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J Neurophysiol 103:2642-2651, 2010. First published 6 January 2010; doi:10.1152/jn.00591.2009

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Submitted 10 July 2009; accepted in final form 1 January 2010

van Kleef JP, Stange G, Ibbotson MR. Applicability of white-noise techniques to analyzing motion responses. *J Neurophysiol* 103: 2642–2651, 2010. First published January 6, 2010; doi:10.1152/jn.00591.2009. Motion processing in visual neurons is often understood in terms of how they integrate light stimuli in space and time. These integrative properties, known as the spatiotemporal receptive fields (STRFs), are sometimes obtained using white-noise techniques where a continuous random contrast sequence is delivered to each spatial location within the cell's field of view. In contrast, motion stimuli such as moving bars are usually presented intermittently. Here we compare the STRF prediction of a neuron's response to a moving bar with the measured response in second-order interneurons (L-neurons) of dragonfly ocelli (simple eyes). These low-latency neurons transmit sudden changes in intensity and motion information to mediate flight and gaze stabilization reflexes. A white-noise analysis is made of the responses of L-neurons to random bar stimuli delivered either every frame (densely) or intermittently (sparsely) with a temporal sequence matched to the bar motion stimulus. Linear STRFs estimated using the sparse stimulus were significantly better at predicting the responses to moving bars than the STRFs estimated using a traditional dense white-noise stimulus, even when second-order nonlinear terms were added. Our results strongly suggest that visual adaptation significantly modifies the linear STRF properties of L-neurons in dragonfly ocelli during dense white-noise stimulation. We discuss the ability to predict the responses of visual neurons to arbitrary stimuli based on white-noise analysis. We also discuss the likely functional advantages that adaptive receptive field structures provide for stabilizing attitude during hover and forward flight in dragonflies.

INTRODUCTION

It has long been the goal of vision science to establish the neural mechanisms that lead to visual motion detection (Exner 1894; Reichardt 1961; for reviews: Borst and Egelhaaf 1989; Clifford and Ibbotson 2003). Many systems have been examined such as the mammalian retina (Barlow and Levick 1965), subcortical visual pathways (Ibbotson and Clifford 2001), and visual cortex (Hubel and Wiesel 1959) along with various insect visual neurons (Egelhaaf and Borst 1993; Hausen 1982; Ibbotson 1991; McCann 1973; Olberg 1981). The focus for most of these studies has been the basic structure of the direction-selective neural circuits. One approach is to use nonmotion stimuli to map how a neuron integrates the contrast sequences presented to it in space and time. These maps, known as spatiotemporal receptive fields (STRFs), can then be used to predict the response to a moving stimulus, and therefore the motion processing ability of the neuron can be understood in terms of its STRF. The STRF structure can be compared, for example, to those employed by phenomenolog-

ical models of motion detection (Adelson and Bergen 1985; Hassenstein and Reichardt 1956; van Santen and Sperling 1985; Watson and Ahmuda 1985).

A stimulus occasionally used to estimate the STRFs of neurons is composed of randomly chosen contrast stimuli presented at many locations within a neuron's receptive field. Each of the stimuli can be dark, bright, or at the mean luminance of the stimulus. Mathematical techniques such as reverse correlation are then used to estimate the linear and nonlinear components of the recorded cell's STRF. This method is broadly termed white-noise analysis (DeAngelis et al. 1993; Emerson et al. 1992; Jones and Palmer 1987; Livingston and Conway 2003, 2007; Marmarelis and McCann 1973; Marmarelis and Naka 1972; McCann 1974; Rust et al. 2005; Touryan et al. 2005; van Kleef et al. 2005, 2008). Using these methods the linear and nonlinear components of a neuron's STRF can be evaluated.

There are several issues related to using white-noise analysis for analyzing motion responses. White-noise analyses assume that STRFs are time invariant, i.e., it is assumed that given the STRF properties of a visual neuron measured using a white-noise stimulus the response to an arbitrary stimulus (e.g., a moving black bar) can be predicted (Wu et al. 2006). This is rarely the case because most visual neurons dynamically change their response properties depending on the stimulus (adaptation) and therefore modify the computational mechanisms that underlie motion detection (Harris et al. 2000; Ibbotson and Clifford 2001; Kalb et al. 2008; Maddess and Laughlin 1985). One way of accounting for adaptation is to use a restricted random stimulus that samples only a component of the stimulus space but the adaptation properties of which can be matched to the motion stimulus of interest (Ringach et al. 1997; Touryan and Dan 2001; Walker et al. 1999). Another problem associated with white-noise analysis is that higher-order nonlinearities are difficult to estimate due to experimental or computational limitations, and in cases where the predictions do not match the responses, it has been suggested that the presence of nonlinearities is the reason for the discrepancies. Certainly various nonlinearities have been previously suggested to underlie directional computations in biological systems (Barlow and Levick 1965; Hassenstein and Reichardt 1956).

Here we sought to establish the relative contribution of adaptation and nonlinearities in modifying the motion response properties of L-neurons in the dragonfly ocelli (simple eyes) (Berry et al. 2006, 2007). Ocelli aid the dragonfly in stabilizing its flight by mediating low-latency head, wing, and body reflexes. The graded responses of ocellar L-neurons have been found to signal fast changes in light intensity around the horizon (Berry et al. 2006, 2007; Chappell and Dowling 1972).

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L-neurons are also directionally selective to moving bars and gratings, an ability that is dependent on the presence of UV light (van Kleef et al. 2008). L-neurons in the dragonfly were selected for the study because the linear STRF maps of L-neurons have been found to adequately predict the responses of the cells to slowly moving patterns (van Kleef et al. 2008). However, as is the case in many motion-sensitive neurons in insects (Ibbotson 2001), L-neurons are sensitive to very high speeds ($>1000^\circ/\text{s}$). At high image velocities, the linear predictions of the STRFs were very poor (van Kleef et al. 2008) for which there are two possible reasons. The first is that L-neuron responses might contain nonlinearities that become significant for very fast moving stimuli. A second explanation is that the STRF structure of L-neurons is fundamentally different during exposure to an infrequently presented bar stimulus compared with exposure to a continuously presented pseudorandom white-noise pattern.

