

Two Methods for Calculating the Responses of Photoreceptors to Moving Objects

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Abstract—The responses of photoreceptor cells to moving stimuli are crucial to understanding motion detection in visual systems. However, these responses are not well characterized quantitatively because they result from a combination of spatial optical behavior in the lens systems with temporal behavior in the phototransduction mechanism. While both these processes can now be modeled quite well by relatively simple equations, their combination cannot be easily obtained in a closed form. Here, we present two approaches to this problem, based on well-established models for the lens and photoreceptors systems of the fly compound eye. The first approach leads to a recursive formula for predicting the photoreceptor response to a moving point object. The second method is approximate, but almost equally accurate and more rapid. © 1998 Biomedical Engineering Society. [S0090-6964(98)00902-3]

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INTRODUCTION

The stationary visual acuity and time-dependent properties of photoreceptors in compound eyes have been measured carefully in many species. However, most studies of motion detection have emphasized behavioral measures such as orientation and tracking, or focused on movement-detecting neurons that are several synapses beyond the photoreceptors.^{1,13,18} In contrast, comparatively little is known about the responses of photoreceptors to moving objects.

When an object moves across the visual field of a compound eye, the optical properties of the lens system at the front of each facet control the resulting change in light intensity falling on the photoreceptors behind it. These changes in light intensity are then converted to changes in membrane potential by a transduction mechanism that is strongly time dependent. Srinivasan and Bernard¹⁴ estimated the responses of locust and *Limulus* photoreceptors to moving objects by combining the op-

tical properties of the lens systems with the photoreceptor impulse responses. Transmission through compound eye lens systems can be quite well approximated by Gaussian functions of space,¹⁵ but the flash responses are more difficult to model. Srinivasan and Bernard used stretched Gaussian functions to fit the impulse responses, because this allowed a closed solution to the convolution. However, it gave a relatively poor description of the impulse responses, compared to the models that are now widely used for this purpose.^{11,19}

Much more complete data are now available on the time-dependent properties of photoreceptors in compound eyes, including accurate measurements in fly photoreceptors and second-order neurons at a range of light adaptation levels.¹⁰ These data have been used recently to obtain estimates of dynamic visual acuity in the two cell layers, using direct convolution of the measured cellular responses with a Gaussian model of optical transmission through the lens system.⁸

The impulse responses of fly photoreceptors can be well approximated by the two-parameter adapting bump model.¹⁷ Convolution of the adapting bump model with a Gaussian function does not yield a closed solution, but here we present two methods that allow calculation of the responses of photoreceptors to moving objects. We show that these methods yield essentially identical results, and use the more rapid method to predict the response amplitude and spatial resolution of fly photoreceptors over a wide range of angular velocities.

THEORY

Predicting Photoreceptor Responses to Moving Objects

Figure 1 illustrates the situation when a moving point object passes through the visual field of a compound eye. Light from the object passes through the lens system at the front of the eye before entering the photoreceptors. Therefore, the resulting electrical response in the photoreceptor membrane is produced by a cascade of two time-dependent processes: First, the intensity of light reaching the photoreceptors changes as the object moves,

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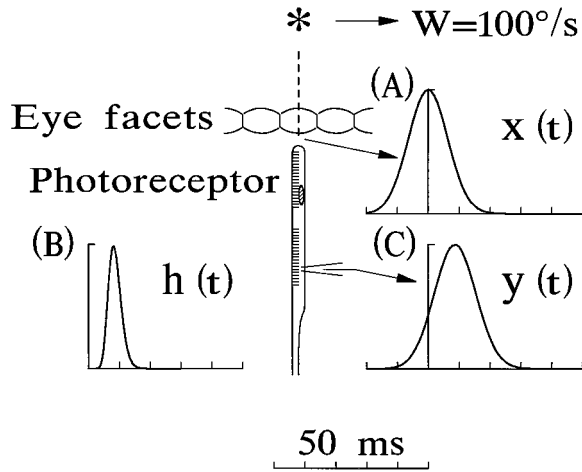


FIGURE 1. A point object (asterisk) moving at constant angular velocity (W) across the visual field of a compound eye causes a change in light intensity on each photoreceptor, $x(t)$, that is approximately a Gaussian function of time (A). The photoreceptors behave nearly linearly with impulse response function, $h(t)$, (B), so that the light signal is transduced to a membrane potential change, $y(t)$, that is a linear convolution of $x(t)$ and $h(t)$ (C).

depending on the object's velocity and the transmission properties of the optics. Second, the phototransduction machinery has strongly time-dependent properties, generally acting as a low-pass filter.

