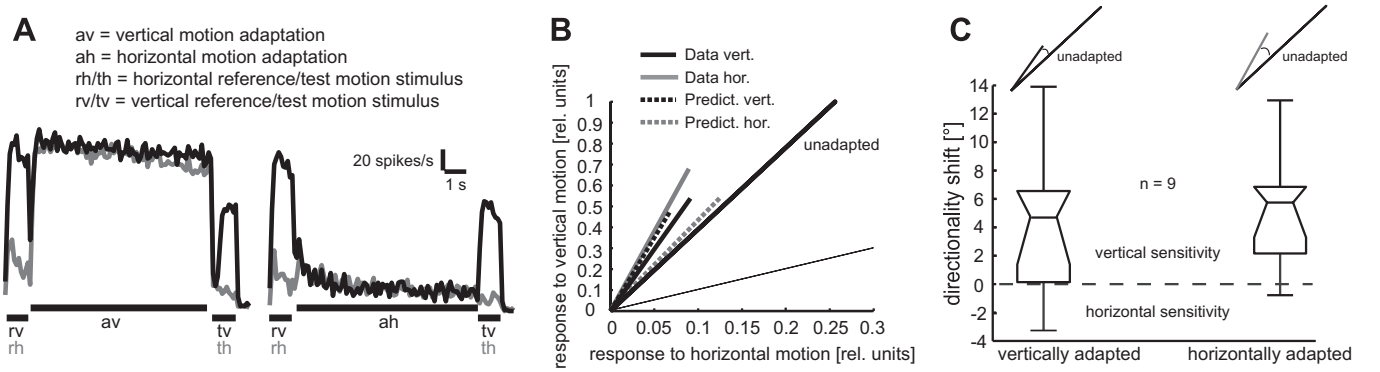

Fig. 2. Neuronal responses of a representative V1-cell to horizontal and vertical motion in the unadapted and in the adapted state. (A) Average spike rates ($n = 10$ traces) during reference and test motion periods before and after either vertical (left) or horizontal (right) motion adaptation. The contrast during reference and test motion periods was 0.20, whereas the contrast during the adaptation periods was 0.53. (B) Directional sensitivities of the example neuron in the unadapted and in the differently adapted states. Directionality vectors express the ratio between normalized horizontal and vertical motion-induced average response amplitudes. The unadapted response to vertical motion was set to one. Note the different scaling of the *x*- and *y*-axis. Unity is indicated by the thin black line: vectors falling on this line indicate equally strong responses to vertical and horizontal motion. Experimentally observed directionality vectors (solid lines) and directionality vectors predicted by the adaptation model (dashed lines, see Section 2 for details) are shown. The directionality shifted towards vertical motion sensitivity regardless of the adapting motion direction. (C) Quantification of experimentally determined shifts in directionality obtained from the responses of 9 V1-cells after vertical and horizontal motion adaptation. The plotted values are the angles enclosed by corresponding unadapted and adapted directionality vectors (see insets). Positive angles indicate shifts towards vertical motion sensitivity, whereas negative values indicate shifts towards horizontal motion sensitivity. Irrespective of the adapting motion direction, the analyzed V1-cells became more sensitive to vertical motion. Box–Whisker plots show the distribution of the shifts in directional sensitivity: the horizontal lines of the boxes indicate the lower quartile, median and upper quartile values. Whiskers show the extent of the rest of the data. Notches provide an estimate of the uncertainty about the means for box-to-box comparisons: the medians are significantly different ($p < .05$) if the corresponding notches do not overlap.

2.4. Calculations of directional sensitivities

Fig. 2 exemplifies our strategy of characterizing directional sensitivities. Mean spike frequencies were averaged over the 1-s period during the presentation of reference and test stimuli. For each adaptation protocol and each V1-cell the average response was obtained from 10 trials.

We calculated the directional sensitivity of a V1-neuron as the ratio between the response magnitudes during vertical and horizontal motion, respectively. The directional sensitivity of the V1-cell can be expressed as a vector ('directionality vector'): its vertical and horizontal component corresponds to the vertical and horizontal motion responses, respectively. Thus, the direction of the vector reflects the directional sensitivity and its length the geometrical mean of the responses to vertical and horizontal motion. Directionality vectors were determined for unadapted as well as horizontally and vertically adapted states. All responses were normalized to the response to vertical motion in the unadapted state, because this stimulus condition led to largest responses. A positive change of the angle of the directionality vector corresponds to an increase in the relative sensitivity to vertical motion. Accordingly, decreased relative sensitivity to vertical motion reflects a negative change of the directionality vector's angle.

