

# Neural image enhancement allows honeybees to see at night

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## SUMMARY

The optical design of most insect apposition compound eyes should restrict activity to daylight because at night the tiny lenses of the isolated ommatidia cannot collect sufficient light. However, several bee species have adopted nocturnal activity, taking advantage of the benefits of night foraging. By measuring behavioural visual performance in honeybees, we show that insects can possess better spatial resolution in dim light than the optics and physiology of their apposition eyes suggest, implying the presence of higher neural mechanisms which enhance vision at night. Theoretical calculations reveal that honeybees improve light capture at night by neurally summing photons in space and time. Even though summation compromises both spatial and temporal resolution, the improved photon capture enhances vision sufficiently for bees to discriminate coarse images in moonlight. This explains how bees and many other insects can adopt a nocturnal lifestyle despite having an eye design typical of a day-active insect.

## 1. INTRODUCTION

Insects that need to see well in dim light face one main obstacle: the small ommatidial lenses of their compound eyes have trouble collecting enough photons to sustain reliable vision (Snyder 1979; Land 1981; Warrant 1996). Many nocturnal insects reduce this problem by having superposition eyes, whose large apertures can collect up to 1000 times more light than the apposition eyes typical of day-active insects, but in so doing often sacrifice spatial resolution (Land 1981; Warrant & McIntyre 1993). Nevertheless, the manifold advantages of foraging at night (Roubik 1989) have driven many insects with apposition eyes to adopt a partly or exclusively nocturnal behaviour. Of honeybee species, two: *Apis mellifera* (especially in Africa) and *Apis dorsata* (in Asia), continue to forage during twilight and throughout the night if a moon at least half-full is present in the sky (Fletcher 1978; Dyer 1985; Kirchner & Dreller 1993). An American solitary bee (*Sphecodogastra texana*) has the same foraging behaviour, but avoids daylight altogether by tightly sealing its burrow during the day (Kerfoot 1967). How do these insects manage to see at night?

Like all eyes, apposition eyes can adapt to the ambient level of illumination (Autrum 1981). As it gets darker, photoreceptors typically respond more slowly and their receptive fields often become broader. Both changes result in a greater photon catch, but only at the expense of spatial and temporal resolution. For

example, in locust apposition eyes the transition from day to night widens the photoreceptor's acceptance angle ( $\Delta\rho$ ) from 2° to 4° (Williams 1983) and lengthens its integration time (the half-width of the impulse response function,  $\Delta t$ ) from 19 ms to 54 ms (Howard 1981). Such dramatic changes are useful for locusts, which are known to have both nocturnal and diurnal activity. In honeybee photoreceptors the changes are probably not so dramatic, although they have never been properly investigated. Nevertheless, dark-adapted values of  $\Delta t$  and  $\Delta\rho$  are known, although these are somewhat smaller than in locusts, respectively 34 ms (drones: Raggenbass 1983) and 2.6° (workers: Laughlin & Horridge 1971; Eheim & Wehner 1972).

On its own, retinal adaptation is not sufficient for reliable nocturnal vision in apposition eyes, even in locusts (Warrant 1996). If insects need to see reliably at night higher visual mechanisms must be present which further improve light capture. One possibility is that the visual system sums photons in space by pooling signals from neighbouring ommatidia (Pirenne 1967; Snyder 1977; Lythgoe 1979; Laughlin 1990), and/or sums photons in time by lengthening the interval during which a sample of photons is counted (Barlow 1958; Lythgoe 1979; Laughlin 1990; Aho *et al.* 1993; Moeller & Case 1995). While the phenomenon of visual summation has been known for many years, its benefits (or otherwise) have never been quantitatively investigated. Recent theoretical work (Warrant 1996) suggests that even though summation significantly compromises both spatial and temporal resolution, the improved photon catch it allows can significantly enhance vision in dim light. The fact that bees can

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forage at night with clearly inadequate eyes suggests that they employ visual summation. Our results imply that they do and provides the optimum summation strategy they should employ. To our knowledge, this is the first quantification of the benefits of spatial and temporal summation for vision in dim light.