The light-transmitting properties of the optical components before the photoreceptors in compound eyes can be approximated by a Gaussian function of two angular dimensions through the center of curvature of the eye surface.^{5,6,15} If movements of the visual world relative to the animal are restricted to one angular dimension, a one-dimensional function can be used.¹⁴ When a point object moves at constant angular velocity, W , across the visual field, the Gaussian approximation predicts that the light intensity passing through each facet and falling on the photoreceptors will be

$$x(t) = e^{-bt^2}, \quad b = (2W/\rho)^2 \ln 2, \quad (1)$$

where t is time relative to the instant at which the point object is directly above the optical axis of the facet, and ρ is the width of the Gaussian function at half-maximum amplitude. Experimental measurements of ρ in fly eyes are available as a function of both light adaptation and position across the surface of the eye.⁷

The responses of light-adapted insect photoreceptors to flashes of light or to smoothly varying input signals are approximately linear.^{2-4,9} Therefore, photoreceptor responses to moving objects may be obtained by convolution of their impulse responses with the function in Eq. (1). Several general models have been proposed to fit

photoreceptor impulse responses. The two most successful are the log-normal model¹¹ and the adapting bump model.¹⁹ Both usually fit experimental flash responses very well, with the same number of parameters. However, the latter model is more suitable for convolution with other functions because it contains exponential terms, while the former model uses a logarithmic function of a Gaussian function. Therefore, we modeled the impulse responses of fly photoreceptors by

$$h_n(\tau) = \frac{1}{an!} (\tau/a)^n e^{-\tau/a}, \quad a > 0, \quad (2)$$

where τ is time after the flash, $n+1$ is the number of stages in a hypothetical sequence of filters, and a is the time constant of the filters.¹⁹

The problem is to obtain the convolution of Eqs. (1) and (2) in a form that is useful for calculating the responses of photoreceptors to moving objects, when parameters are available for both equations. In the following section, we present two solutions to this problem.

A Recursive Method of Convolution

If the photoreceptor response to an object crossing the visual field at constant angular velocity is $y(t)$, we can write

$$y_{n+1}(t) = \int_0^\infty h_{n+1}(\tau) x(t-\tau) d\tau \quad (3)$$

$$= \frac{1}{(n+1)! a^{n+2}} \int_0^\infty \tau^{n+1} e^{-b(t-\tau)^2 - \tau/a} d\tau \quad (4)$$

$$= -\frac{1}{(n+1)! 2ba^{n+2}} \int_0^\infty \left(-\frac{1}{a} - 2b(\tau-t) \right) \times \tau^n e^{-b(t-\tau)^2 - \tau/a} d\tau + \frac{2bt - 1/a}{(n+1)! 2ba^{n+2}} \int_0^\infty \tau^n e^{-b(t-\tau)^2 - \tau/a} d\tau. \quad (5)$$

This becomes, after integrating by parts the first term immediately above,

$$y_{n+1}(t) = \frac{1}{2ba^2(n+1)} \frac{1}{a^n(n-1)!} \int_0^\infty \tau^{n-1} \times e^{-b(t-\tau)^2 - \tau/a} d\tau + \frac{2bt - \frac{1}{a}}{2ab(n+1)} y_n(t). \quad (6)$$

Therefore

$$y_{n+1}(t) = \frac{1}{2a^2b(n+1)} \{y_{n-1}(t) + (2abt - 1)y_n(t)\}, \quad n = 1, 2, \dots \quad (7)$$

Equation (7) provides a recursive solution if expressions for $y_0(t)$ and $y_1(t)$ can be obtained. For $y_0(t)$,

$$y_0(t) = \int_0^\infty h_0(\tau)x(t-\tau)d\tau = \int_{-\infty}^t h_0(t-\tau)x(\tau)d\tau. \quad (8)$$

Let

$$u = \sqrt{2b} \left(\tau - \frac{1}{2ab} \right), \quad du = \sqrt{2b} d\tau. \quad (9)$$