In order to test the significance of the adaptation-induced changes in the angles of the directionality vectors, we applied a two-sided sign test to our data. This test is usually applied to linear data, but not to angular data. The latter would normally require circular statistics. However, since in the most extreme case only half of the circle is covered by the experimentally determined angles (which is only theoretically the case if a neuron exclusively responds to either vertical *or* horizontal motion), application of the sign test is valid. This is due to the fact that in our case the projection of the angles on a linear scale would yield different numerical values but identical rank values. Only the latter are relevant in a sign test.

3. Results

The V1-cell combines the motion signals from four identified motion-sensitive Vertical System (VS) cells (Kurtz, Warzecha, & Egelhaaf, 2001; Kalb, Egelhaaf, & Kurtz, 2006; Warzecha, Kurtz, & Egelhaaf, 2003). These presynaptic VS-cells differ within their large receptive fields in the sensitivity to the direction of local motion: whereas all presynaptic VS-cells are predominantly sensitive to vertical downward motion, the presynaptic VS1-cell is additionally sensitive to horizontal back-to-front motion in a specific region of its receptive field (Krapp et al., 1998; for simplification in the following text the term 'vertical' is used for 'vertical downward' and 'horizontal' is used for 'horizontal back-to-front'). As a consequence, the V1-cell is sensitive to vertical motion in large parts of the visual space and to horizontal motion in another, smaller part (for comparison see the receptive fields of VS-cells in Krapp et al. (1998) and that of the V1-cell illustrated in Fig. 1A as modified from Karmeier et al. (2003)). This receptive field organization and its suitability for long-term recordings makes the V1-cell an ideal candidate to analyze whether motion adaptation alters the directional sensitivity: if for instance adapting motion in one direction affected the response to subsequent motion in the same direction more than to motion in other directions, the directional sensitivity of the V1-cell would change. We tested this hypothesis by comparing the directional sensitivity of the V1-cell before and after either vertical or horizontal motion adaptation.

Fig. 2 outlines our experimental procedure on the basis of representative sample recording. Fig. 2A shows the mean spike rates of the V1-cell to adaptation either by horizontal or by vertical motion of a high-contrast grating. Whereas the V1-cell was strongly excited by vertical motion during the reference, adaptation and test phase, its responses were weaker during horizontal motion stimulation. Fig. 2B shows as vectors the directional sensitivity of the V1-cell before and after horizontal and vertical adaptation. These vectors are defined by the ratio of the response magnitudes to vertical and horizontal motion ('directionality vector', see Section 2). Shortening of the adapted vector length indicates how much the response is reduced as a consequence of motion adaptation. The length of the directionality vectors obtained from spike responses decreased after both horizontal (see Fig. 2B, dashed black vector) and vertical (solid black vector) motion adaptation. Hence, adaptation strongly attenuated the response of the V1-cell to subsequent test motion irrespective of the response amplitudes during motion adaptation (cf. Fig. 2A left and right).

However, not only the lengths of the adapted directionality vectors change, but also their directions. A change of the vector direction reflects the adaptation-induced change of directional sensitivity. For example, if motion adaptation attenuated the sensitivity of the V1-cell for the adapted direction more than that for the unadapted direction, the adapted directionality vector is predicted to shift away from the adapting motion direction. Our data, however, did not meet this most obvious prediction. After

both vertical and horizontal motion adaptation, the directionality vector shifts toward vertical motion, indicating that the relative sensitivity of the cell for vertical motion is increased regardless of the direction of the adapting motion. Hence, the relative increase in the sensitivity for vertical motion after vertical motion adaptation clearly contradicts the expectation that adaptation would attenuate the responsiveness of the V1-cell in the adapted direction more than in other motion directions.

Basically the same results were obtained with 8 further V1-cells (see Table 1). Although there is a large variability in experimentally determined changes in individual directionality vectors, their median is clearly shifted towards a relative increase in sensitivity for vertical motion, irrespective of the adapting motion direction (see Fig. 2C). The variability of measured directional sensitivities of individual V1-cells is most likely the consequence of varying strengths of motion adaptation. The change in directionality was significant after both vertical and horizontal motion adaptation (two-sided sign test, $p < .05$).

