

Sexual dimorphism matches photoreceptor performance to behavioural requirements

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Differences in behaviour exist between the sexes of most animal species and are associated with many sex-specific specializations. The visual system of the male housefly is known to be specialized for pursuit behaviour that culminates in mating. Males chase females using a high-acuity region of the fronto-dorsal retina (the 'love spot') that drives sex-specific neural circuitry. We show that love spot photoreceptors of the housefly combine better spatial resolution with a faster electrical response, thereby allowing them to code higher velocities and smaller targets than female photoreceptors. Love spot photoreceptors of males are more than 60% faster than their female counterparts and are among the fastest recorded for any animal. The superior response dynamics of male photoreceptors is achieved by a speeding up of the biochemical processes involved in phototransduction and by a tuned voltage-activated conductance that boosts the membrane frequency response. These results demonstrate that the inherent plasticity of phototransduction facilitates the tuning of the dynamics of visual processing to the requirements of visual ecology.

Keywords: photoreceptor; frequency response; sexual dimorphism; housefly; *Musca domestica*; visual ecology

1. INTRODUCTION

Several studies on invertebrate photoreceptors have demonstrated correlations between photovoltage response dynamics and visual ecology (Autrum 1950, 1984; Howard *et al.* 1987; Laughlin & Weckström 1993; De Souza & Ventura 1989). Fast-moving species possess photoreceptors that respond rapidly, thus enabling them to code the higher temporal frequencies present in rapidly moving images. The photoreceptors of slower-moving species respond more slowly, presumably because the detection of high-temporal frequency signals is not necessary (Laughlin 1996). Studies on dipteran species by Laughlin & Weckström (1993) have demonstrated that, not only is there a correlation between photoresponses and the dictates of an organism's visual ecology, but that the electrical properties of photoreceptor membranes are tuned in step with the desired response dynamics. In particular, rapidly responding photoreceptors possess membranes with a predominantly non-inactivating, delayed rectifier potassium conductance, while the membranes of photoreceptors of slowly moving species mostly contain a quickly inactivating potassium conductance. One might therefore expect two very closely related animals (i.e. males and females of the same species) with distinct lifestyles to exhibit differences in photoreceptor performance. Preliminary evidence from the marchfly (Bibionidae, Diptera) has suggested that this is true (Laughlin & Weckström 1993). Furthermore, O'Carroll *et al.* (1997) found that, at higher levels of visual processing, the temporal properties of the same neuron class (HS-like) in different sexes of the syrphid fly (*Eristalis tenax*)

were consistent with individual behaviour. They showed that neurons from males were tuned to higher temporal frequencies than those in females. Here we provide a new example of sex-specific differences in neural function in the visual system of the housefly (*Musca domestica*) that relates photoreceptor response dynamics and spatial acuity to retinal image velocities and metabolic cost.

The visual system of the housefly provides a classic example of sexual dimorphism in photoreceptor structure and function. Male and female houseflies differ in their visual behaviour (Land & Collett 1974; Wehrhahn 1979; Wehrhahn *et al.* 1982; Wagner 1986). Males pursue flying females vigorously and successful chases lead to interception followed by mating. This sexual pursuit behaviour is associated with pronounced differences in visual tracking. Males undertake tortuous high-speed manoeuvres while chasing their targets from below with the aid of a specialized fronto-dorsal region of their compound eyes, the 'love spot'. Females lack this love spot and track targets infrequently, with episodes that are brief and poorly controlled. The visual system of males is uniquely adapted for this chasing behaviour, starting with the defining characteristic of the love spot, the larger ommatidial facet lenses (Beersma *et al.* 1975; Land & Eckert 1985). These larger lenses are indicative of higher sensitivity and better acuity (Land 1981). Furthermore, while photoreceptors within an individual ommatidium of the fly compound eye are normally differentiated into achromatic (six receptors, i.e. R1–R6) and chromatic (two receptors, i.e. R7 and R8) pathways (Hardie 1985), within the love spot of the male housefly photoreceptors R1–R7 contribute nearly identically to the achromatic pathway (Franceschini *et al.* 1981; Hardie *et al.* 1981). This adaptation is believed to improve the detectability of dark targets. The love spot drives a set of male-specific, higher-order