## 2. MATERIALS AND METHODS

To test whether visual summation is used to enhance nocturnal vision, we measured the spatial resolution of freely walking honeybees (*Apis mellifera carnica*) as a function of light intensity. A colony of about 20000 honeybees was kept in an indoor flight room. Single marked foragers were trained to fly to a dark chamber and to walk there on a horizontal Y-maze (90° between the arms) towards one of two screens (20 cm by 20 cm). Both screens consisted of a black-and-white stripe grating of set spatial frequency (a higher spatial frequency is equivalent to a higher visual stripe density). The gratings were illuminated from behind with white light of various intensities emitted from a halogen lamp. Light intensities were calibrated at the decision point of the Y-maze using an International Light 760 Photo-multiplier and a 567 nm interference filter ( $\Delta\lambda = 10$  nm). These calibrations were made to relate intensities in the Y-maze with natural intensities measured in the same way (see Warrant & McIntyre 1993, figure 5). To determine the spatial resolution, one of the gratings was presented horizontally, the other one vertically. The bees were trained to search for a sucrose reward in front of the horizontal grating, which was presented on the left or right side in a pseudo-random order. A total of 44 bees was trained and tested and the experimental data presented in figure 1 are based on a total of 3758 decisions. A threshold light intensity was defined as the lowest intensity at which the bees significantly preferred the rewarded pattern ( $p < 0.01$ ,  $\chi^2$  test). Below this intensity the bees showed no preference for either pattern. Threshold intensities were measured at each of several spatial frequencies.

## 3. RESULTS AND DISCUSSION

The threshold intensity at which bees significantly prefer the rewarded grating increases for increasing spatial frequency (figure 1). In other words, visual performance declines with decreasing light intensity, as is the case in all visual systems (see Pirenne 1967). In bright light, the finest gratings visible to bees have spatial frequencies ( $\nu_{max}$ ) of around 0.25 cycles  $\text{deg}^{-1}$  (figure 1), which is in good agreement with a recent behavioural study (Srinivasan & Lehrer 1988). Bees continue to see the finest grating at all light intensities down to mid-dusk levels, below which  $\nu_{max}$  systematically declines (i.e. the finest gratings visible to the bee become coarser and coarser). The ability of honeybees to see in dim light has also been revealed in other behavioural studies. Freely flying bees maintain colour discrimination down to late-dusk intensities, with achromatic vision taking over down to moonlight intensities (Rose & Menzel 1981; Menzel 1981). Walking bees show positive phototaxis to monochromatic light sources as dim as starlight (Kaiser *et al.* 1977).

This behavioural visual performance can now be compared to the performance expected if the amount of light captured by the eye is limited by the optics and dark-adapted receptor physiology of each omma-

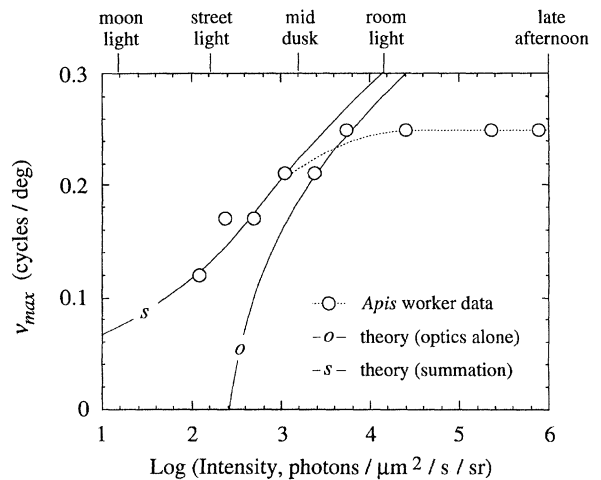


Figure 1. Spatial resolution in the honeybee as a function of light intensity. Spatial resolution is represented by the finest spatial frequency detectable by the bees ( $\nu_{max}$ ). Data points are shown as open circles. If light is collected by the optics of isolated ommatidia in the bee's apposition eye (no spatio-temporal summation), spatial resolution is predicted to decline with intensity faster than the data. With optimum spatial and temporal summation spatial resolution is predicted to decline less rapidly with intensity, a prediction which fits the data quite well below mid-dusk intensities. Above these intensities the theoretical curves continue to rise, but the data plateau to 0.25 cycles  $\text{deg}^{-1}$ . This plateau frequency is lower than expected on the basis of the optics (Srinivasan & Lehrer 1988), and may represent a behavioural upper limit imposed at some higher level of processing. The theoretical curves continue to rise until  $\text{Log } I = 5.5$ , when they plateau to 0.38 cycles  $\text{deg}^{-1}$ , the optical limit ( $\Delta\rho^{-1}$ ). Because the theory does not account for transduction saturation in bright light, the curves may also rise faster than they should at higher intensities. However at the dim intensities we are interested in, this is not a problem.