Here we show that the addition of nonlinear terms to our STRF model does not account for the responses to single bars moving at high speed. These bars take 19.2 ms to traverse the display and are interspersed with constant luminance of 1-s duration. Given this, a random bar stimulus was created that matches the spatial and temporal characteristics of the moving bar stimulus. This random stimulus produces a state of visual adaptation in L-neurons similar to that produced by a moving bar stimulus while allowing us to measure their STRFs. The STRFs obtained using this stimulus were significantly better at predicting the L-neuron responses to moving bars than the STRFs obtained using a standard dense stimulus. We conclude that L-neuron STRFs are dependent on the stimulus history and therefore those obtained from dense white-noise analysis are unsuitable for predicting responses to motion. This may also be the case in other analyses of motion processing visual systems where the statistical properties of the stimulus used to measure the STRFs are not closely matched to the motion stimulus and therefore our results have wider significance (Carandini et al. 2005). We also provide a functional interpretation of these findings in terms of dragonfly behavior.

METHODS

Animal preparation and intracellular recordings

Animals were obtained, mounted before the display, and recorded from as described in previous studies (Berry et al. 2006; van Kleef et al. 2008). Intracellular recordings were obtained from median ocellar L-neurons that produced responses of >10 mV to a flash of bright light, consistent with previous recordings of dragonfly L-neurons (Berry et al. 2006; Chappell and Dowling 1972; Simmons 1982). A total of 46 cells were recorded: 37 were presented with upward and downward moving negative and positive contrast bars, 23 of those were separately shown pseudorandom UV and green contrast patterns, while 23 were shown separately sparse and dense UV contrast patterns.

LED display

The LED display consisted of an array of 12×9 pairs of UV ($\lambda_{\text{max}} = 383$ nm) and green ($\lambda_{\text{max}} = 528$ nm) light-emitting diodes (LEDs) mounted on a hemisphere. LEDs were refreshed independently at a rate of 625 Hz (for details, see Berry et al. 2006). We estimated that at the center where the ocellus is mounted, each UV LED produced a maximum flux of $\sim 1.2 \times 10^{14}$ photons $\text{cm}^{-2}\text{s}^{-1}$, and each green LED produced a maximum flux of $\sim 0.9 \times 10^{14}$ photons $\text{cm}^{-2}\text{s}^{-1}$. Both UV

and green LEDs were circular with diameters of 2.7° . These were centered at intervals of 6° in elevation and 12° in azimuth, a resolution sufficient to sample the average ocellar photoreceptor, the spatial sensitivity functions of which have full-width at half-maximum of 15° in elevation and 30° in azimuth (Van Kleef et al. 2005). The display has a range of -33 – 33° in elevation and -48 – 48° in azimuth. The display was centered on the median ocellus such that the optical axis of the eye lies at zero elevation.

Directional stimuli and directional index

Directional stimuli were restricted to UV bars moved up and down at 3,750°/s (van Kleef et al. 2008). For these stimuli, the responses of L-neurons is poorly predicted by their linear STRFs (van Kleef et al. 2008). Bars were 6° wide and either positive contrast (+0.82) or negative contrast (−0.82) using UV LEDs. Directional selectivity of the responses to bars was assessed using the directional index (DI) defined as $\text{DI} = (r_u - r_d)/(r_u + r_d)$ where r_u and r_d are the peak-to-peak responses to an upward moving bar and downward moving bar, respectively (Jagadeesh et al. 1993; Livingston and Conway 2003; van Kleef et al. 2008).

Pseudorandom stimuli

Two types of pseudorandom stimuli were used. The first was a white-noise stimulus, termed a dense stimulus, and consisted of a sequence of UV or green contrasts at each point of elevation $[\theta_i = -33^\circ + (i - 1) \cdot 6^\circ, \text{ for } i = 1, 2, \dots, 12]$ and at times $t_n = n\Delta t$ where $\Delta t = 1.6$ ms and $n = 0, \dots, 24,511$. The contrast value $c(\theta_i, t_n)$ at each elevation θ_i and time t_n is defined in terms of the light intensity at that point $I(\theta_i, t_n)$ and the time-averaged intensity at the same elevation $\bar{I}(\theta_i)$ by the equation $c(\theta_i, t_n) = [I(\theta_i, t_n) - \bar{I}(\theta_i)]/\bar{I}(\theta_i)$. Contrasts were selected with equal probability in the range ± 0.82 (variance, 0.22). Contrast sequences from any two spatial locations were statistically independent. Although this stimulus is called a white-noise stimulus it is only “white” over the bandwidth of the display which ranges from 0 to 322.5 Hz. By restricting the stimulus space to a particular range of stimuli, the estimation times are also kept within practical limits.

The second type of stimulus, termed sparse, was designed to match the bar stimulus in power and sparseness and was composed entirely of either positive or negative contrasts. It consisted of short “pulses” separated by 1,000 ms of mean luminance. Each “pulse” consisted of 12 contrasts equal in magnitude to the moving bar contrast (0.82) and presented in random order at each point of elevation. Each contrast is displayed for 1.6 ms, and therefore it takes 19.2 ms to display a complete pulse that covers all spatial locations. Locations were chosen with equal probability, and, as with the dense stimulus, contrast sequences from two different locations were statistically independent. The complete stimulus included 50 pulses. The dense and sparse stimuli therefore differ in their spatial and temporal characteristics. In the case of the sparse stimulus, only one spatial location is stimulated at any time with a single 1.6-ms bar stimulus, whereas for the dense stimulus, every point in the receptive field is simultaneously stimulated with white noise. During the sparse stimulus, the neuron is stimulated during short pulses, while it is continuously stimulated for the dense stimulus.