As a consequence of the directional sensitivity of the V1-cell, the overall strengths of responses to vertical and to horizontal motion differed dramatically in our first series of experiments (see Fig. 2A and B and Table 1). To make the magnitude of unadapted vertical and horizontal motion responses more equal we raised the contrast of horizontal reference and test stimuli above that of the corresponding vertical motion stimuli. Fig. 3A illustrates the experimentally determined adaptation-induced changes in the directional sensitivity of a sample V1-cell. Now the horizontal-to-vertical response ratio was much larger than with the first protocol. However, vertical motion adaptation now led to a relative increase in the sensitivity for horizontal motion (solid black line), whereas horizontal motion adaptation left the response ratio of the two tested motion directions unchanged (solid gray line). We repeated the same analysis described above on 7 further V1-cells. With this stimulation protocol the response to test stimuli moving in horizontal direction had about half the magnitude of the response to vertical test motion (see Table 1). Horizontal-to-vertical response ratios closer to one could be obtained by lowering the contrast of the vertical stimulus even more. Such low contrast, however, led to very low spike rates in the adapted state, rendering quantitative analysis too unreliable.

Fig. 3B illustrates the measured changes in the directionality vectors of all V1-cells that were analyzed with the second adaptation protocol: both vertical and horizontal motion adaptation now induced a relatively stronger *horizontal* responsiveness in all cells, which is expressed in negative median values. The change in directionality was significant both after vertical and after horizontal motion adaptation (two-sided sign test, $p < .05$). Similar to the results obtained with the first stimulation protocol, motion adaptation strongly affects the directional sensitivity of adapted cells independent of the adapting motion direction. However, with the second protocol the change in the directionality vector was in the opposite direction than with the first protocol (cf. Fig. 2C with Fig. 3B). Thus, it depends largely on the stimulus conditions whether adaptation leads to a relative increase in sensitivity for vertical or for horizontal motion.

How can the observed adaptation-induced changes in directional sensitivity be explained? Harris et al. (2000) identified three prominent components (termed here for simplicity 'Harris components') of adaptation in a TC of the hoverfly *Eristalis tenax*. These adaptation components do not represent directionality-changing adaptation in a strict sense, because they affect responses to subsequent motion independent of its direction. To pinpoint putative interactions between direction and contrast adaptation we used a simple model based on the changes in contrast sensitivity with motion adaptation of HS-neurons in *Eristalis* (Harris et al., 2000; see Section 2). Although the V1-neuron tested in the present study has many common properties with the HS-cells tested by Harris et al. (2000), these neurons differ in several aspects from each other: first, the HS-cells respond best to horizontal motion instead of vertical motion, the preferred direction of the V1-cell. Second, the axonal response of HS-cells is, to a large extent, a graded membrane potential change rather than spike trains as is a characteristic of the V1-cell. Third, species differences in neuronal properties between *Eristalis* and *Calliphora* cannot be excluded. Because of these differences we did not adjust the model parameters to obtain a quantitative fit of our data. In the following, we will show that despite these differences in properties between HS-cells and the V1-cell, the model can account for our major findings on changes in directionality induced by motion adaptation.

The predicted effect of motion adaptation, when taking the 'Harris components' into account, is not only a reduction of the response magnitude, but also a change in the relative sensitivity for vertical and for horizontal motion of the V1-cell (see Figs. 2B and 3A, dashed lines): in our model prediction with the first stimulation protocol a strong shift of the directionality vector of the example cell towards vertical motion sensitivity is induced by vertical adaptation (see Fig. 2B, dashed black line) and a weak shift in the same direction is induced by horizontal adaptation (see Fig. 2B, dashed gray line). In contrast, an increased sensitivity for horizontal motion relative to vertical motion is predicted for the neuron stimulated according to the second protocol (see Fig. 3A, dashed black and gray lines). In both cases, the directions of the predicted shifts of directionality vectors are in accordance with the experimentally observed shifts. This observation is corroborated by the similarity of the adaptation-induced changes in directionality between experimental data and model predictions for the entire cell samples analyzed with the two stimulation protocols: although there are quantitative differences, both the experimentally measured and the predicted vectors shift towards the same direction after both horizontal and vertical motion adaptation (cf. Fig. 2C with Fig. 4A and Fig. 3B with Fig. 4B). Thus, our data reveal that even without postulating a new component of adaptation that explicitly changes direction sensitivity, the changes in contrast sensitivity with motion adaptation can induce profound changes in directional sensitivities.