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interneurons that respond selectively to moving targets and probably guide pursuit behaviour (Hausen & Strausfeld 1980; Land & Eckert 1985). The ability to detect rapidly moving targets during male pursuit behaviour will be maximized when the higher acuity provided by the larger facet lenses of the love spot is paired with a faster electrical response to reduce motion blur (Laughlin 1981*b*). In order to investigate this functional relationship between spatial and temporal resolution we compared the coding properties of male photoreceptors (R1–R6) from the love spot with photoreceptors from the corresponding frontal region of the female eye.

2. METHODS

(a) *Animals*

Musca domestica were collected in the wild near Cambridge, UK, and used for establishing a culture in the Department of Zoology at the University of Cambridge. Animals were used 3–14 days after emergence.

(b) *Electrophysiology and frequency responses*

Intracellular recordings were made from fully light-adapted R1–R6 photoreceptors in the fronto-dorsal retina of intact male and female animals using conventional microelectrode recording techniques (Weckström *et al.* 1991). All experiments were performed at room temperature (22–24°C). Photoreceptors were stimulated with the light from a 505 nm ultrabright light-emitting diode (LED) (LEDTronics, Inc., Torrance, CA, USA) that was focused onto the tip of a fluid-filled light guide whose other end projected the light onto the eye via a lens (subtending > 12.5° visual angle). The LED intensity (controlled by a voltage-to-current converter) was driven by a computer in order to produce Gaussian white noise modulations about a mean intensity that evoked *ca.* 5×10^5 quantum bumps receptor⁻¹s⁻¹. The photoreceptors' temporal coding ability was determined by measuring the average voltage response ($v(t)$) to repeated presentations ($n = 100$) of a 512 ms stimulus sequence with contrast modulation ($c(t)$). The mean contrast of this modulation, which was defined as the standard deviation of the intensity modulation divided by the mean intensity, was 0.28. The responses of fully light-adapted photoreceptors to modulations of this contrast are essentially linear (De Ruyter van Steveninck & Laughlin 1996). Each cell was presented with five different white noise sequences and these were used for obtaining photoreceptor transfer functions as follows. Both stimulus and response were filtered by a four-pole, Butterworth filter with a cut-off frequency of 500 Hz and sampled at 2 kHz. Ensemble averages of the five sets of stimulus and response waveforms were saved to disk. The saved time-series were (fast) Fourier transformed ($v(t) \rightarrow V(f)$ and $c(t) \rightarrow C(f)$) and the average power spectra were calculated. Square roots of the power spectra were used to derive the amplitude of the linear photoreceptor transfer function, i.e. $|H(f)|$, where $|H(f)| = |V(f)|/|C(f)|$.

The dynamic impedance of the membrane was determined by injecting 512 ms sequences of Gaussian white-noise-modulated current ($i(t)$) about a mean of zero into the light-adapted photoreceptor cell using a single-electrode, discontinuous, current clamp technique (Weckström *et al.* 1992). The standard deviation of the injected current was chosen so that the voltage response ($v(t)$) was similar in amplitude to that elicited during stimulation by light. The same protocol and analysis as described above for deriving the photoreceptor transfer function were used here in

order to derive the dynamic impedance of the membrane, i.e. $|Z(f)|$, where $|Z(f)| = |V(f)|/|I(f)|$.

(c) *Angular sensitivity experiments*

Response intensity functions ($V/\log I$) were generated for each cell studied by measuring peak response amplitudes to flashes of a point source placed in the centre of the receptive field that subtended 0.25° at the eye, the intensity of which could be accurately varied over a 3 log unit range. An appropriate flash intensity was used for measurement of angular sensitivities (i.e. one that was high enough to allow for a useful response range but which did not saturate the response peak). Sensitivities were determined by referring the peak of the voltage response elicited by this fixed flash intensity at a specific angular position in the photoreceptors' receptive field to a dark-adapted response intensity function in order to obtain the effective intensity of the flash (Hardie 1979). The angular position of the point source was adjusted in 0.25° steps and was always measured in the vertical plane. Angular sensitivities were calculated (as percentages) by dividing the effective intensity of the stimulus at each position by the effective intensity at the point in the visual field of maximum response, and multiplying by 100. Angular sensitivity functions were fitted with a Gaussian distribution that minimized the sum of squared error.