Model estimation

A Wiener kernel model (Wiener 1958) of second-order was used to describe the relationship between the measured L-neuron response $y(t_n)$ (mV) and its contrast inputs. Wiener kernel models encompass a general class of time-invariant nonlinear model. Their parameters can be efficiently estimated using multiple linear regression (James 2003; van Kleef et al. 2005, 2008). While a general Wiener model includes terms of all orders, the more terms that are included the longer the

sequence required to estimate the kernels. Therefore in practice, the number of Wiener terms estimated is truncated to produce smaller required recording times. Here we restricted our analysis to the first- and second-order kernels (linear and nonlinear STRFs) (van Kleef et al. 2005). Terms were added to the model to remove slow drifts in the mean potential over the 40-s recording interval and sinusoidal signals with frequencies of 50 Hz (the frequency of mains power supply in our laboratory). Although the addition of these trend terms does not significantly alter the kernels, it significantly reduces the error estimates for some cells (van Kleef et al. 2008). The relationship between the L-neuron response $y(t_n)$ (mV) and its contrast inputs is modeled by the equation

$$y(t_n) = f_1(t_n) + f_2(t_n) + f_d(t_n) + \varepsilon(t_n) \quad (1)$$

where the linear term f_1 is given by

$$f_1(t_n) = \sum_{m=1}^M \sum_{i=1}^{12} h_1(\theta_i, \tau_m) c(\theta_i, t_n - \tau_m) \quad (2)$$

the second-order term f_2 is given by

$$f_2(t_n) = \sum_{i=1}^{12} \sum_{j=1}^{12} \sum_{m=1}^M \sum_{p=1}^M h_2(\theta_i, \theta_j, \tau_m, \tau_p) [c(\theta_i, t_n - \tau_m) c(\theta_j, t_n - \tau_p) - V_c \delta(\theta_i - \theta_j, \tau_m - \tau_p)] \quad (3)$$

the term f_d represents the trend (modeled as a 4th-order polynomial in time and 50-Hz sinusoidal and cosinusoidal functions) and the term $\varepsilon(t_n)$ represents the remaining noise.

The quantity $h_1(\theta_i, \tau_m)$ is the first-order Wiener kernel (or linear STRF) that describes the linear relationship between the response y at time t_n and the contrast inputs at each elevation θ_i for previous times $t_n - \tau_1, t_n - \tau_2, \dots, t_n - \tau_M$ where τ_M is the memory of the kernel.

The second-order Wiener kernel, $h_2(\theta_i, \theta_j, \tau_m, \tau_p)$ (which in this study is the nonlinear STRF) describes the nonlinear relationship between the response y at time t_n and the two contrast inputs at times $t_n - \tau_m$ and $t_n - \tau_p$, either at the same spatial location ($\theta_i = \theta_j$) or at different locations ($\theta_i \neq \theta_j$). The term $-V_c \delta(\theta_i - \theta_j, \tau_m - \tau_p)$ subtracts the variance of the stimulus at points in the summation where $\tau_m = \tau_p$ and $\theta_i = \theta_j$ and is otherwise zero.

For each trial, h_1 and h_2 were obtained by fitting the recorded $y(t_n)$ to Eqs. 1–3 using multiple linear regression, and the predictive capacity of the model was evaluated using cross-validation methods as described previously (Berry et al. 2006, 2007; James 2003; van Kleef et al. 2005, 2008). In brief, the trend (f_d) is subtracted from the measured data to obtain the detrended measured data $y_d(t_n)$. The predicted response $y_p(t_n)$ was obtained by taking the mean of $f_1(t_n) + f_2(t_n)$ from all but one trial (usually 4 of 5), and this prediction was then compared with the remaining trial. Thus trials used to estimate both h_1 and h_2 , were separated from those used to test their predictive capacity. The percentage mean squared prediction error (%MSPE) was used as a measure of this predictive capacity. It is reported as a percentage of the signal power of the detrended measured data and defined as (Berry et al. 2006; Juusola et al. 2003; van Kleef et al. 2005, 2008)

$$\% \text{MSPE} = 100 \times \frac{\overline{(y_p(t_n) - y_d(t_n))^2}}{\overline{(y_d(t_n) - \bar{y}_d(t_n))^2}} \quad (4)$$

where the bar represents the temporal mean. Note that the %MSPE, although greater than or equal to zero, can be >100%. For example, in the case when $y_p(t_n) = -y_d(t_n)$ and $\bar{y}_d(t_n) = 0$ the %MSPE is 400%.

A similar error function is used to quantify the error in the Wiener kernel prediction of the response to moving bars. The formula is the same as in Eq. 4, but $y_p(t_n)$ is obtained using the mean of the $f_1(t_n) + f_2(t_n)$ from all trials, and $y_d(t_n)$ is the mean of measured responses (usually 2 trials) to a moving negative or positive contrast bar.

Receptive field characteristics

Estimates of the spatial $S(\theta_i)$ and temporal $T(\tau_m)$ components of the STRF such that $h_1(\theta_i, \tau_m) = S(\theta_i)T(\tau_m)$ were obtained using singular value decomposition (Depireux et al. 2001; van Kleef et al. 2008). The maximum value of $T(\tau_m)$ was then used to estimate the time to peak and first zero crossing after the peak and $S(\theta_i)$ was used to estimate the full width at half the maximum response (FWHM).

Statistics

The normality of sample distributions was tested using Lilliefors' test. If this was applicable at an alpha of 5%, the unpaired two-tailed Student *t*-test was used to compare the sample distribution against single values and a two-tailed paired *t*-test to compare two distributions. If distributions were not normal, a two-tailed Wilcoxon rank test was used to evaluate the similarity of the two distributions.