Then

$$y_0(t) = \frac{1}{a\sqrt{2b}} e^{1/(4a^2b)} e^{-t/a} \int_{-\infty}^{\sqrt{2b}[t-1/(2ab)]} e^{-u^2/2} du. \quad (10)$$

For $y_1(t)$,

$$y_1(t) = \int_0^\infty h_1(\tau)x(t-\tau)d\tau = \int_{-\infty}^t h_1(t-\tau)x(\tau)d\tau. \quad (11)$$

Therefore,

$$y_1(t) = \left(\frac{t}{a} - \frac{1}{2a^2b} \right) y_0(t) + \frac{1}{2a^2b} e^{-bt^2} \quad (12)$$

$$= \frac{1}{2a^2b} \{e^{-bt^2} + (2abt - 1)y_0(t)\}. \quad (13)$$

The integral in Eq. (10) can be obtained from the area under the normal curve. Therefore, $y_0(t)$ and $y_1(t)$ can

be obtained and used in Eq. (7) to yield $y_{n+1}(t)$, $n = 1, 2, \dots$. Since this method ultimately depends on estimating the area under portions of the normal curve, it does involve an approximation. It is interesting to note from Eq. (7) that for all $n = 1, 2, \dots$, the ratios $\{(n+1)y_{n+1}(t)\}/y_n(t)$ intersect at $t = 1/(2ab)$, where they each have the value $1/(2a^2b)$.

A Fast Method of Convolution

Note that the Laplace transform of $h_n(t)$ is

$$H_n(s) = \frac{1}{(as+1)^{n+1}}. \quad (14)$$

So, letting $X(s)$, $Y_0(s)$, $Y_1(s)$, ..., be the Laplace transforms corresponding to $x(t)$, $y_0(t)$, $y_1(t)$, ..., we obtain the cascade

$$X(s) \rightarrow \left[\frac{1}{as+1} \right] \rightarrow Y_0(s) \rightarrow \left[\frac{1}{as+1} \right] \rightarrow Y_1(s) \rightarrow \text{etc.}, \quad (15)$$

where

$$y_0(t) = \frac{1}{a} \int_0^\infty e^{-r/a} x(t-r) dr. \quad (16)$$

Now, let Δ be a small time increment:

$$y_0(t+\Delta) = \frac{1}{a} \int_0^\infty e^{-r/a} x(t+\Delta-r) dr. \quad (17)$$

Let $u = r - \Delta$; then

$$y_0(t+\Delta) = \frac{1}{a} \int_{-\Delta}^\infty e^{-(u+\Delta)/a} x(t-u) du \quad (18)$$

$$= \frac{1}{a} e^{-\Delta/a} \int_{-\Delta}^0 e^{-u/a} x(t-u) du + e^{-\Delta/a} y_0(t) \quad (19)$$

$$\approx e^{-\Delta/a} y_0(t) + e^{-\Delta/a} \frac{\Delta}{a} x(t). \quad (20)$$

Similarly,

$$y_1(t+\Delta) \approx e^{-\Delta/a} y_1(t) + e^{-\Delta/a} \frac{\Delta}{a} y_0(t), \quad (21)$$

and, in general,

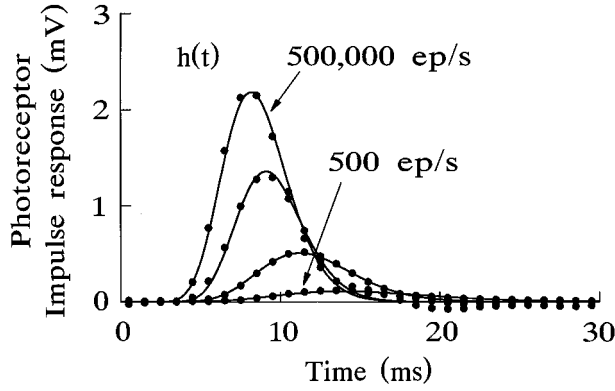


FIGURE 2. The adapting bump model of Eq. (2) (Ref. 19), fitted to photoreceptor responses from the fly compound eye (Ref. 10) at background light levels of 500, 5000, 50,000, and 500,000 ep/s. The data are shown as filled circles and the model as continuous lines. Fitting was performed using a minimum X^2 procedure, and the fitted parameters for eight different background light levels are shown in Table 1.