3. RESULTS

Figure 1*a* shows the frequency responses obtained from intracellular recordings of photoreceptor membrane potentials in response to Gaussian white noise modulations in light intensity. The brightness and contrast of the stimulus (see §2) matched those that photoreceptors normally experience during natural behaviour (Laughlin 1981*a*; De Ruyter van Steveninck & Laughlin 1996). The normalized amplitudes of the frequency responses ($|H(f)|$) measured from male and female photoreceptors showed clear differences, with male photoreceptors responding to higher temporal frequencies than those of females. The corner frequency, which is defined as the frequency at which the amplitude falls to $1/\sqrt{2}$ of maximum, provides a useful comparative measure of temporal acuity (Laughlin & Weckström 1993). The average (\pm s.e.) corner frequency for male photoreceptors is 75.9 \pm 3.2 Hz ($n = 9$), whereas the average for females is 46.7 \pm 0.9 Hz ($n = 9$), giving a sex difference in corner frequency for the voltage response to light of 29.2 \pm 3.3 Hz (Student's *t*-test, $p < 0.001$). This constitutes a 60% improvement in bandwidth and temporal resolution for the male. On an absolute scale this improvement allows male photoreceptors to achieve a greater gain than females' at higher temporal frequencies. For example, at a frequency of 100 Hz, the male:female ratio of gains is *ca.* 1.80.

The voltage response to light can be decomposed into two underlying components: the photocurrent generated by the action of the biochemical processes of phototransduction on light-gated channels, and the electrical properties of the membrane that converts this current to voltage. The membrane's dynamic impedance is determined by both passive and active components, i.e. capacitance and voltage-gated ion channels, respectively. By injecting Gaussian white-noise-modulated current ($i(t)$) into fully light-adapted photoreceptors and recording the resulting voltage fluctuations across the membrane, ($v(t)$),