Why do the 'Harris components' of motion adaptation affect the directional sensitivity of the V1-cell although they are at first sight *not* expected to change the relationship between

Table 1
Mean spike rates (± standard deviation) during stimulation of V1-neurons with the two adaptation protocols, which differed in the contrasts of the moving grating patterns

Condition	Ref	Adapt	Test
1st adaptation protocol (n = 9)			
rv-av-tv	rv = 196 ± 36	av = 186 ± 41	tv = 100 ± 58
rh-av-th	rh = 57 ± 23	av = 189 ± 37	th = 19 ± 14
rv-ah-tv	rv = 194 ± 35	ah = 34 ± 15	tv = 129 ± 39
rh-ah-th	rh = 58 ± 27	ah = 35 ± 13	th = 22 ± 11
2nd adaptation protocol (n = 8)			
rv-av-tv	rv = 92 ± 33	av = 167 ± 43	tv = 10 ± 9
rh-av-th	rh = 53 ± 23	av = 167 ± 40	th = 17 ± 11
rv-ah-tv	rv = 87 ± 26	ah = 26 ± 16	tv = 22 ± 11
rh-ah-th	rh = 48 ± 23	ah = 48 ± 12	th = 24 ± 11

In the first protocol the contrast of reference and test stimuli was 0.20. In the second protocol the contrast of reference and test stimuli was 0.06 when moving in vertical direction, but 0.53 when moving in horizontal direction. The contrast of the adapting stimuli was 0.53 in all cases. Mean spike frequencies were averaged over the entire period of 1 s for reference and test stimuli and 8 s for adapting stimuli. See Section 2 for details. Use of abbreviations as in Fig. 2.

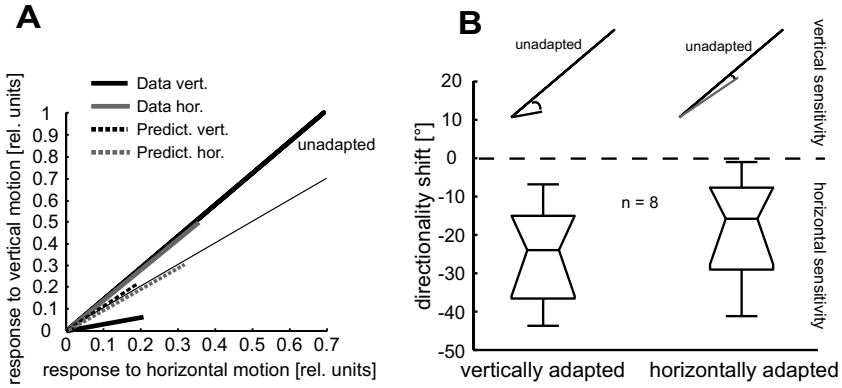

Fig. 3. Effects of motion adaptation on measured directional sensitivity of 8 V1-cells using the second adaptation protocol. The contrast of horizontal reference and test motion was higher than that of vertical motion. Data were analyzed as described in Fig. 2. (A) Directionality vectors of an example V1-cell. Line styles as in Fig. 2. (B) Population data showing the experimentally determined directionality shifts after vertical and after horizontal motion adaptation. In general, the directionality of the V1-cell shifted towards horizontal sensitivity in both adaptation conditions.

horizontal and vertical responsiveness (see Fig. 5)? The reason for this effect is the subtractive nature of one of the three 'Harris components' (see Section 2): because of its mainly downward preferred direction the V1-cell responds stronger to vertical motion than to horizontal motion. The generally weaker horizontal test response is relatively more affected by the subtractive shift than the stronger vertical one, because the same value is subtracted from the vertical and the horizontal

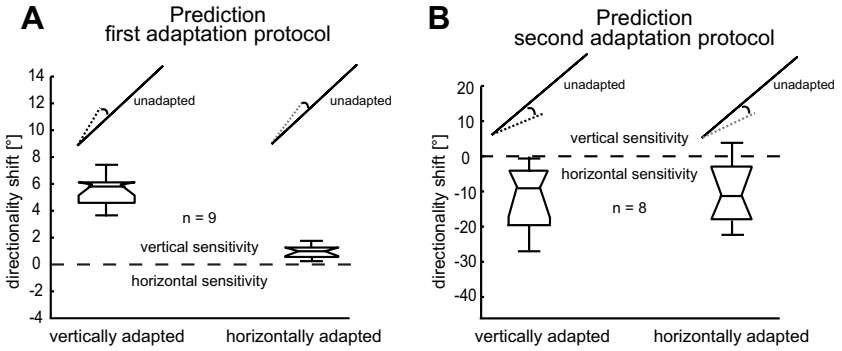

Fig. 4. Predicted shifts in directionality of V1-cells analyzed with the first (A) and the second (B) adaptation protocol. The shifts are qualitatively similar to the experimentally observed shifts. Predictions are based on a simple adaptation model (see Section 2 for details) incorporating only adaptation components underlying the reduced contrast sensitivity reported by Harris et al. (2000). Data presentation as in Figs. 2C and 3B.

