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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).

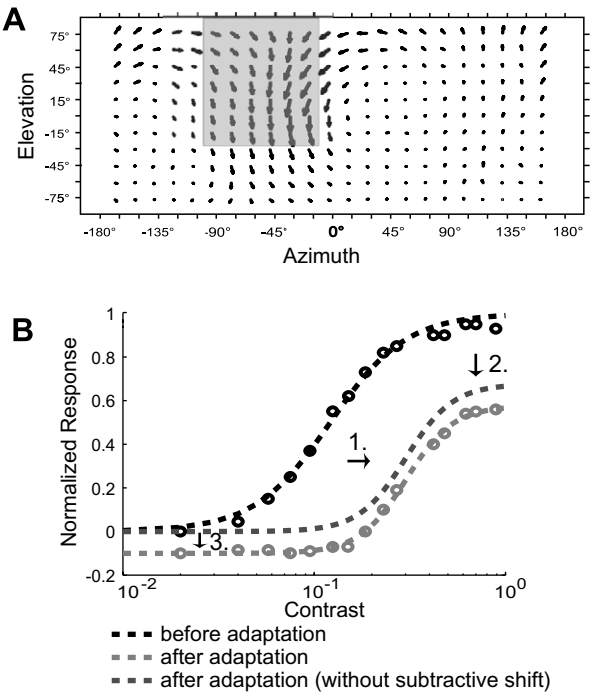

Fig. 1. (A) Reproduction of receptive field profile of the V1-cell determined by the analysis of local visual motion sensitivities by Karmeier et al. (2003). Each arrow indicates the preferred direction of motion at a particular position within the visual field of the fly. Arrow lengths show the normalized 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.