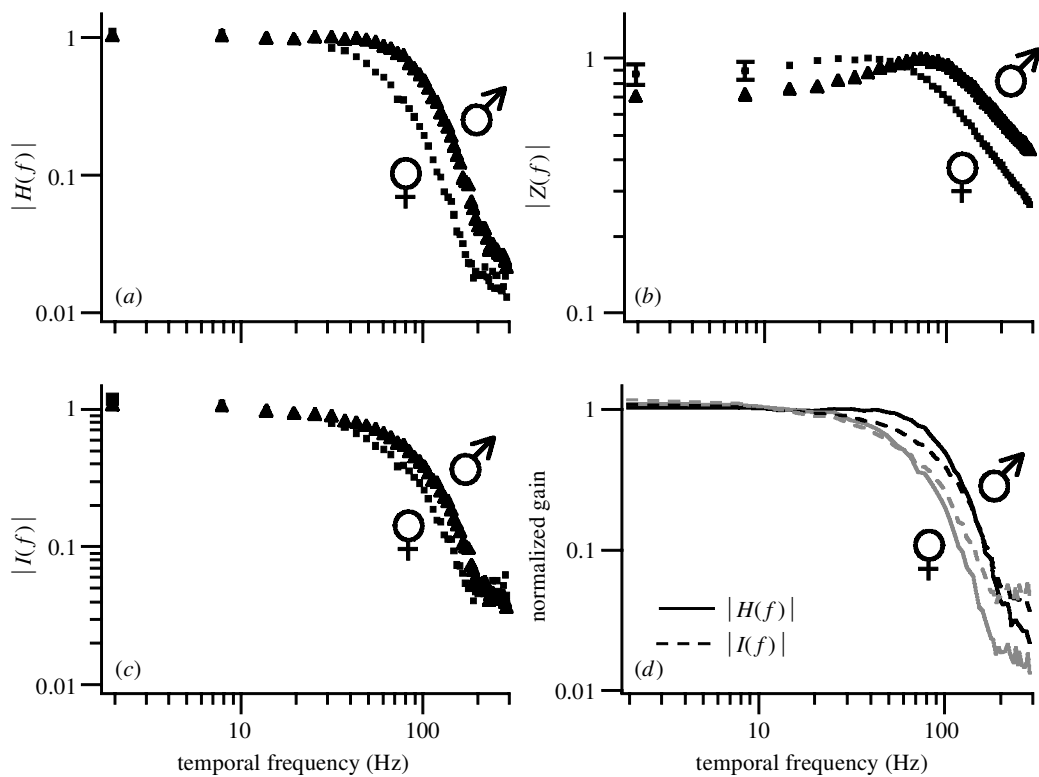


Figure 1. Average temporal resolution of seven fully light-adapted male and female photoreceptors. Sizes of the data points in (a)–(c) are equal to or larger than 95% confidence intervals, except where noted by error bars. (a) Normalized voltage gains ($|H(f)|$) demonstrating that male photoreceptors code for higher temporal frequencies than female photoreceptors. (b) Normalized membrane dynamic impedances ($|Z(f)|$) demonstrating that male photoreceptor membranes are tuned to pass higher temporal frequencies than those in females and that males have a more powerful voltage-activated potassium conductance (see text). (c) Normalized photocurrent gains ($|I(f)|$) demonstrating that the phototransduction cascade of males codes higher frequencies. (d) Comparison of photovoltage and photocurrent frequency responses for males (black lines) and females (grey lines). The data are the same as those presented in (a) and (c) and continuous curves represent lines drawn through the data points. The frequency responses in (a) and (c) were normalized by the average gain between 10 and 20 Hz, while those in (b) were normalized by the maximum value.

we could determine the dynamic impedance of the membrane as a frequency response directly. Figure 1b shows the mean normalized amplitude spectra ($|Z(f)|$) for male and female photoreceptor membranes. The mean (\pm s.e.) corner frequency of the male photoreceptor membranes was 156.8 ± 8.1 Hz ($n = 7$) compared with 95.7 ± 3.9 Hz ($n = 7$) for the females', giving a sex difference in membrane corner frequency of 61.1 ± 9.0 Hz (Student's *t*-test, $p < 0.001$). Measurements of light-adapted photoreceptor input resistances showed that they are lower in males (7.89 ± 0.51 M Ω) ($n = 7$) than in females (13.1 ± 1.12 M Ω) ($n = 7$), giving a difference of -5.21 ± 1.23 M Ω (Student's *t*-test, $p = 0.001$). Evidence that at least part of the underlying conductance was carried through a non-inactivating delayed rectifier by potassium ions comes from the observation that both male and female dynamic impedances show attenuation at low frequencies. The greater attenuation at low frequencies in male photoreceptors indicates that these cells have a larger potassium conductance (see §4).

An estimate of the frequency response of the photocurrent ($I(f)$) was obtained by dividing the frequency response for light-induced voltage ($H(f)$) (figure 1a) by the membrane impedance ($Z(f)$) (figure 1b). Figure 1c shows the mean normalized amplitude spectra ($|I(f)|$) for male and female photocurrents. This frequency response

also has a higher mean (\pm s.e.) corner frequency in males of 57.8 ± 2.3 Hz ($n = 7$) versus 44.2 ± 1.3 Hz ($n = 7$) in females, giving a sex difference of 13.6 ± 2.6 Hz (Student's *t*-test, $p < 0.001$). On an absolute scale, this improvement led to a greater gain in the male photocurrent compared with that in the female in response to higher temporal frequency signals. For example, at a frequency of 100 Hz, the male:female ratio of gains is *ca.* 1.68. Thus, the biochemical machinery that converts light to photocurrent in male photoreceptors operates more rapidly with a higher gain.