tidium. If the behaviour indicates a performance in dim light greater than that expected from the optics and physiology alone, then this implies a strategy of visual summation in space and/or time. By using reliable anatomical and physiological parameters for the dark-adapted worker bee eye it is possible to calculate the number of photons absorbed by the rhabdom from a grating of given spatial frequency and light intensity (Warrant 1996). This, together with the expected magnitudes of thermal and shot noise, makes it possible to predict the finest grating spatial frequency ( $\nu_{max}$ ) visible to bees at each light intensity (Appendix). This calculation shows that the optical visual performance of the fully dark adapted eye declines with intensity more rapidly than the behavioural performance (figure 1), with bees becoming blind at light intensities lower than street-light levels ( $\nu_{max} = 0$ ). The behavioural results imply that bees continue to see gratings at intensities much lower than street-light levels, and this suggests summation in space, or time, or both. These three summation possibilities were tested using the theoretical model (Appendix) to see if any of them could explain the observed behavioural data.

Without attempting to fit the data, the model was allowed to freely choose the summation strategy that was optimum for the bee apposition eye at each light

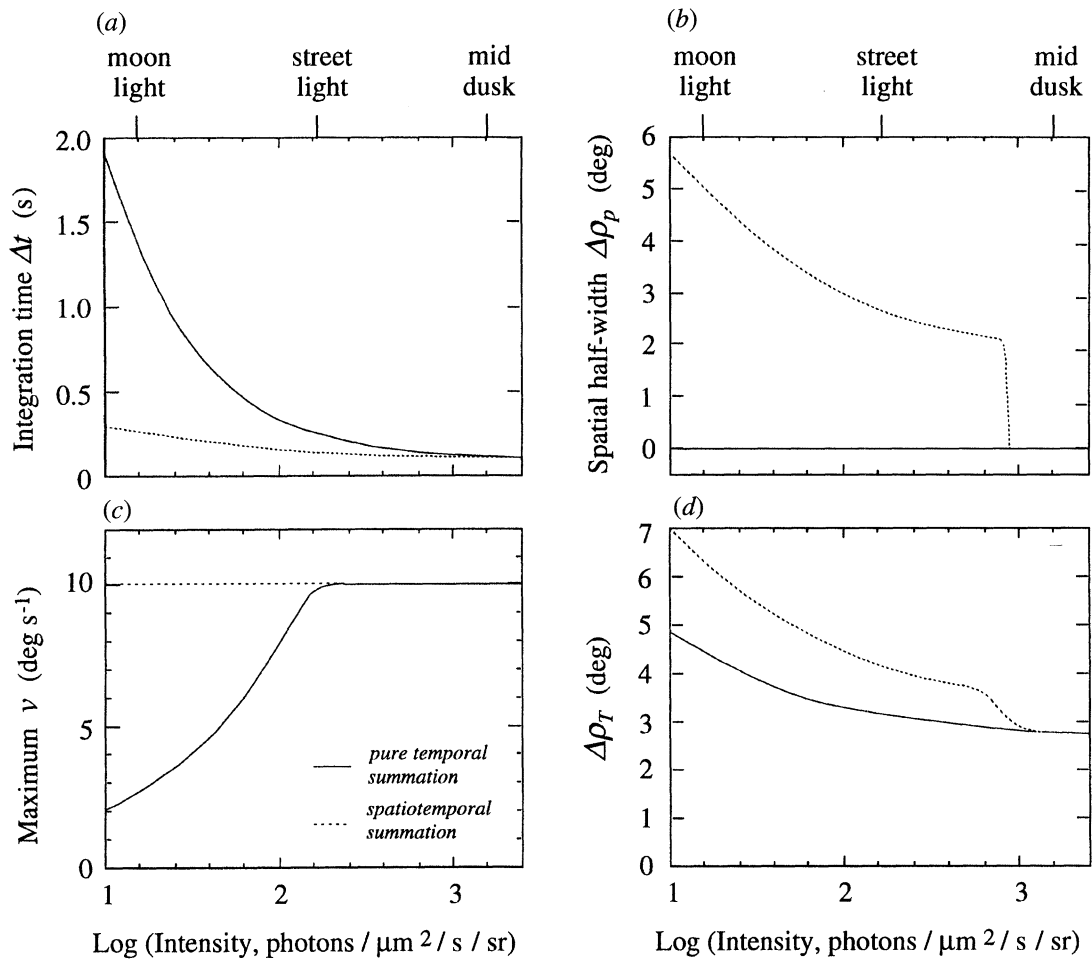


Figure 2. The optimum (a) temporal and (b) spatial summation that determines the optimum  $\nu_{max}$  (shown in figure 1) for strategies of spatiotemporal summation (dashed lines) and pure temporal summation (solid lines). For both strategies of summation, the integration time ( $\Delta t$ ) is predicted to increase as the light intensity falls, this increase being much larger for pure temporal summation. For spatiotemporal summation, the extent of ommatidial channel coupling ( $\Delta\rho_p$ ) is also predicted to increase with decreasing light intensity, but for intensities above mid-dusk it is predicted to become inactive (i.e.  $\Delta\rho_p = 0$ ). At these higher intensities the receptive fields of isolated ommatidia (with acceptance angles  $\Delta\rho$ ) are responsible for light capture and for setting the spatial properties of each visual channel. (c) The highest image velocity  $\nu$  perceivable by bees using strategies of spatiotemporal summation (dashed lines) and pure temporal summation (solid lines). The highest image velocity at each intensity is calculated for the finest spatial frequency visible to behaving bees at the same intensity (obtained from the theory curve in figure 1). (d) The half-width of the channel's total receptive field  $\Delta\rho_T$  (Appendix, equation (4)) using strategies of spatiotemporal summation (dashed lines) and pure temporal summation (solid lines).