RESULTS

L-neurons produce a directional response, such that there is greater modulation of the response when a bar moves upward than when it moves downward (Fig. 1A). The two traces in Fig. 1A represent the intracellular response to a 6° positive contrast bar (bright bar against a gray background) moved up and down at

FIG. 1. *A* and *B*: directional responses to positive contrast bars (*A*) and negative contrast bars (*B*) moving upward (left) and downward (right). The horizontal and vertical bars represent 100 ms and 5 mV, respectively, for *A*–*C*. *C*: a 100-ms interval of the dense pseudorandom stimulus together with the response to 12 randomly modulated UV bars. *D*: the linear spatiotemporal receptive field extracted from the recording in *C* using reverse-correlation analysis. *A* and *B* show representative locations for 2 bars (elevation) the nonlinear interactions of which are expanded. The nonlinear actions for this cell are summarized in *E*. *E*, top, middle, and bottom, respectively: the interactions between 2 flashes; both at *A*, at *A* and *B*, and both at *B*. Blue shading indicates suppression and the red-orange shading indicates facilitation. The most significant directional interaction is the asymmetric facilitation for a bar flashed at *B* around 5 ms before a bar is flashed at *A* than the reverse, demonstrating directional preference for upward motion. The data from *C*–*E* are from the same cell. *F* and *G*: the 2-flash interactions as shown in *E*; however, *F* shows the average interaction plot for 23 cells shown UV bars alone and *G* shows the same for 23 cells shown green bars alone. Note that *F* shows prominent asymmetries between *A* and *B*, whereas *G* shows almost none. Colorbar: the value of *h* in the colorbar is $0.4 \text{ mV}(\text{C} \cdot \text{ms})^{-1}$ in *D*, $0.29 \text{ mV}(\text{C} \cdot \text{ms})^{-2}$ in *E*, $0.14 \text{ mV}(\text{C} \cdot \text{ms})^{-2}$ in *F*, and $0.25 \text{ mV}(\text{C} \cdot \text{ms})^{-2}$ in *G*.

3750°/s. The two traces in Fig. 1B show another example of a directional response, but this time a negative contrast bar (dark bar against a gray background). In addition to the moving bar, we used a random bar stimulus (Fig. 1C), which attempted to replicate the contrast of the moving bars. We assessed the linear and nonlinear STRFs using first- and second-order Wiener kernels in an attempt to capture the full characteristics of the L-neuron responses.

STRFs measured using a dense stimulus

We investigated the nonlinear interactions in 23 L-neurons from the dragonfly median ocellus. These cells were shown a dense random bar stimulus. That is, a stimulus where the contrast at each bar was updated every 1.6 ms under different conditions of green or UV stimulation. The green and UV stimuli were presented separately. Multiple linear regression (James 2003; van Kleef et al. 2005) was used to estimate the linear and nonlinear STRFs from the response to stimulation with 12 UV and 12 green independently and randomly modulated bars (see Fig. 1C for a diagram of the stimulus and an example recording of the response to this stimulus). The estimated linear STRF is shown in Fig. 1D. This map shows, for example, that a small flash of a positive contrast bar at position A will produce a hyperpolarization (at ~17 ms) followed by a depolarization (at 27 ms). The time course of the response to other positions is also mapped.

Increases or decreases in the responses that occur, apart from those predicted from the linear STRF are known as nonlinear interactions and are mapped by the nonlinear STRFs (2nd-order Wiener kernels; Fig. 1E). The *top box* in this figure shows the nonlinear interactions between two flashes that occur at A, the *middle* one shows those that occur between flashes at A and B, and the *bottom* shows those that occur between two flashes at B. The time of the flash at A is denoted $t(A)$, whereas the time of the flash at B is denoted $t(B)$. These times denote the time in milliseconds until the nonlinear response occurs. Facilitation, or increase in the response, is represented by orange-red and suppression, or decrease in the response, is represented by blue. The second-order Wiener kernels allow us to distinguish between the nonlinear responses to changes in contrast (for example, 2 bars at locations A and B delivered at the same time), or simulated downward motion (A followed by B) or upward motion (B followed by A).

From working along the diagonal of Fig. 1E, *top*, it can be seen that two flashes presented concurrently produce a suppression of the response at ~15 ms that is followed by a relatively small facilitation of the response at 20 ms that continues for >20 ms. This kernel is by its nature symmetric because the flashes occur at the same spatial point. Nonlinear interactions between two separate spatial locations A and B are shown in Fig. 1E, *middle*. This map shows that there is a greater facilitation response to the sequence of bars A followed by B (interval: 5 ms) and a small amount of suppression seen if B is followed by A (interval: 10 ms). These asymmetric nonlinearities are even more strongly demonstrated in Fig. 1F, *middle*, which shows the average data for 23 cells presented with the UV stimulus. However, when green light is used, there is very little asymmetry between the response to a flash at A followed by B and the reverse (see Fig. 1G, *middle*, which shows the average data for 23 cells). Thus as with the linear

mechanisms of directionality (Van Kleef et al. 2008), these nonlinearities are dependent on UV light. The nonlinear STRFs improved the predictive capacity of the model when either UV or green stimuli were used. In the case of UV stimuli, the error in the prediction, as measured by the %MSPE, fell from 23.6 ± 9.2 to $17.0 \pm 8.3\%$ (means $\pm$ SD, $n = 23$) and in the case of the green stimuli, the %MSPE fell from 34.5 ± 12.5 to $13.9 \pm 11.4\%$ ($n = 23$).

Nonlinear STRF predictions of bar responses

Despite the fact that the prediction of the nonlinear STRF was a significant improvement over that of the linear STRF, the nonlinearities did not significantly improve the prediction of the response to moving bars at high speeds. Figure 2, A and B, show example predictions of the linear STRF (black trace) and addition of linear and nonlinear STRFs (dashed trace). The contribution of the nonlinear terms is so small that the dashed trace is obscured. The gray trace is the measured response to a moving bar. Over the population of cells, shown in Fig. 2C, the average %MSPE of the predicted response to bars based on the linear kernels alone was $44 \pm 22\%$ ($n = 23$) for positive contrast bars and $35 \pm 11\%$ ($n = 23$) for negative contrast bars. The %MSPE was worse for nonlinear kernels in both cases: it was $51 \pm 26\%$ ($n = 23$) for positive contrast bars and $38 \pm 22\%$ for negative contrast bars.