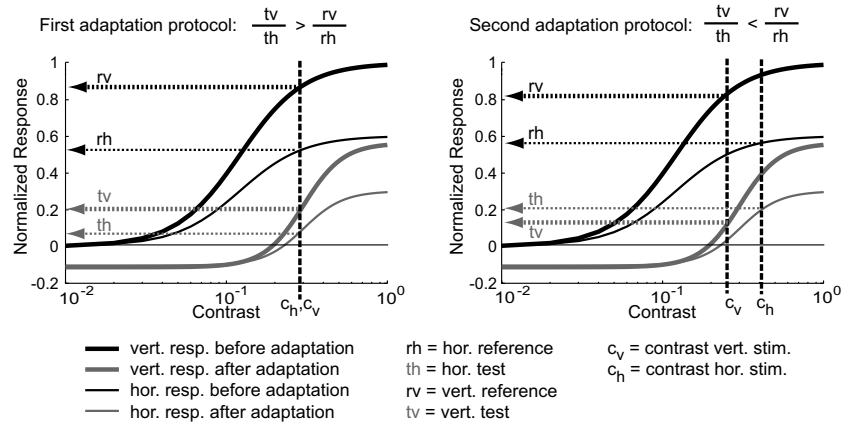

Fig. 5. Scheme illustrating how changes in contrast sensitivity with motion adaptation as reported by Harris et al. (2000) can induce shifts in directionality. In the first adaptation protocol the same contrast was used for all reference and test stimuli. The vertical-to-horizontal response ratio increased with adaptation. In the second adaptation protocol the contrast of vertical reference and test stimuli was higher than that of horizontal reference and test stimuli. In this case, the vertical-to-horizontal response ratio decreased with adaptation. See main text for details.

response. This effect is particularly strong with the first stimulation protocol. As a consequence, the ratio between vertical and horizontal motion sensitivity changes towards vertical motion (see Fig. 2C). The change in directional sensitivity towards horizontal motion responsiveness observed with the second stimulation protocol (see Fig. 3B) can, although surprising at first sight, also be explained when considering the components contributing to the reduced contrast sensitivity after motion adaptation (Harris et al., 2000; Section 2): the lateral shift in the contrast–response function can be expected to affect the response to the weak-contrast vertical stimulus more than the response to the high-contrast horizontal stimulus (see Fig. 5). Thus, the directional sensitivity will change towards an increased sensitivity for horizontal motion relative to vertical motion.

All in all, the previously described changes in contrast sensitivity with motion adaptation seem to have the potential to induce strong changes of the directionality of fly motion-sensitive neurons. This unexpected finding allows us to explain experimentally observed changes in directional sensitivity after motion adaptation in a parsimonious way.

4. Discussion

We demonstrated that motion adaptation changes the directional sensitivity of the V1-cell, a motion-sensitive neuron in the fly brain. Surprisingly, opposite changes in directional sensitivity can occur in one and the same neuron. Depending on stimulus parameters responses to test stimuli moving in the same direction as the adaptor were either attenuated or enhanced relative to the responses to test stimuli moving orthogonally with respect to the adapted direction.

Since we determined the direction of a shift from the measurement of only two directions of motion two possible changes in the direction tuning curves can account for the measured shifts: first, a sideward shift of the tuning curve and a resulting change in the neuron's preferred direction and, second, an up- or downward shift of the tuning curve. The latter effect can in principle also lead to a change in the ratio between the responses to two different motion directions without changing the neuron's preferred direction. Which of these two explanations applies to the adaptation-induced change in directional sensitivity in the V1-neuron can only be assessed in future experiments by measuring responses of the V1-neuron to a larger spectrum of motion directions. Nevertheless our results might show parallels to results obtained from different types of cortical neurons. Here, depending on the brain area, either relative enhancements or relative attenuations of neuronal responses to stimuli moving in the same direction as the adaptor have been reported (Kohn & Movshon, 2004; Tolias, Keliris, Smirnakis, & Logothetis, 2005).

4.1. Model explanation of adaptation-induced changes in the relative sensitivity for different motion directions

Surprisingly, we could reproduce in a qualitative way the major effects of motion adaptation on the directional sensitivity of V1-cells with a general model of TC adaptation, which solely included the components underlying contrast sensitivity reduction (Harris et al., 2000). Thus, the previously described phenomena underlying contrast sensitivity reduction in fly motion adaptation bear the potential to change the directional sensitivity of the V1-neuron. Similar adaptation-induced changes of contrast–response functions have been demonstrated in neurons in the visual cortex (Carandini & Ferster, 1997; Crowder et al., 2006; Ohzawa et al., 1982). Consequently, the possibility has to be considered that changes in directional sensitivity in these neurons also result from contrast adaptation.