$$y_{n+1}(t+\Delta) \approx e^{-\Delta/a} y_{n+1}(t) + e^{-\Delta/a} \frac{\Delta}{a} y_n(t),$$

$$n=0, 1, 2, \dots \quad (22)$$

Therefore, Eq. (20) can be used to generate $y_0(t)$, and then Eq. (22) can be used to generate the succeeding $y_{n+1}(t)$, at $t = -M\Delta, (-M+1)\Delta, (-M+2)\Delta, \dots$. To use Eqs. (20) and (22), start with the initial conditions $y_n(-M\Delta) = 0, n=0, 1, \dots$. Here, M is sufficiently large so that the Gaussian function in Eq. (1) has negligible area to the left of $-M\Delta$. Note that $x(t)$ can be any arbitrary function and is not restricted to a Gaussian function.

RESULTS

Figure 2 shows examples of impulse response functions from fly photoreceptors at four different levels of light adaptation. These data were taken from a study using pseudorandomly modulated light to measure impulse responses in photoreceptors at eight different levels of light adaptation.¹⁰ Photoreceptor responses are always contaminated by noise, which varies from cell to cell and with light intensity. A detailed description of the noise and signal-to-noise levels of the recordings used here have been described previously.¹⁰ Noise was reduced by averaging in the frequency domain before inverse Fourier transforming the frequency responses to obtain impulse responses.

Figure 2 also shows the fitted curves from Eq. (2), which gave very good visual agreement with the data. The fitting parameters for all of the eight background

TABLE 1. Parameters obtained by fitting the model of Eq. (2) to fly photoreceptor impulse response functions. The background light level is expressed in effective photons per second. Fitting was performed using a minimum X^2 procedure, with the parameter n constrained to be an integer.

Background level (ep/s)	n	a (ms)
160	14	1.11
500	10	1.40
1600	15	0.86
5000	15	0.75
16,000	22	0.47
50,000	21	0.43
160,000	17	0.50
500,000	16	0.51

light levels are shown in Table 1. Background light levels are given in units of effective photons per second (ep/s), which were calibrated for each photoreceptor by counting photon arrivals in the cell at a low light level, using neutral density filters applied to the light source.

Values of ρ , the width of the Gaussian light acceptance function at half-amplitude, were taken from previously published data for fly eyes. At the front of the eye, ρ was approximately 1.5° during dark adaptation. This value decreased during light adaptation to a minimum of about 1.2° , due to pigment migration in the lens system.⁷

Both the recursive and the rapid methods of calculating the convolution were programmed using the ‘‘C’’ language and implemented on an IBM compatible personal computer using floating point arithmetic (24 bit mantissa). For the recursive method, the area under the normal curve was calculated using a Chebyshev approximation.¹² Both methods worked satisfactorily. A temporal resolution of 0.2 ms was used for calculating all photoreceptor responses. At this resolution, a time step Δ in Eqs. (20) and (22) of less than $50 \mu\text{s}$ gave very good agreement between the results obtained by the two methods. Figure 3 shows a comparison of the responses obtained from both methods using values of $\rho = 1.5^\circ$, $W = 1000^\circ/\text{s}$, $n = 10$, and $a = 1$ ms, which were typical for the range of interest, and it can be seen that the agreement was excellent.

Temporal and Spatial Responses to a Moving Point Object

Peak responses in single photoreceptors as functions of angular velocity are shown in Fig. 4 for two background light levels, using values of $\rho = 1.5^\circ$ at 500 ep/s and $\rho = 1.2^\circ$ at 500,000 ep/s. The other parameters were taken from Table 1. Responses were then calculated from Eqs. (20) and (22). As an object moves more rapidly across the visual field, it provides a more rapidly changing input to the photoreceptors, which behave approximately as low-pass filters.^{2,3} Responses were, there-

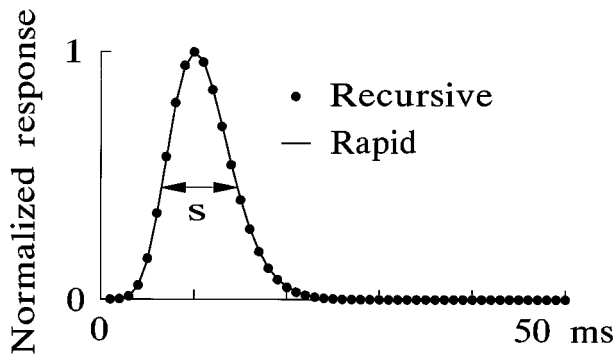


FIGURE 3. Comparison of the two methods of calculating the convolution of Eq. (3). In both cases, the parameters used were: $W=1000^\circ/\text{s}$, $n=10$, and $a=1$ ms. Both calculations are shown at 1 ms intervals and the time step, Δ , was 10 μs for the rapid method. Filled circles show the results obtained from the recursive method, and the solid line shows the rapid method.