Over the population of 23 cells there were no significant differences between the direction indices (DIs) predicted by either model for either positive or negative contrasts (shown in Fig. 2D). The mean DI predicted for positive contrast bars was 0.16 ± 0.06 for the linear STRFs and 0.15 ± 0.06 for the nonlinear STRFs (no significant difference, t -test, $P > 0.2$).

FIG. 2. A recorded responses to moving bars (gray traces) and the response to moving bars predicted by the linear spatiotemporal receptive field (STRF, black trace) and nonlinear predicted STRF (dashed trace) for a positive contrast bar moving up (left top) and down (right top). Arrows indicate the bar directions. Bottom traces show the same quantities for negative contrast bars. B: another example cell as in A. C: the error of the linear STRF against the error of the nonlinear STRF in predicting the response to a fast bar moving up and down for 15 cells. D: the direction index (DI) of the responses the errors of which are shown in C.

FIG. 3. *A–C*: the difference among the dense stimulus (*A*), sparse negative contrast stimulus (*B*), and the sparse positive contrast stimulus (*C*). In each case, 100 ms of stimulus is shown. The dense stimulus continues in a similar manner, the sparse stimulus contains a 1-s gap until another 19-ms “pulse” of random bars is delivered. To the right of the sample stimuli are the linear STRFs from the same sample cell. The normalized spatial and temporal components of these STRFs are shown in blue (dense), red (sparse negative), and green (sparse positive). Colorbar: values of h for 1st column: top, $0.69 \text{ mV}(\text{C}\cdot\text{ms})^{-1}$; middle, $9.5 \text{ mV}(\text{C}\cdot\text{ms})^{-1}$; and bottom, $9.2 \text{ mV}(\text{C}\cdot\text{ms})^{-1}$; 2nd column: top, $1.0 \text{ mV}(\text{C}\cdot\text{ms})^{-1}$; middle, $3.2 \text{ mV}(\text{C}\cdot\text{ms})^{-1}$; bottom, $2.3 \text{ mV}(\text{C}\cdot\text{ms})^{-1}$.

The mean DI predicted for negative contrast bars was 0.15 ± 0.06 for the linear STRFs and 0.15 ± 0.06 for the nonlinear STRFs (no significant difference, t -test, $P > 0.8$). Thus although Fig. 2*D* presents some nonlinear STRFs that show directional components, the response component predicted by the nonlinear terms is not significant.

STRFs estimated with a sparse stimulus

To test the idea that because the bars were sparsely presented (with 1 s between presentations), the receptive fields were different to those during the dense pseudo-random stimulus (shown in Fig. 3*A*), we used a random bar stimulus exactly matched to the negative and positive contrast bar stimuli (Fig. 3, *B* and *C*). Specifically, the 12 negative or positive contrast bars were, in random order, flashed for 1.6 ms, which takes a total of 19.2 ms. These 19.2-ms stimulus periods were separated by 1 s of mean luminance. We estimated the linear STRFs for each L-neuron using both the sparse and the dense stimulus and compared the results.

Examples of the linear STRFs estimated from the data obtained from two cells are shown in Fig. 3, *A–C*, right. The most obvious difference (not shown because the contour plots are normalized) is that the maximum gains in the linear STRFs shown in the first column (*B* and *C*) are around 10 times the maximum gain of the kernel in *A*. For the STRFs of another cell, shown in the second column, the ratio of the maximum gains is around 3. These cells show only a small amount of change in the temporal profile of their linear STRFs (obtained using SVD, see METHODS) when the sparse negative (Fig. 3*B*) or positive (*C*) contrast stimulus is used compared with the case where the dense stimulus was used (Fig. 3*A* - demonstrated by

the colored horizontal traces). The spatial profile of these cells becomes narrower as shown by the colored vertical traces.

Parameters describing the changes in linear STRF structure with changes in the density of the stimulus, are shown for 23 L-neurons in Fig. 4, *A–D*. Figure 4*A* is a scatter plot of the gain of the linear STRFs measured using sparse negative ($\times$) or

FIG. 4. *A–D*: the STRF parameters from 23 L-neurons shown dense (ordinate in each panel) and sparse (abscissa in each panel) pseudorandom stimuli. *A*: the gain of the STRF (maximum value). $\times$, negative contrast sparse stimuli; $\circ$, positive contrast sparse stimuli. *B*: time to peak of the STRF ($\times$, negative contrast sparse stimuli; $\circ$, positive contrast sparse stimuli). *C*: the 0 crossing that occurs immediately after the peak ($\times$, negative contrast sparse stimuli; $\circ$, positive contrast sparse stimuli). *D*: the full-width at half-maximum for the spatial component of STRFs measured using negative ($\times$) and positive ($\circ$) contrast sparse stimuli against the same quantity measured from the spatial profile of STRFs obtained using a dense stimulus.

positive ($\circ$) contrasts against the gain of the linear STRF obtained using a dense stimulus. The gain is measured as the millivolts per step in stimulus contrast per millisecond [mV/(Cms)]. The mean gain for the latter is 1.3 ± 0.5 mV/(Cms), which is significantly different to the mean for STRFs obtained using a sparse positive contrast stimulus [3.5 ± 1.6 mV/(Cms), t -test, $P < 2 \times 10^{-7}$] and to the gain of the STRFs obtained using a negative sparse contrast stimulus [4.2 ± 1.8 mV/(Cms), t -test, $P < 7 \times 10^{-9}$].