The electrical properties of the membrane play a role in extending the frequencies to which male photoreceptors are tuned (black lines in figure 1d). The sex difference in photocurrent corner frequency was statistically significant, but is less than half of the total difference in corner frequency seen in the voltage response to light. The larger part resulted from improved transmission by the membrane of male photoreceptors in the band 30–200 Hz. This can be clearly seen in figure 1d where normalized photocurrent and photovoltage frequency responses are compared. The limited temporal response properties of the photocurrent were overcome by specialization in the membrane that produced a voltage frequency response with an extended dynamic range (the space between dashed and solid black lines represents total improvement

due to the membrane). In comparison, the temporal resolution of the voltage response to light in female photoreceptors was limited by the dynamics of phototransduction (grey lines in figure 1*d*). Moreover, the female membrane served to low-pass filter the photocurrent signal, thus slowing it down even further.

The superior frequency response of the male photoreceptor is consistent with the males' need to detect, chase and intercept fast-moving, point-like objects (preferably female houseflies). However, the ability to track small, rapidly moving targets also depends on the quality of spatial resolution. The large facets of love spot ommatidia have a smaller, diffraction-limited, point-spread function and the rhabdomeres (photosensitive segments) of R1–R6 photoreceptors in these ommatidia are narrower (Hardie 1985). We confirmed that these factors reduce blur by measuring the angular sensitivity functions of male and female photoreceptors directly (Hornstein 1998) (figure 2*a*). As commonly found in insects, the functions were approximately Gaussian (Hardie 1985; Wilson 1975) and could therefore be compared by their half-width, i.e. the 'acceptance angle'. The male acceptance angle ($1.44 \pm 0.12^\circ$) ($n = 5$) was much narrower than that found in the female ($2.39 \pm 0.05^\circ$) ($n = 5$), giving a sex difference of $-0.95 \pm 0.13^\circ$ (Student's *t*-test, $p < 0.001$). These measurements were from dark-adapted photoreceptors. Activation of an intracellular pupil mechanism by bright light narrows the acceptance angle by *ca.* 0.3° (Hardie 1985). By applying this correction to the fitted Gaussians (solid lines in figure 2*a*) and taking their Fourier transforms we derived the modulation transfer functions of light-adapted male and female photoreceptors (figure 2*b*). The modulation transfer functions described transmission as a function of spatial frequency and demonstrated that male photoreceptors were capable of coding higher spatial frequencies.

By combining spatial and temporal frequency responses into a spatio-temporal contour plot of gain, we can realize the ability of the visual system to code objects moving at different velocities (O'Carroll *et al.* 1996, 1997), as shown in figure 3. The numbers corresponding to the individual contours indicate the spatio-temporal gain normalized with respect to a maximum value of unity. Thus, the plot indicates the relative sizes of photoreceptor responses to various combinations of spatial frequency (f_s) and temporal frequency (f_t), as given on the abscissa and ordinate. Each point that makes up a contour is derived from the product of a single point on the temporal frequency response function and a single point on the spatial frequency response function. Note that for every spatial and temporal frequency pair (f_s, f_t), a particular velocity is defined by the equation:

$$V = f_t/f_s. \quad (1)$$

The superior spatial and temporal resolutions of male photoreceptors combine to increase the range of velocities over which a given spatial signal can be resolved (compare figures 3*a, b*). This is best illustrated by figure 3*c* which shows the spatio-temporal corner frequency (the pairs of spatial and temporal frequencies that produce a product of $1/\sqrt{2}$ of the maximum response amplitude) derived for both males and females. Thus, not only can