intensity. Two parameters were optimised: the integration time ( $\Delta t$ ) reflecting the extent of temporal summation, and the ommatidial channel coupling ( $\Delta\rho_p$ ) reflecting the extent of spatial summation. The parameter  $\Delta t$  is the time during which the visual system counts a sample of photons: a longer  $\Delta t$  means greater temporal summation. The parameter  $\Delta\rho_p$  is the angular half-width of the function describing the extent of coupling (Appendix): a greater  $\Delta\rho_p$  means more extensive spatial summation. Both  $\Delta t$  and  $\Delta\rho_p$  were varied over a wide range and for each combination  $\nu_{max}$  was calculated. At each light intensity, the combination of  $\Delta t$  and  $\Delta\rho_p$  which resulted in the highest  $\nu_{max}$  (i.e. the finest grating perceivable) was taken as the optimum summation strategy (see Appendix).

The optimum strategy chosen by the model involves both spatial and temporal summation. Using this

strategy, the finest spatial frequencies visible to bees lie close to the behavioural data (figure 1). The extents of spatial and temporal summation predicted to be optimal depend on light intensity (figure 2a, b; dashed lines): as light levels fall, the theory predicts a longer integration time ( $\Delta t$ ) and a more extensive coupling of ommatidial channels ( $\Delta\rho_p$ ). For intensities greater than mid-dusk spatial summation is predicted to be inactive (figure 2b). In street light the calculation predicts that bees should sum photons during integration times of 117 ms from channels coupled with a  $\Delta\rho_p$  of  $3.0^\circ$ . This extent of spatiotemporal summation cannot be explained by the finer spatial and temporal properties of the dark adapted bee retina. Instead, long integration times might be generated by specialised integrating mechanisms in the optic lobe. Such mechanisms have recently been found in the optomotor pathways of nocturnal hawkmoths (E. J. Warrant &



D. C. O'Carroll, unpublished data), and may explain how some crabs are able to track extremely dim point sources moving incredibly slowly (Horridge & Sandeman 1964; Sandeman & Erber 1976; Doujak 1985). Neural circuits mediating ommatidial coupling in dim light have been implicated in the lamina (Dubs *et al.* 1981) and optomotor system (Pick & Buchner 1979; Srinivasan & Dvorak 1980) of flies and crabs (Doujak 1985), but their cellular basis remains unknown.