Figure 4B is a scatter plot of the time to peak of the temporal profile of linear STRFs measured using sparse negative ($\times$) or positive ($\circ$) contrasts against the time to peak of the linear STRF obtained using a dense stimulus. The mean time to peak for the latter is 18.6 ± 2.1 ms, which is significantly different to the mean for STRFs obtained using a sparse positive contrast stimulus (17.0 ± 2.1 ms, Kruskal-Wallis, $P < 0.03$) but not to STRFs obtained using the negative sparse contrast stimulus (17.8 ± 2.1 ms, t -test, $P > 0.3$). In Fig. 4C, the time at which the temporal profile crosses zero is shown for STRFs measured using sparse negative ($\times$) or positive ($\circ$) contrasts against those obtained from the STRF obtained using the dense stimulus. The mean time for zero crossings from positive contrast bars was 22.2 ± 3.2 ms, which is significantly earlier than for the dense stimuli (24.7 ± 4.1 , t -test, $P < 0.02$). There were no significant differences between the times of the zero crossings for STRFs obtained using negative contrast bars (Kruskal-Wallis, $P > 0.3$).

Figure 4D is a scatter plot of the full width at half the maximum response (FWHM) obtained using the sparse negative stimuli ($\times$) and positive stimuli ($\circ$) against the FWHM obtained using the dense stimulus. The mean FWHM ($20.1 \pm 3.0^\circ$) was significantly larger than either the STRF obtained from the sparse negative contrast bars ($16.5 \pm 2.6^\circ$, $P < 1 \times 10^{-4}$) or sparse positive contrast bars ($17.1 \pm 6.1^\circ$, $P < 4 \times 10^{-4}$).

We have shown here that there are significant differences between the linear STRFs (1st-order Wiener kernels) measured using dense and sparse stimuli. Although in the dense case we have fitted the second-order Wiener kernel, this could not be achieved for the sparse stimulus because this stimulus provides few nonlinear stimulus combinations. For this reason, it seems unlikely that nonlinear terms would significantly improve the model prediction in the case of the sparse stimulus. In fact, responses to sparse stimuli were extremely well described by their linear STRFs (negative contrast, %MSPE 10.1 ± 7.2 and positive contrast %MSPE, 7.0 ± 7.8).

The mean membrane potential during the two different stimuli (dense and sparse) were not significantly different from each other. This was irrespective of whether the sparse stimulus was composed of positive ($P > 0.17$, $n = 23$, Wilcoxon rank test) or negative ($P > 0.20$, $n = 23$, Wilcoxon rank test) contrast bars.

Sparse pseudorandom stimulus predictions of bar responses

We measured the ability of the STRFs estimated using the sparse random stimulus to predict the measured responses of the L-neuron to moving bars. Two examples are shown in Fig. 5, A and B. In these figures, the continuous gray line is the measured response to a bar, the continuous black line represents the linear-sparse-STRF prediction and the dashed line indicates the nonlinear-dense-STRF prediction. Clearly the

FIG. 5. A: example responses (gray trace) and the nonlinear predicted STRF(dense) predicted (dashed trace) and linear predicted STRF(sparse; black trace) for a positive contrast bar moving up (left top) and down (right top). Bottom: the same quantities for negative contrast bars. B: another example cell as in A. C: the error (%MSPE) of the nonlinear STRF(dense) against the error of the linear STRF(sparse) in predicting the response to a fast bar moving up and down for 14 cells. D: the DI of the responses the errors for which are shown in C.

actual response (gray trace) is better predicted by the linear-sparse-STRF (black trace).

For 13 of the 14 cells from which we recorded responses to bars, the linear-sparse STRFs were better predictors of the response to the bars (shown in Fig. 5C) than the nonlinear-dense STRFs. For white bars, the MSPE of the response predicted by the STRF obtained from the sparse stimulus was 16 ± 10 , which was significantly better than the error for the STRF obtained from the dense stimulus (46 ± 21 , t -test, $P < 1 \times 10^{-9}$). For dark bars, the improvement was not significant (t -test, $P > 0.1$) and neither was a good predictor of the response (average MSPE of $94 \pm 42\%$ for sparse and $106 \pm 45\%$ for dense).

The linear-sparse STRFs predicted larger direction indices for white bars (0.10 ± 0.04 , shown in Fig. 5D) than the nonlinear-dense STRFs (0.05 ± 0.02 , Kruskal-Wallis, $P < 1 \times 10^{-4}$). There were no significant differences for the DIs predicted for the dark bars (sparse: 0.08 ± 0.04 ; dense: 0.07 ± 0.03 , $P > 0.06$), but overall the predictions did follow the trend seen for white bars.

DISCUSSION

In this study, the linear and nonlinear STRF properties of ocellar L-neurons were estimated from a second-order Wiener kernel analysis of their intracellular responses to two different types of random stimuli (continuous and intermittent). The spatial and temporal properties of the STRFs obtained from the two different types of random sequence were compared. The

STRFs were used to predict the responses of L-neurons to fast moving bars.

Our data suggest that nonlinear response properties, while present during a continuous random sequence, do not account for the responses of L-neurons to moving bars. On the other hand, using an intermittent (sparse) random sequence with characteristics matched to those of the moving bar, we provide strong evidence that the gain and spatiotemporal structure of the STRFs of L-neurons change significantly from the case where a continuous random sequence has been used. The effects are stronger for the positive contrast (ON) receptive fields. These changes are likely to be due to contrast adaptation because in the case of the dense white-noise stimulus, the L-neurons were constantly stimulated by modulated contrast and therefore experienced substantial periods of adaptation. The results demonstrate that L-neurons adapt not only to color (van Kleef et al. 2008) but to the configuration of the contrast sequence with which it is stimulated. Changing the configuration of the sequence from continuous to intermittent alters the spatial, temporal, and direction tuning properties of L-neurons.

Although we recorded from L-neurons in the ocellar plexus, we cannot exclude that some of the physiological responses in this study are dependent on signals from the compound eye: for the case of flies, it was found that ocellar L-neurons and compound eye interneurons can be electrically coupled to premotor neurons (Haag et al. 2007). Although the compound eyes were not covered in the current study, they were painted over in a previous study (van Kleef et al. 2008), which established that, in dragonflies, the directional selectivity of these cells is not dependent on compound eye input.