The first set of experiments in our study (see Fig. 2) demonstrated a strong impact of one of the previously identified mechanisms reducing the contrast sensitivity of adapted TCs, namely the subtractive shift in the response function (Harris et al., 2000). The subtractive shift is caused by an excitation-dependent hyperpolarization and is therefore mainly elicited by preferred direction motion. The influence of the subtractive shift on directional sensitivity, in spite of the fact that it affects test stimuli moving in any direction, can be explained by a differential effect on strong and weak response magnitudes: since the V1-cell is a predominantly vertical motion sensitive element, it responds weaker to horizontal than to vertical motion. Thus, the weaker horizontal test responses were more affected by the subtractive shift than the corresponding vertical responses. As a consequence, the ratio of the cells' overall motion sensitivity changed towards vertical sensitivity irrespective of the adapting motion direction (see Fig. 5).

In a second set of experiments, we tried to equalize the horizontal and vertical motion-induced responses by reducing the contrast of the vertical stimulus (see Fig. 3). As a consequence, motion adaptation led to an increased horizontal motion sensitivity of adapted V1-cells, regardless of the motion direction during the adaptation period. Here, the directional sensitivities were mainly influenced by the lateral shift of the contrast–response functions of TCs with adaptation: the responses to the weak-contrast vertical test stimulus were more affected than those to the corresponding high-contrast horizontal motion stimulus. The stronger reduction of vertical motion responses both after horizontal and after vertical motion adaptation changed the response ratios towards horizontal motion sensitivity (see Fig. 5).

The major conclusions obtained from the two sets of experiments were reproduced by a simple, general model of adaptation in TCs although this model is based on adaptation of graded-potential TCs in *Eristalis tenax*, a hoverfly species. Moreover, a correspondence between the model predictions and our main experimental findings was given despite the fact that this model was not specifically fitted to the adaptation properties of the V1-cell. A more specific model incorporating actual contrast–response functions of V1-cells might lead to a quantitatively much closer fit of our experimental data. However, there is no reason to believe that contrast–response functions and their adaptation differ significantly between different fly species and between different types of TCs. First, the unadapted contrast–response function of HS-neurons is similar in *Eristalis* (Harris et al., 2000) and *Calliphora* (Egelhaaf & Borst, 1989). Second, experiments with *Drosophila* mutants in which specific types of neurons in the lamina, a neuropile upstream of TCs, were rendered non-functional (Rister et al., 2007) suggest that contrast sensitivity in the motion pathway is to a large extent shaped peripheral to TCs rather than in individual TCs themselves. It is therefore plausible to assume that different TCs have similar contrast sensitivity. Moreover, HS-neurons and neurons of the Vertical System (VS), the latter of which provide input to the V1-cell, have been shown to be very similar in their biophysical properties (Haag, Theunissen, & Borst, 1997). And finally, signal transfer from VS-cells to the V1-cell has been shown to operate linearly during excitatory stimulation (Kurtz et al., 2001; Warzecha et al., 2003; Beckers, Egelhaaf, & Kurtz, 2007), which was the only type of stimulation used in the present study. Nevertheless, it has to be considered that in contrast to graded-potential HS- and VS-cells the response properties of the V1-cell are affected by the spike threshold non-linearity. A spike threshold might limit the influence of the adaptation-induced subtractive shift in the contrast–response function when the responses are small. Thus,

with our model we might have overestimated the influence of the subtractive shift on the directional sensitivity of the V1-neuron. We therefore did not expect this simple model to reproduce our experimental data in a quantitative way. However, as a purely phenomenological model it allowed us to highlight general principles of how the adaptation-induced changes in directional sensitivity of the V1-neuron, which seem counterintuitive at first sight, can be explained in a parsimonious way. In this sense our model was successful, because principal experimental findings were reproduced without the need to introduce new adaptation components.