Optimum spatiotemporal summation would allow bees to maintain reasonable vision even in moonlight (figure 1), a prediction supported by the moonlight foraging observed in the wild (Kerfoot 1967; Fletcher 1978; Dyer 1985; Kirchner & Dreller 1993). That vision necessarily becomes slower in dim light is supported by the observation that European honeybees become clumsier and fly slower at intensities below room light. European honeybees are even seen hovering at intensities between mid-dusk and street light (Rose & Menzel 1981).

Although the model predicts spatiotemporal summation to be optimal for bees, it may nevertheless be possible that purely spatial or purely temporal summation could explain the behavioural data. Attempts to fit the data using pure spatial summation failed. Using  $\Delta t = 34$  ms (the dark adapted photoreceptor integration time: Raggenbass 1983) it was impossible to reach the level of visual performance displayed by our bees. On the other hand, a strategy of pure temporal summation ( $\Delta\rho_p = 0$ ) can fit the data, but the integration times needed are unacceptably large, reaching 1.5 s in moonlight (figure 2*a*, solid line), which is about six times longer than the integration times predicted to be optimal for spatiotemporal summation. This long integration time takes its toll on the highest image velocity which is perceivable by bees in dim light (figure 2*c*): less than  $3 \text{ deg}\cdot\text{s}^{-1}$  in moonlight, compared with  $10 \text{ deg}\cdot\text{s}^{-1}$  if optimal spatiotemporal summation is used. If the half-width  $\Delta\rho_T$  of the total channel visual field is considered (which depends on the receptive field of the photoreceptor  $\Delta\rho$ ,  $\Delta\rho_p$ ,  $\Delta t$  and the image velocity  $v$  (Appendix)), temporal summation results in a narrower visual field than spatiotemporal summation (figure 2*d*), but the difference is not huge. We conclude, that for flying insects such as bees, reliable perception of higher image velocities would probably favour spatiotemporal summation over pure temporal summation.

Nocturnal foraging by flower-visiting insects has several advantages, each of which might have driven the evolution of visual systems suitable for nocturnal flight activity (Roubik 1989). There are diurnal changes in the availability of nectar and pollen in most flowering plants, and this allows nocturnal flower visitors to exploit these plants more efficiently. Another advantage for nocturnal foraging is the lower ambient temperature at night. Diurnal flight activity of flower visiting insects ceases when the ambient temperature exceeds about  $40^\circ\text{C}$ , as these insects need a temperature gradient between their thorax and the air to shed the heat produced by the flight motor. Nocturnal foragers also avoid potential predators, most of which

are diurnal or crepuscular. Because most flower visitors are diurnal, the most important advantage of nocturnal foraging seems to be reduced competition. The predominance of diurnal foraging may be the result of two constraints, both of which seem to restrict nocturnal flight activity to insects of larger body size. One constraint is the visual system, as photon capture is generally greater in larger eyes (Land 1981). The other constraint is the low night-time air temperature, as flight requires a thoracic temperature of at least  $25\text{--}30^\circ\text{C}$  in most insects.

Our results suggest that honeybees enhance their vision in dim light by summing photons in space and time. While not giving them a visual performance equal to that of truly nocturnal insects with superposition eyes (Warrant 1996), it does allow them to discriminate coarse images in moonlight and thus to forage at night. Enhanced nocturnal vision is probably of great benefit to many different kinds of insects with apposition eyes, not only those which forage. The many examples of nocturnally active insects with apposition eyes (such as the locust) suggest that visual summation is probably a widespread strategy.