Using STRFs to predict directionality

One of the benefits of using white-noise analysis is that the Wiener kernels (STRFs) estimated from the responses encompass a general class of models, known as nonlinear time-invariant models, which includes linear and LN (linear-nonlinear) models. Our results suggest that STRFs of L-neurons in the dragonfly median ocellus are not time invariant but depend on the particular stimulus used to measure them. Thus like other visual neurons, adaptation plays an important role in forming their STRF properties. It is possible then that STRF predictions of responses to motion stimuli will be more accurate when the random stimulus used to estimate the STRFs matches the spatial and temporal characteristics of the motion stimulus so as to hold the cell in an equivalent state of adaptation. We have demonstrated that this is the case when using STRFs to predict the responses of L-neurons to moving bars presented intermittently. STRF predictions were significantly improved when a matched random stimulus was used. This random stimulus is less general than white noise but general enough to encompass the moving bar stimulus.

The novel stimulus allows an analysis to be made that is a significant improvement on previous analyses. These have compared, for example, responses to sparse presentations of gratings and bars with predictions from STRFs measured using dense pseudorandom stimuli (DeAngelis et al. 1993; Emerson et al. 1992; Marmarelis and McCann 1973; Rust et al. 2005; Touryan et al. 2005; van Kleef et al. 2008). In cases where the predictions do not match the responses, it is sometimes suggested that the presence of higher-order nonlinearities is the

reason for the discrepancy between these quantities. Here we have demonstrated that discrepancies between the STRF-predicted and actual response can be explained not by the presence of higher-order nonlinearities, but by the fact that the spatial and temporal properties and gain of the neuronal receptive fields are not invariant to the stimulus being used. In the present case, changes in the STRFs came about because of the absence of a stimulus between bar presentations, a common experimental approach used for maximizing responses.

Adaptation and changing STRFs

The adaptation of visual neurons to the characteristics of their sensory inputs produces persistent changes in their STRF properties. These changes enable neurons to maintain high sensitivity over a wide range of inputs, avoid saturation, and optimize their coding efficiency (Brenner et al. 2000; David et al. 2004; Laughlin 1981; Shapley and Enroth-Cugell 1984; Sharpee et al. 2006; Srinivasan et al. 1982). Two particularly well-studied examples of adaptation are: light adaptation, adapting to the mean luminance of the stimulus (Mante et al. 2005; Norman and Werblin 1974; Shapley and Enroth-Cugell 1984), and contrast adaptation, also known as contrast gain control (Albrecht 1995; Chander and Chichilnisky 2001; Harris et al. 2000; Nolt et al. 2004; Ohzawa et al. 1985; Sakai and Naka 1987; Sceniak et al. 1999; Shapley and Victor 1978; Smirkanis et al. 1997). Some studies have also considered the adaptation of neurons to the spatial and higher-order statistics of the stimulus (Bonin et al. 2006; Smirkanis et al. 1997) as well as adaptation to motion (Harris et al. 2000; Maddess and Laughlin 1985; ölvéczy et al. 2007; Ibbotson et al. 1998).

In this study, we have shown that changes in the spatial and temporal properties of the contrast stimulus have the consequence that L-neurons are more sensitive to changes in contrast, faster (shorter time to peak and shorter time to cross zero after peak), more narrowly spatially tuned, and more directional to extremely fast movements. Several changes in the linear STRFs are consistent with previous studies that have investigated the effects of altering the contrast of the stimulus. Changes in contrast sensitivity have been observed in flies (Brenner et al. 2000; Harris et al. 2000), catfish retina (Sakai and Naka 1987), salamander and rabbit retina (Smirkanis et al. 1997), primate retina (Chander and Chichilnisky 2001), cat lateral geniculate nucleus (Ohzawa et al. 1985), and mammalian visual cortex (Albrecht 1995; Ohzawa et al. 1985; Solomon et al. 2004). In these studies, an increase in the contrast of the stimulus resulted in a decrease in the sensitivity of the neurons, as measured by their gain (spike rate or voltage membrane amplitudes). This type of neural adaptation makes sense because it means a wider range of intensity fluctuations can be encoded by the same amplitude of neural fluctuations. In other words, the adaptation allows the range of intensities to be matched by the full range of neural responses available, which are ultimately bounded by the saturation of the neural response.

Changes in the temporal response properties with changes in image contrast have been observed in salamander and rabbit retina (Smirkanis et al. 1997) and primate retina (Chander and Chichilnisky 2001). In these cases, the time to peak became smaller and the zero crossing occurred earlier with increases in contrast. Our results, on the other hand, suggest that presenting

long periods of zero contrast interleaved with shorter periods of random bar stimuli produces linear STRFs with slightly shorter time to peak and zero crossing time values than those evaluated using a white-noise stimulus. The differences perhaps reflect the different functions of these neurons. It seems that integrating over time and gaining an increased signal-to-noise ratio while sacrificing temporal resolution is an acceptable compromise in the retina of vertebrates where information is yet to be processed by several layers of neural circuitry. On the other hand, as we have demonstrated here in the ocellar system, where latency and temporal resolution are of a premium, the retinal cells mostly increase their temporal resolution.

Changes in the spatial resolution also suggest that the ocellar system differs from other visual systems because when a sparse system is used, the area of spatial summation actually decreases. In the mammalian visual cortex, spatial summation is increased at low contrasts (Sceniak et al. 1999), as it is to a lesser extent in the retina and LGN (Nolt et al. 2004). Again the increase in the signal-to-noise ratio gained from having a greater summation area in the vertebrate visual system does not seem to be present in the ocellar system of the dragonfly. This is perhaps understandable because the ocellar system already has a great deal of optical blur and neural convergence making signal-to-noise ratios extremely high (Berry et al. 2006, 2007). It is interesting to note that the FWHM of L-neurons STRFs estimated with the sparse stimulus is close to the limit set by the photoreceptors ($\sim 15^\circ$) (van Kleef et al. 2005).