4.2. Relation to previous studies on motion adaptation in fly TCs

At first sight our results seem to be in contrast to those of Neri and Laughlin (2005), who also tested directional tuning of the V1-cell before and after adaptation with vertical motion. In their study significant changes in directional gain (i.e., in the modulation depth of the direction tuning curve), but no prominent changes in the peak location of directional tuning curves were found. The seemingly conflicting results can be reconciled in the following way: Neri and Laughlin (2005) observed a decrease in directional gain after local adaptation within a small circular region located centrally within the large receptive field of the V1-cell. This gain reduction would express itself as a relative enhancement of the responses to horizontal motion relative to vertical motion, as we found with our second experimental protocol irrespective of the direction of adapting motion. However, a more specific comparison of our results with those of Neri and Laughlin (2005) is difficult, because horizontally moving adaptors were not tested in the latter study and because stimulus area and contrast differ considerably between the two studies. In a recent study, Neri (2007) demonstrated that the directional tuning of the V1-cell shifts away from the adapting direction, again using stimulation within small patches. This effect was a fast-scale adaptive effect, building up after only 220 ms of stimulation. Although this effect is likely to contribute to the long-term effects demonstrated in our study, we did not isolate it with our protocol, using adapting stimuli of several seconds duration and quantifying responses within time windows of one second.

4.3. Functional significance of adaptation-induced changes in directional sensitivity

We have shown that the history of previous motion stimuli can influence the directional sensitivity of the V1-cell. In principle, directionality-changing adaptation might help motion-sensitive neurons to selectively decrease their sensitivity to ongoing motion in one direction, but at the same time to remain sensitive to motion in other directions. This ability could allow a motion-sensitive neuron to detect disturbances within temporally continuous optic flow patterns, as might be elicited by a sudden change in flight trajectory or by the approach of objects in the environment. The V1-neuron has indeed been found to code certain stimulus properties with a remarkable robustness against superposition with other stimuli (Karmeier et al., 2003). Similarly, Dragoi et al. (2002) suggested that the adaptation-induced shifts of preferred orientation away from the adapting orientation found in orientation selective neurons in the primary visual cortex might help these neurons to enhance their ability to discriminate different pattern orientations. Fast-scale adaptation of direction tuning similar to that found in the V1-cell (Neri, 2007) has been interpreted to enhance the sensitivity for sudden changes in motion direction in area MT neurons of monkeys, because their responsiveness to preferred direction motion was enhanced immediately after presentation of motion in non-preferred direction (Perge et al., 2005).

Our data clearly demonstrate that the overall effect of motion adaptation on the directional sensitivity of the V1-cell can be opposite to a relative enhancement of responses to stimuli moving in directions other than the adaptor: in the V1-cell the relative directional sensitivity changed in the same way, irrespective of the motion direction during adaptation. It is unclear whether in the V1-cell a functional benefit results from adaptation with respect to the plasticity of directional tuning.

References

Beckers, U., Egelhaaf, M., & Kurtz, R. (2007). Synapses in the fly motion-vision pathway: Evidence for a broad range of signal amplitudes and dynamics. *Journal of Neurophysiology, 97*, 2032–2041.

Borst, A., & Haag, J. (2002). Neural networks in the cockpit of the fly. *Journal of Comparative Physiology [A], 188*, 419–437.

Carandini, M., & Ferster, D. (1997). A tonic hyperpolarization underlying contrast adaptation in cat visual cortex. *Science, 276*, 949–952.

Clifford, C. W., & Ibbotson, M. R. (2002). Fundamental mechanisms of visual motion detection: Models, cells and functions. *Progress in Neurobiology, 68*, 409–437.

Crowder, N. A., Price, N. S. C., Hietanen, M. A., Dreher, B., Clifford, C. W. G., & Ibbotson, M. R. (2006). Relationship between contrast adaptation and orientation tuning in V1 and V2 of cat visual cortex. *Journal of Neurophysiology, 95*, 271–283.

Dragoi, V., Rivadulla, C., & Sur, M. (2001). Foci of orientation plasticity in visual cortex. *Nature, 411*, 80–86.

Dragoi, V., Sharma, J., Miller, E. K., & Sur, M. (2002). Dynamics of neuronal sensitivity in visual cortex and local feature discrimination. *Nature Neuroscience, 5*, 883–891.

Dragoi, V., Sharma, J., & Sur, M. (2000). Adaptation-induced plasticity of orientation tuning in adult visual cortex. *Neuron, 28*, 287–298.

Egelhaaf, M., & Borst, A. (1989). Transient and steady-state response properties of movement detectors. *Journal of the Optical Society of America A, 6*, 116–127.

Egelhaaf, M., Kern, R., Krapp, H. G., Kretzberg, J., Kurtz, R., & Warzecha, A.-K. (2002). Neural encoding of behaviourally relevant visual-motion information in the fly. *Trends in Neuroscience, 25*, 96–102.