fore, constant at low velocities, but decreased at higher angular velocities. These data indicate that fly photoreceptors begin to reduce their output above $100^\circ/\text{s}$ and the output is reduced to 10% by about $200^\circ/\text{s}$. However, a strong background light intensity improves the performance at higher velocities significantly, shifting the half-amplitude velocity to higher values by a factor of about 1.5, although there is also a reduction in the response at low velocities.

As a single point object moves across the visual field of a compound eye, each photoreceptor responds similarly, but with a delay relative to its neighbor that has already received the change in light intensity. If the photoreceptors were regularly spaced, with infinitely high angular resolution, we could calculate a spatial distribution of photoreceptor responses:

$$Y(\phi, t) = y(t - \phi/W), \quad (23)$$

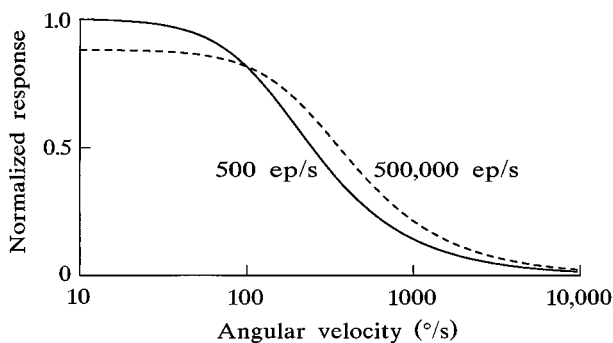


FIGURE 4. Peak photoreceptor responses to moving point objects calculated by the rapid method. Responses for two background light levels are shown, and the data were normalized to unity at low angular velocity for the low background light intensity.

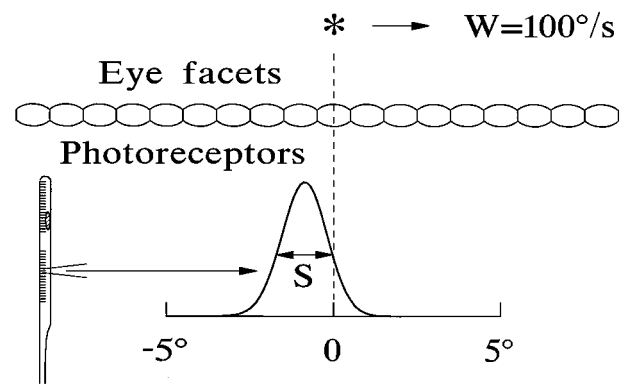


FIGURE 5. A moving point object evokes a series of responses in neighboring photoreceptors that can be viewed as a spatial response having the same form as the temporal response, but as a negative function of angular distance. The spatial response can be characterized by its spatial half-width S , defined as the width at half maximum amplitude. The example shown here is for an object moving at $100^\circ/\text{s}$. The more rapid the movement, the broader the spatial response.

where ϕ is the angular distance from the photoreceptor immediately below the moving point. This is the same function as the temporal response in the photoreceptor, but is applied to the spatial dimension, ϕ , having the opposite sign to time, and varying with velocity, W , as well as time. An example of this function using discrete time and space resolutions of 1 ms and 0.2° is illustrated in Fig. 5. The moving point object creates a spatial wave of membrane potential changes in the photoreceptors, most of which lags behind the object itself. However, a small part of the response leads the object because of the Gaussian angular acceptance function.

The spatial wave can be characterized by its half-width, the width of the function at half its peak amplitude. Because the spatial response is a linear transform of the temporal response, its half-width, $S(W)$, can be obtained directly from the corresponding temporal half-width, $s(W)$, of the photoreceptor response,¹⁴

$$S(W) = s(W)W. \quad (24)$$

Therefore, spatial half-widths could be calculated directly from the temporal responses without the need to calculate the actual spatial responses.