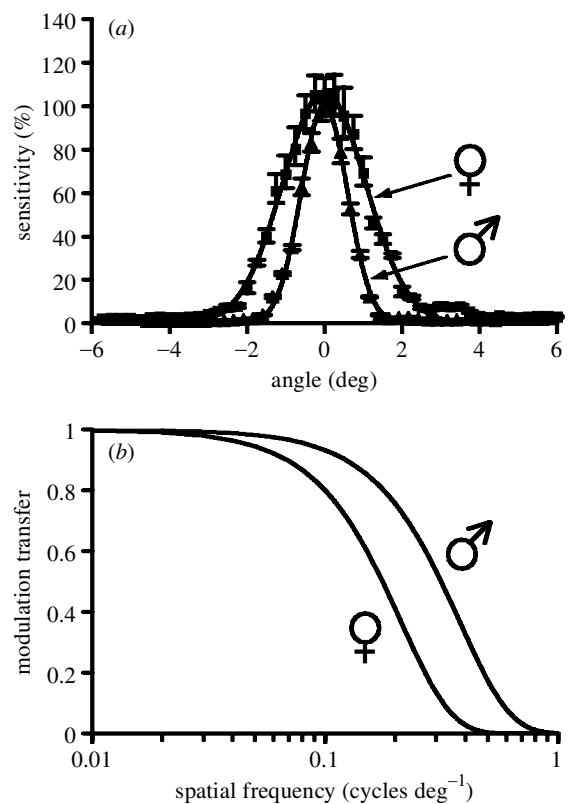


Figure 2. Photoreceptor spatial resolution. (a) Angular sensitivity functions for a dark-adapted male and female photoreceptor. The width of the angular sensitivity function at the 50% level for the male photoreceptor is 1.4° while that for the female is 2.4° . Error bars represent standard errors ($n = 6$) and solid lines are the best Gaussian fits to the data. (b) Light-adapted modulation transfer functions derived from the above angular sensitivity functions after adjustment for the reduction in half-width under light-adapted conditions.

males extract detail from images moving at higher speeds, they can do so at higher spatial frequencies, allowing for better resolution of smaller targets.

4. DISCUSSION

We have described several new components of sexual dimorphism in the visual system of the housefly. Our comparison of photoreceptors in the love spot, the specialized region of the male eye that is used to chase females, with photoreceptors in the corresponding frontal region of the female eye, showed that both the phototransduction cascade and the membrane of male photoreceptors are specialized to produce a faster voltage response. This leads to a 60% improvement in temporal resolution, as measured by the corner frequency of the photovoltage frequency response. The male corner frequency is similar to the highest values previously published for any insect (Laughlin & Weckström 1993) and, thus, among the highest observed in any animal. These male-specific specializations in cell signalling mechanisms are a substantive adjunct to the anatomical enlargement of the male frontal eye, which we have shown leads to photoreceptors with better acuity in males compared with females. Male photoreceptors have a 40% narrower point-spread function than that in females and