Evidence of changes in the directional tuning with contrast has been reported in the literature, albeit in more complicated neural systems than the median ocellus. Ohzawa et al. (2005) showed that direction selectivity increased in simple and complex cells of cat visual cortex as stimulus contrast was decreased. Livingstone and Conway (2007) have shown in macaque cortical neurons that the space-time slant of the STRFs predicts that optimal speeds will be higher at higher contrasts. However, optimal speed tuning was found to be variable in cat primary visual cortex with adaptation to high speeds most often generating a reduction in the optimal speed tuning of the cells, while at the same time influencing contrast coding (Hietanen et al. 2007a,b).

Functional benefits

The ocelli of many flying insects have been shown to mediate compensatory head and body movements to facilitate flight and gaze stabilization (Goodman 1981; Schuppe and Hengstenberg 1993; Stange 1981; Taylor 1981a,b; review Hengstenberg 1991). This is primarily achieved by detecting the changes in light intensity that occur with changes in attitude. However, as shown in flies, motion information can be obtained by combining the signals from the two lateral ocelli (Parsons et al. 2006) and in dragonflies individual ocelli are directionally selective (van Kleef et al. 2008).

While bees and flies are optimized to detect light coming from above, dragonfly and locust ocelli are directed toward the horizon with the median ocellus and lateral ocelli optimally located to measure changes in pitch and roll, respectively (Berry et al. 2006, 2007; Wilson 1978; review Goodman 1981). Focusing on the horizon, rather than integrating over a wide area of visual space, is an optimal strategy for fine resolution of elevation because this is the area in visual space

with the greatest change in intensity with elevation (Wilson 1978). On the other hand, by spatially integrating over a wider angle, ocelli are more robust to objects that might obscure a part of the field of view or of deviations in the skyline due to the terrain or vegetation (Stange et al. 2002; Wehner 1987). Given that L-neurons in the median ocellus increase their spatial acuity when the stimulus is delivered intermittently suggests that under these conditions they are tuned to provide greater resolution of elevation at the expense of robustness.

The instabilities inherent in small flying animals mean that dragonflies require the ability to detect very rapid movements and respond to them quickly (Wakeling and Ellington 1997; Wang et al. 2003). Intermittent contrast stimuli are likely to be encountered by a hovering or forward-flying dragonfly, which successfully fixates on the horizon because during fixation little or no visual stimulation will occur. Therefore relatively long periods (e.g., 1 s) of successful fixation followed by a sudden movement across the horizon will produce visual stimuli similar to the sparse stimuli used here. Thus the decreases in L-neuron latency that occur with a sparser stimulus would aid during hover or forward flight when the requirements for low-latency responses to attitude changes are at a premium.

The high angular velocities used here ($3,750^\circ/\text{s}$) are comparable to those observed in free-flying dragonflies (Wang et al. 2003). Using high-speed video cameras, Wang et al. (2003) have shown that the pitch velocity of the body of forward flying dragonflies can exceed $4,000^\circ/\text{s}$. The angular velocity of the dragonfly head may be even greater as active control of the dragonfly head can produce angular velocities of $>500^\circ/\text{s}$ (Stange 1981). It has also been shown in other visual systems that motion processing neurons can respond strongly at very high speeds. Certain descending visual neurons in the honeybee, thought to provide input for flight stability, have been shown to respond strongly to speeds up around $1,000^\circ/\text{s}$ (Ibbotson 1991, 2001). Also neurons in the mammalian visual system have been shown to respond at speeds associated with high speed saccadic eye movements (subcortical: Price and Ibbotson 2001; cortical: Price et al. 2005a,b).

Potential physiological mechanisms

Contrast adaptation has been attributed to a number of different underlying mechanisms including changes in membrane properties of the neuron (Carandini and Ferster 1997; Kim and Rieke 2003; Sanchez-Vives et al. 2000a,b), synaptic transfer properties (Rieke 2001), and pattern of synaptic connectivity (Nauhaus et al. 2009).

In mammalian cortical neurons, evidence suggests that contrast adaptation activates sodium-gated potassium channels in the cell membrane, which produces a tonic hyperpolarization (Carandini and Ferster 1997; Sanchez-Vives et al. 2000a,b). Our data show that there is no change in the mean potential of L-neurons with changing contrast, neither a tonic hyperpolarization or depolarization. However, without further experiments we cannot rule out changes in the membrane properties.

Changes in the synaptic transfer function of cells may also be responsible for adaptation (Rieke 2001). L-neurons synapse with a large number of cells within the ocellar nerve plexus, these include photoreceptors and small neurons (S-neurons) as well as other L-neurons (Laughlin 1981). Although it is unclear how the responses of S neurons change with contrast, photo-

receptors do not appear to have temporal dynamics that are contrast dependent (van Kleef et al. 2005), suggesting that the mechanism responsible for contrast adaptation in dragonfly ocellar L-neurons occurs at or after the L-neuron-to-photoreceptor synapse. This would be consistent with studies of the retina showing that contrast adaptation does not occur at the photoreceptor level (Rieke 2001; Smirkanis et al. 1997).

Several theoretical studies have shown that nonlinear models are able to produce adaptive type changes in the linear and nonlinear receptive field properties in response to changes in the contrast of the stimulus without a change in their parameters (Bair and Movshon 2004; Borst et al. 2005; Yu and Lee 2003). These include the nonlinearities involved in models of directional selectivity (Bair and Movshon 2004; Borst et al. 2005) and spike generation (Yu and Lee 2003). It is important to note therefore that changes in the STRF properties measured using the Wiener method (as used here) do not automatically imply that there is a change in the value of the parameters that describe the biophysical properties of the neuron.

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