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## APPENDIX

The maximum detectable spatial frequency,  $\nu_{max}$  (Warrant & McIntyre 1993), is given by (Warrant 1996):

$$\nu_{max} = \frac{0.530}{\Delta\rho_T} \sqrt{\ln mN - \frac{1}{2} \ln [N + \sigma_D^2]}, \quad [1]$$

where  $m$  is the contrast of the grating (measured at 0.9),  $N$  is the total number of photons sampled by a visual channel during one integration time,  $\sigma_D^2$  is the total dark variance, and  $\Delta\rho_T$  is the half-width of the Gaussian spatial receptive field resulting from spatial and temporal summation. These parameters are given by

$$N = 0.890 \kappa \tau \left( \frac{kl}{2.3 + kl} \right) \Delta t \left( \frac{dA}{f} \right)^2 I \quad (\text{no summation}) \quad [2a]$$

$$= 1.269 \kappa \tau \left( \frac{kl}{2.3 + kl} \right) \Delta t \left( \frac{\Delta\rho_p dA}{\Delta\phi f} \right)^2 I \quad (\text{summation}) \quad [2b]$$

$$\sigma_D^2 = 0.79 \omega l \Delta t d^2 \quad (\text{no summation}) \quad [3a]$$

$$= 1.13 \omega l \Delta t \left( \frac{\Delta\rho_p d}{\Delta\phi} \right)^2 \quad (\text{summation}) \quad [3b]$$

$$\Delta\rho_T = \sqrt{\Delta\rho^2 + (\nu\Delta t)^2} \quad (\text{no summation}) \quad [4a]$$

$$= \sqrt{\Delta\rho^2 + \Delta\rho_p^2 + (\nu\Delta t)^2} \quad (\text{summation}) \quad [4b]$$

The *summation* model has only three variables: the light intensity ( $I$ ), the half-width ( $\Delta\rho_p$ ) of the Gaussian function specifying the extent of spatial summation, and the integration time ( $\Delta t$ ) which specifies the extent of temporal summation. At each light intensity, a range of values of  $\Delta\rho_p$  and  $\Delta t$  were used to calculate  $\nu_{max}$ . The combination of  $\Delta\rho_p$  and  $\Delta t$  which resulted in the largest  $\nu_{max}$  at each intensity was then considered the optimum extent of spatial and temporal summation. The optimum values of  $\nu_{max}$ ,  $\Delta t$  and  $\Delta\rho_p$  are plotted in figures 1, 2a and 2b respectively. The optimum spatial receptive field half-width because of spatial and temporal summation ( $\Delta\rho_T$ ) is plotted in figure 2d. The other parameters are anatomical or physiological whose values for worker honeybees are taken from the literature. These are the focal length  $f$  (70  $\mu\text{m}$ : Varela & Wiitanen 1970), the interommatidial angle  $\Delta\phi$  (1.9°: van Hateren *et al.* 1990), the facet lens diameter  $A$  (32  $\mu\text{m}$ : Varela & Wiitanen 1970), the rhabdom length  $l$  and diameter  $d$  (250  $\mu\text{m}$

and  $2\ \mu\text{m}$  respectively: averaged from data in Snyder *et al.* 1973; Kirschfeld 1974; Land 1981; Wehner & Meyer 1981), the photoreceptor acceptance angle  $\Delta\rho$  ( $2.6^\circ$ : Laughlin & Horridge 1971; Eheim & Wehner 1972), the absorption coefficient of the rhabdom  $k$  (taken as  $0.0067\ \mu\text{m}^{-1}$ : Bruno *et al.* 1977), the quantum capture efficiency of the transduction process  $\kappa$  (taken as 0.5: Lillywhite 1977), the fraction of incident light transmitted by the optics of the eye  $\tau$  (taken as 0.8), and the *specific* dark variance  $\omega$  (taken as  $1.3 \cdot 10^{-6}$  equivalent photons  $\mu\text{m}^{-3}\ \text{s}^{-1}$ : Lillywhite 1977; Lillywhite & Laughlin 1979). For spatiotemporal

summation calculations, the image velocity  $\nu$  seen by the walking bee in our apparatus was estimated as  $10\ \text{deg}\ \text{s}^{-1}$ . Coincidentally, this was also the highest velocity which allowed theoretical summation curves to reach the behavioural data (see figure 2*c*, dashed line): higher velocities result in theoretical curves which lie below the data points in figure 1. For pure temporal summation calculations the highest  $\nu$  was chosen which still enabled a fit (see figure 2*c*, solid line). In the dark-adapted state, without summation, honeybees have a photoreceptor integration time of 34 ms (Raggenbass 1983).