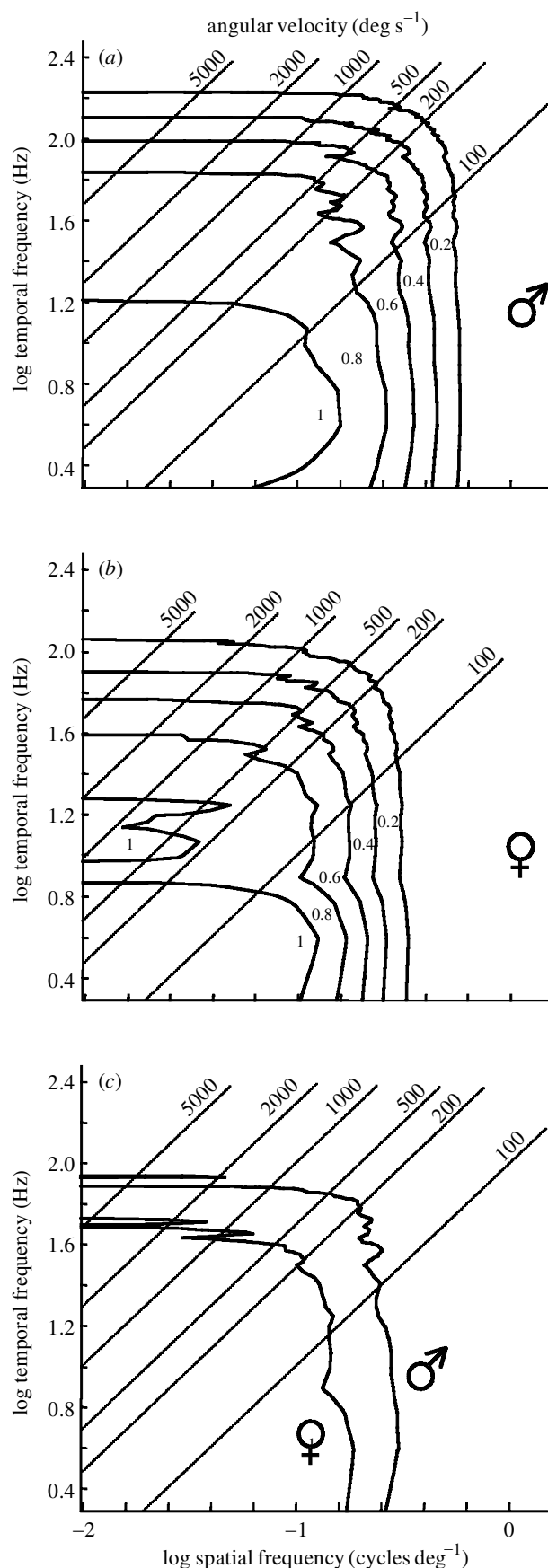


Figure 3. Spatio-temporal contour plots. Contour levels represent the fraction of the maximum photoreceptor response gain to incoming spatio-temporal information. (a) Contour plots for a fully light-adapted male photoreceptor. (b) Contour plots for a fully light-adapted female photoreceptor.

this extends their modulation transfer to higher spatial frequencies. These measurements thus confirm that a defining feature of the love spot, its larger ommatidial facet lenses, together with narrower R1–R6 rhabdoms (Hardie 1985), leads to an improved spatial frequency response that increases the bandwidth of the love spot. This must enhance the male's ability to locate and pursue small targets (such as females) because they contain power at all spatial frequencies and, when moving, all temporal frequencies. Without the faster voltage response, the fine spatial detail captured by the better optics of the love spot would be lost during rapid image movements. Because high rates of turn (in excess of 5000 s^{-1}) are generated during the pursuit of females (Land & Collett 1974; Wehrhahn *et al.* 1982), the superior spatial and temporal performance of male photoreceptors will make a substantial contribution to fitness. For example, at the level of response depicted in figure 3c, a spatial frequency of $0.1\text{ cycles deg}^{-1}$ is moving at 750 s^{-1} in the male compared with only 200 s^{-1} in the female.

Male photoreceptors achieve such a high temporal resolution because their membranes sacrifice the ability to pass low frequencies for an increased bandwidth and this allows the improved performance of the phototransduction cascade to go mostly unattenuated. An analysis of the shape of the photocurrent frequency responses (figure 1c) revealed that the male and female curves are similar (compare this to the difference in shape between the photovoltage responses in figure 1a). This suggests that the basic processes in the IP_3 signalling pathway responsible for mediating the opening and closing of light-sensitive channels are similar in males and females but are just faster in males. Calcium may play a critical role in producing this faster response because its entry through light-activated channels is involved in regulating the kinetics of the photoresponse via an early positive feedback mechanism and a delayed negative feedback mechanism (Hardie 1991; Ranganathan *et al.* 1995). Stronger feedback mechanisms within the phototransduction cascade of males compared with females could account for its increased temporal resolution.