Spatial half-widths for a wide range of velocities and two background levels were calculated, using the rapid method [Eqs. (20) and (22)]. The results indicate that photoreceptors have significantly better resolving power for moving objects of all velocities when they are strongly light adapted (Fig. 6). The resolution was approximately constant for angular velocities below $100^\circ/\text{s}$, but then deteriorated linearly with velocity, so that ob-

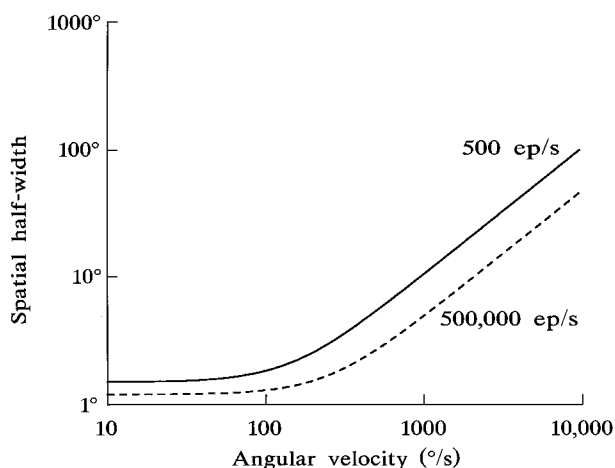


FIGURE 6. Spatial half-width was calculated for a range of angular velocities, and two background light levels, using the rapid method. Above about $100^\circ/\text{s}$, the resolution deteriorated approximately linearly with angular velocity.

jects moving faster than $1000^\circ/\text{s}$ would be quite poorly resolved.

DISCUSSION

Both of the methods described here performed satisfactorily, and the rapid method can determine the output responses for an arbitrary $x(t)$ and not merely for a Gaussian function. It should be emphasized that these methods are not restricted to compound eyes, or invertebrate eyes. It should also be noted that these results were obtained under relatively natural conditions, because the stimuli had constant contrast at varying mean light intensities, which would be close to the conditions occurring in nature. However, it must also be said that these methods are based on linear models of phototransduction. While linear models generally give good descriptions of fly photoreceptors, there is also evidence for some nonlinearities,¹⁷ so that more complete nonlinear models would be desirable in the future.

The calculated temporal and spatial responses agree well with data obtained by direct convolution in the fly eye.⁸ The data for spatial resolution of fly photoreceptors are qualitatively similar to analogous data from the locust eye.¹⁴ However, the spatial half-width in the locust began to increase significantly at about $20^\circ/\text{s}$, compared to about $100^\circ/\text{s}$ in the fly. This reflects the faster temporal properties of fly photoreceptors.¹⁶

The calculated temporal and spatial responses reflect the two major processes involved, i.e., light acceptance by the lens system, and temporal spreading by the voltage responses of the photoreceptors. Below about $100^\circ/\text{s}$, the spatial half-width depends mainly on the Gaussian angular acceptance of light. Above $100^\circ/\text{s}$, the voltage

responses can no longer follow the rapid changes in intensity caused by the moving object. The amplitude of the response decreases and the spatial response becomes spread across the eye. Thus, the temporal response of these cells not only limits the ability of the animal to detect changes in light intensity, but also its ability to perceive a moving object or to see while moving relative to its background.

For an object moving relative to a stationary animal, angular velocity depends on the distance from the animal and the linear velocity of the object. Movements of an object very close to a fly's head could easily produce angular velocities exceeding $1000^\circ/\text{s}$. However, most visual movement detection may occur when flies are in flight. Wehrhahn¹⁸ used high-speed cinematography to show that flies can turn at angular velocities exceeding $2000^\circ/\text{s}$. Flies have also been made to track moving stimuli while held in a stationary position, with the tracking measured by torque production. Under these conditions, flies tracked objects moving relative to themselves at $>200^\circ/\text{s}$.¹³ The present results suggest that motion at an angular velocity of $1000^\circ/\text{s}$ already significantly compromises a fly's resolving ability, with the spatial response being more than twice as large as when stationary. This agrees quite well with the maximum angular velocities observed for free flight.

The methods presented here allow rapid assessment of the responses of photoreceptors to moving objects. They should be useful for measuring the resolution of photoreceptors in many species, as data become available for the optical properties of the lens systems and the temporal properties of the receptor transduction processes. They may also be extended to other visual neurons, if their temporal responses can be well fitted by the adapting bump model.

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