Franceschini, N. (1975). Sampling of visual environment by the compound eye of the fly: Fundamentals and applications. In A. W. Snyder & R. Menzel (Eds.), *Photoreceptor Optics* (pp. 98–125). New York: Springer.

Haag, J., & Borst, A. (2004). Neural mechanisms underlying complex receptive field properties of motion-sensitive interneurons. *Nature Neuroscience, 7*, 628–634.

Haag, J., Theunissen, F., & Borst, A. (1997). The intrinsic electrophysiological characteristics of fly lobula plate tangential cells: II. Active membrane properties. *Journal of Computational Neuroscience, 4*, 349–369.

Hammond, P., Mouat, G. S., & Smith, A. T. (1985). Motion after-effects in cat striate cortex elicited by moving gratings. *Experimental Brain Research, 60*, 411–416.

Harris, R. A., O'Carroll, D. C., & Laughlin, S. B. (2000). Contrast gain reduction in fly motion adaptation. *Neuron, 28*, 595–606.

Hausen, K. (1976). Functional characterization and anatomical identification of motion sensitive neurons in the lobula plate of the blowfly *Calliphora erythrocephala*. *Zeitschrift für Naturforschung, 31c*, 629–633.

Kalb, J., Egelhaaf, M., & Kurtz, R. (2006). Robust integration of motion information in the fly visual system revealed by single cell photoablation. *Journal of Neuroscience, 26*, 7898–7906.

Karmeier, K., Krapp, H. G., & Egelhaaf, M. (2003). Robustness of the tuning of fly visual interneurons to rotatory optic flow. *Journal of Neurophysiology, 90*, 1626–1634.

Kohn, A., & Movshon, J. A. (2004). Adaptation changes the direction tuning of macaque MT neurons. *Nature Neuroscience, 7*, 764–772.

Krapp, H. G., Hengstenberg, R., & Egelhaaf, M. (2001). Binocular contributions to optic flow processing in the fly visual system. *Journal of Neurophysiology, 85*, 724–734.

Krapp, H. G., Hengstenberg, B., & Hengstenberg, R. (1998). Dendritic structure and receptive-field organization of optic flow processing interneurons in the fly. *Journal of Neurophysiology, 79*, 1902–1917.

Kurtz, R., Dürr, V., & Egelhaaf, M. (2000). Dendritic calcium accumulation associated with direction-selective adaptation in visual motion-sensitive neurons in vivo. *Journal of Neurophysiology, 84*, 1914–1923.

Kurtz, R., Warzecha, A.-K., & Egelhaaf, M. (2001). Transfer of visual motion information via graded synapses operates linearly in the natural activity range. *Journal of Neuroscience, 21*, 6957–6966.

Maddess, T., & Laughlin, S. B. (1985). Adaptation of the motion-sensitive neuron H1 is generated locally and governed by contrast frequency. *Proceedings of the Royal Society B, 228*, 251–275.

Neri, P. (2007). Fast-scale adaptive changes of directional tuning in fly tangential cells are explained by a static nonlinearity. *Journal of Experimental Biology, 210*, 3199–3208.

Neri, P., & Laughlin, S. B. (2005). Global versus local adaptation in fly motion-sensitive neurons. *Proceedings of the Royal Society B, 272*, 2243–2249.

Ohzawa, I., Sclar, G., & Freeman, R. D. (1982). Contrast gain control in the visual cortex. *Nature, 298*, 266–268.

Perge, J. A., Borghuis, B. G., Bours, R. J. E., Lankheet, M. J. M., & van Wezel, R. J. A. (2005). Temporal dynamics of direction tuning in motion-sensitive macaque area MT. *Journal of Neurophysiology, 93*, 2104–2116.

Rister, J., Pauls, D., Schnell, B., Ting, C. Y., Lee, C. H., Sinakevitch, I., et al. (2007). Dissection of the peripheral motion channel in the visual system of *Drosophila melanogaster*. *Neuron, 56*, 155–170.

Tolias, A. S., Keliris, G. A., Smirnakis, S. M., & Logothetis, N. K. (2005). Neurons in macaque area V4 acquire directional tuning after adaptation to motion stimuli. *Nature Neuroscience, 8*, 591–593.

Van Wezel, R. J., & Britten, K. H. (2002). Motion adaptation in area MT. *Journal of Neurophysiology, 88*, 3469–3476.

Warzecha, A.-K., Kurtz, R., & Egelhaaf, M. (2003). Synaptic transfer of dynamic motion information between identified neurons in the visual system of the blowfly. *Neuroscience, 119*, 1103–1112.