We have not identified the mechanisms responsible for increasing the membrane corner frequency in male photoreceptors. Nonetheless, our membrane frequency responses were similar to curves from other insects, where it has been shown that the frequency response is largely shaped by membrane capacitance and a voltage-activated potassium conductance (Weckström *et al.* 1992). A slowly activating, delayed rectifier, potassium conductance improved signal transmission in the frequency band of 30–200 Hz in R1–R6 photoreceptors of the blowfly, the most thoroughly analysed insect photoreceptor membrane (Weckström *et al.* 1991; Anderson 2000). Activation of this conductance by depolarization (e.g. by light-induced current) in combination with the voltage-independent

(Cont.) (c) Male and female photoreceptor contour plots at a level that is $1/\sqrt{2}$ the maximum. Due to higher spatial and temporal resolution, male photoreceptors have the ability to respond to a wider range of spatial frequencies at any given velocity, and to higher velocities at any given spatial frequency.

conductance raised the membrane corner frequency by reducing the membrane time-constant. The slowly activating, non-inactivating potassium conductance also served to attenuate low frequencies because it effectively shunted the membrane, thereby lowering its resistance. Thus, the higher corner frequency and increased attenuation at low frequencies observed in love spot photoreceptors compared with female photoreceptors (figure 1*b*) suggest that the membranes of these cells have a larger delayed rectifier potassium conductance, possibly because they express channels at a higher density. The extent to which voltage-gated inward currents enhance high-frequency signals, as described in drone honeybee photoreceptors (Coles & Schneider-Picard 1989; Vallet *et al.* 1992), has not been established.

Our demonstration of sexual dimorphism in the physiological properties of housefly photoreceptors confirms the proposal, based on studies from a wide variety of insect species (see Laughlin & Weckström 1993), that photoreceptor response dynamics are tuned to specific properties of the image and to behavioural requirements. Gender differences that have been commonly observed in the structure, optics and photopigment distribution of compound eyes (Kirschfeld 1976; Zeil 1983; Hardie 1985; Land & Eckert 1985; Menzel *et al.* 1991; Stavenga 1992) have previously been found in the physiological properties of photoreceptors. There are differences in photoreceptor response dynamics and potassium conductance in bionids (Laughlin & Weckström 1993) and these correlate with differences in the spatial resolution of female and male eyes (Zeil 1983). The dorsal photoreceptors in the drone honeybee are specialized for detecting small targets by having larger lenses, longer rhabdoms and membranes that use a tetrodotoxin-sensitive sodium conductance to amplify the small signals generated by over-flying queens (Praagh *et al.* 1980; Menzel *et al.* 1991; Vallet & Coles 1993). In addition to functional differences between cells in different sexes and species, there are more subtle changes within a single retina. The R1–R6 photoreceptors in the male blowfly vary in frequency response according to position (Burton *et al.* 2000) and, within a single ommatidium, again of a blowfly, the achromatic (R1–R6) and chromatic (R7 and R8) photoreceptors differ in frequency response and potassium conductance (Anderson 2000; Anderson & Laughlin 2000). Thus, our account of differences between photoreceptors in male and female houseflies fits into a general pattern of adaptation of photoreceptor temporal performance to visual ecology in insects.

What does the adaptation of form to function in male love spot photoreceptors cost? Differences in optics and eye size between a wide variety of insect species suggest compromises between the benefits of improved sensitivity and resolution and the metabolic costs of supporting the eye (Land 1981). The diversity of optical systems reflects the diversity of body plans, behavioural patterns and photic niches. Similar factors govern temporal acuity. Improvements in temporal resolution are metabolically costly. A rapid response requires that the photoreceptor membrane has a short time-constant and this in turn requires a high specific membrane conductance that leads to large ion fluxes across the membrane (Laughlin & Weckström 1993; Laughlin *et al.* 1998). All other factors

being equal, the metabolic cost of generating signals is proportional to a photoreceptor's input resistance (Laughlin *et al.* 1998). The extra metabolic cost of improving the temporal response of love spot photoreceptors is considerable. Love spot photoreceptors have input resistances that are nearly 40% lower than in corresponding female cells. One must add to this the cost of enlarging the facet lens to improve spatial resolution. It is therefore likely that the specialization of photoreceptors in the male's love spot represents a balance between the benefits of better vision and the energetic demands made by non-visual functions that are unique to females, such as egg production and laying. Such an explanation is consistent with sex-specific differences in behaviour, time-management and energy budgeting seen in other animals (Krebs & Davies 1997).

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